Eesti Maaülikool
Estonian University of Life Sciences

THE STRUCTURING ROLE OF LAKE CONDITIONS FOR AQUATIC MACROPHYTES

Järvedes valitsevad tingimused veetaimestiku kujundajatena

TÕNU FELDMANN

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

Väitekiri
Filosoofiadoktori kraadi taotlemiseks hüdrobioloogia erialal

Tartu 2012

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II. Nõges, P., Tuvikene, L., Feldmann, T., Tõnno, I., Künnap, H., Luup, H., Salujõe, J. & Nõges, T. **2003**. The role of charophytes in keeping the water clear in a shallow lake. Hydrobiologia 506-509 (1): 567-573.

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V. Feldmann, T. & Nõges, P. **2007**. Factors controlling macrophyte distribution in large shallow Lake Võrtsjärv. Aquatic Botany 87: 15–21.

VI. Feldmann, T. & Nõges, P. **2009**. Seasonal and vertical changes in the surface area/biomass ratio of *Potamogeton lucens* L. in a clear and a turbid shallow lake. Journal of Aquatic Plant Management 47: 116-121.

VII. Nõges, T., Luup, H. & Feldmann, T. **2010**. Primary production of aquatic macrophytes and their epiphytes in two shallow lakes (Peipsi and Võrtsjärv) in Estonia. Aquatic Ecology 44: 83-92.

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Author´s contribution to the papers:

	I	**II**	**III**	**IV**	**V**	**VI**	**VII**	**VIII**
Original idea			*		*	*		
Study design			*		*	*		
Data collection	*	*	*	*	*	*	*	*
Data analysis	*	*	*	*	*	*		
Manuscript preparation	*	*	*		*	*	*	*

1. INTRODUCTION

Macrophytes have an important and sometimes a key role in lake ecosystems. Large stands of emergent and floating-leaved macrophytes along lake shores can modify the hydrodynamics of lakes by dampening wave action and slowing down water currents (Fonseca et al., 1982; Gregg & Rose, 1982; Madsen & Wrancke, 1983) that leads to increased sediment accumulation in the littoral (Barko & James, 1998). Vegetation carpeting lake bottoms suppresses sediment resuspension (Berg et al., 1997; Scheffer, 1998) and modifies nutrient fluxes between water column and sediments (Jaynes & Carpenter, 1986 James & Barko, 1990; Sand-Jensen & Borum, 1991; Horppila & Nurminen, 2001). Submerged plants create a complex structure in the water column that affects light penetration by shading (Binzer & Sand-Jensen, 2006) offers hiding places for zooplankton and small fish from their predators (Scheffer, 1998, Timms & Moss, 1984, Heck & Crowder, 1991; Mittelbach & Osenberg, 1993; Persson, 1993; Persson & Eklöv, 1995) and serves as food for a large variety of animal species. In oligo-mesotrophic shallow lakes, aquatic macrophytes are the principal primary producers, whereas in eutrophic–hypertrophic lakes their role gradually decreases with increasing phytoplankton turbidity causing poor light conditions (Mitchell, 1989; Blindow et al., 2006; Allende et al., 2009). Rooted aquatic macrophytes have a particularly large effect in small and shallow lakes (Carpenter & Lodge, 1986; Blindow et al., 1998) where they may cover most of the lake area and be important in maintaining the clear water state (Moss, 1990; Scheffer et al., 1993; Jeppesen et al., 1997).

The publication of the book "The Structuring Role of Submerged Macrophytes in Lakes" in Ecological Studies (Jeppesen et al., 1998) became an important milestone in aquatic ecosystem research summarising the ideas of a new paradigm, which emphasised the active role of macrophytes as edificators in lakes according to which macrophytes are the main structuring component in lake ecosystems creating habitat conditions for other species. Undoubtedly, that aspect is continually highly relevant because of the overwhelming fraction of the world's lake population being comprised of small (Downing et al., 2006) and shallow lakes with the littoral area constituting up to 95% of the lake area (Wetzel, 1990).

On the other hand, aquatic macrophytes have a passive role being strongly controlled by abiotic and biotic conditions of the ecosystem in a broad sense. The distribution patterns of species and ecological zones in the littoral result from a combination of biotic and abiotic factors reflected in aquatic macrophytes parameters, such as height, shoot number or coverage, and species composition. The sessile way of life and relative longevity of aquatic macrophytes (compared to planktonic organisms) and their sensitivity to environmental conditions makes them valuable indicators, especially for medium- and long-term impacts, e.g. their species richness and proportion of various growth forms reflect changes in the trophic state of lakes (Sculthorpe, 1971; Toivonen & Huttunen, 1995). The European Water Framework Directive (European Commission. 2000) induced a new wave of studies on impact-response relationships aiming at using aquatic organisms, including aquatic macrophytes, as indicators of water body status.

The papers forming the bulk of this dissertation are connected with various passive aspects of macrophytes in lakes, i.e. with questions how the plant architecture, species composition and distribution in lakes are shaped by environmental conditions. As the original studies cover only a tiny area in this large field of research, the synthesis part of the dissertation is written as a review, which enables a more balanced approach to the underlying questions, offering at the same time an umbrella for the papers included in the dissertation. In this review, the results achieved in the original papers are linked with references. The materials and methods used and the major conclusions drawn based on the original studies are summarised separately. The title of the dissertation paraphrasing the title of the epochal book by Jeppesen et al. (1998) is a tribute to the authors and editors of this book but highlights the other complementary side of aquatic macrophyte research.

2. AIMS OF THE STUDY

The general aim of the synthesis part of the dissertation is to demonstrate how the multitude of ecological factors affecting aquatic macrophytes in temperate lake ecosystems is reflected in plant parameters at individual, population, and community levels creating lake specific or lake type specific distribution patterns of plant communities. The spectrum of macrophyte related topics analysed and discussed in the original publications is wide ranging from eco-physiological aspects (papers II, IV, VII) and aspects of autecology (paper VI) to population ecology (paper VIII) and synecology (papers I, III, V). Studies were performed mainly in the large and shallow Lake Võrtsjärv and in two smaller lakes, Prossa and Kaiavere, the first being macrophyte dominated and the other phytoplankton dominated. The following specific questions were addressed in these lakes:

1. Which factors determine the observed distribution of macrophytes in Võrtsjärv (Paper V) and which macrophyte parameters are most sensitive to spatial differences of these factors? (Paper III).

2. Which long-term trends have been evidenced in the macrophyte vegetation of Võrtsjärv and what are their driving factors? (Papers I, III, VIII).

5. What is the role of macrophytes among primary producers in large and shallow lakes and are the seasonal patterns in different lakes coherent? (Paper VII)

6. What is impact of meteorological forcing on macrophyte distribution in lakes and how this impact scales with lake morphometry (Papers II, IV, V).

7. What is the role of macrophytes in the formation of clear-water periods in small hard water lakes and what are the potential governing mechanisms? (Papers II, IV).

8. What are the differences in plant architectonics and seasonal growing patterns occurring between macrophytes in clear and turbid water lakes? (Paper VI).

Given the broad thematic spread of the underlying papers, the thesis follows the format of a review paper that enables better integration of the original publications still maintaining the thematic integrity.

3. MATERIALS AND METHODS

The material for the present thesis was collected during 14 years (1997 – 2011) mainly from three lakes located in Central Estonia – the large and shallow Võrtsjärv (papers I, III, IV, V, VII & VIII), and two small drumlin lakes in the Vooremaa landscape protection area – Prossa and Kaiavere – the first being a macrophyte dominated lake and the other a phytoplankton dominated lake (papers II, IV &VI). Material from Lake Peipsi, the largest lake in Estonia, was used only in one paper (VII). In paper IV, data on macrophytes and their epiphyton was collected from 9 Estonian lakes of different size and type. More detailed descriptions of the study sites are given in paper VII for lakes Võrtsjärv and Peipsi, and in paper VI for lakes Prossa and Kaiavere.

As the methods are described in detail in the papers, the basic methods used are only shortly listed here with references to the corresponding papers.

- The basic method used for describing the macrophyte community in most papers has been the combined transect and sampling quadrat method used in geobotanical studies (papers I, III, IV & V).
- An original similarity index was used to compare the historical list of species with nowadays data (paper I).
- The weight of the calcite crust on *Chara* plants reflecting the role of these algae in precipitation of calcium carbonate was measured as the dry weight difference created by dissolving the calcite by hydrochloric acid (paper II).
- For studying plant architecture (paper VI), the plants were dissected and scanned with following image analysis for estimating various plant morphometry parameters.
- In two papers (IV & VII) macrophytes were studied together with their epiphyton. In a set of 9 lakes, the lake-specifity and plant species-specifity of the epiphyton was studied comparing epiphytic communities collected from different macrophyte species within the same lake and similar plant species from different lakes. In lakes Võrtsjärv and Peipsi, the role of macrophytes, epiphyton and phytoplankton in the total primary production was analysed using the ^{14}C technique.
- Long-term changes in reed areas (paper VIII) were analysed from retrospective series of satellite images.

4. LITERATURE REVIEW AND SYNTHESIS

4.1. INFLUENCE OF LAKE CONDITIONS ON THE DISTRIBUTION OF AQUATIC MACROPHYTES

The structuring role of lake conditions for aquatic macrophytes may be divided into three large categories – physical, chemical and biological – with corresponding limnological, metabolic and biotic effects on plants (Figure 1). Limnological effects are related to physical conditions in the water and sediment, metabolic effects are related to nutrient cycling and production of organic matter, and biotic effects are connected with biological interactions and community structure. That division used by Gasith and Hoyer (1998) to describe the changing influence of aquatic macrophytes along lake size and depth gradients, is suitable as well in the other way round – for describing the structuring role of lake conditions for macrophytes.

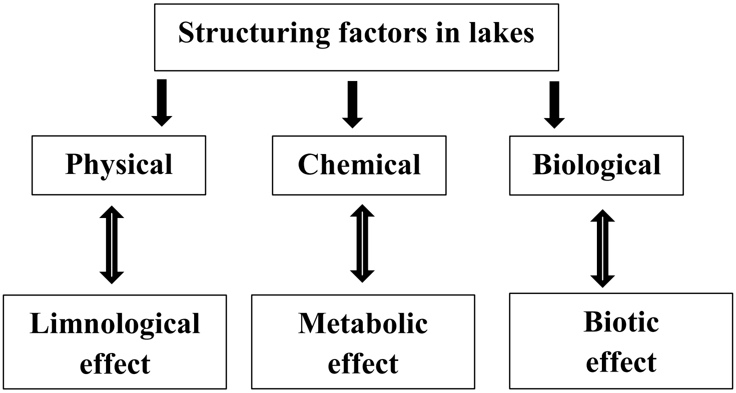

Figure 1. Structuring factors in lakes and their effects on macrophytes.

4.1.1. Limnological factors

Lake morphometry, composition of bottom sediments, water movement, light, temperature have a major effect on aquatic macrophytes and create a clear zonation in their distribution in the littoral area (Figure 2).

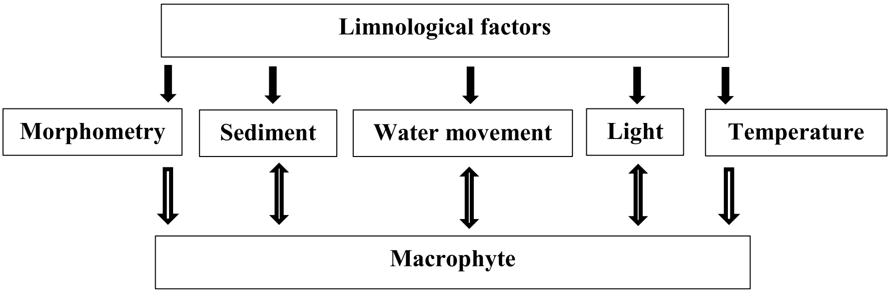

Figure 2. Limnological factors affecting the distribution of macrophytes in lakes.

4.1.1.1. Lake morphometry

The question how the distribution of macrophytes varies among lakes of similar trophic status that differ in size and depth has not been exhaustively studied yet. In general, large and deep lakes have less macrophytes than small and shallow lakes (Gasith & Hoyer, 1998). Light availability and the mechanical impact of water movement are directly and indirectly influenced by lake morphometry. Due to exponential light attenuation in water, depth is one of the most critical environmental factors determining the growth of macrophytes and their species richness (Chambers & Kalff, 1985; Duarte & Kalff, 1986). The biomass of submerged macrophytes is inversely related to the slope of the bottom in the littoral (Duarte & Kalff, 1986) that affects the relative area suitable for plant growth and creates differences in sediment stability and quality between gently sloped (sedimentation zone) and steeply sloped (erosion zone) littoral zones. Also the area of littoral zone available for growth of emergent plants declines with increasing slope of the basin (Gasith & Hoyer, 1998). Basin slope (square root of the area divided by mean depth), surface area, and basin configuration are among the most important morphological features that influence the potential development of macrophytes in lakes (Spence, 1982; Duarte & Kalff, 1986). The proportion of the littoral zone in total lake area declines with increasing depth and lake size (Gasith, 1991) and increases with increasing shoreline irregularity. Therefore, highly irregular lakes may have a higher proportion of vegetation zones compared with lakes of similar area but with a simpler shoreline. These factors interact directly and indirectly with other environmental factors such as light, nutrient availability, substrate characteristics, and wind-generated erosion to determine the site-specific extent of plant development and macrophyte types (Gasith & Hoyer, 1998).

Coming back to the active role of macrophytes, it was shown by Gasith & Hoyer (1998) that the limnological and metabolic effects of macrophytes decline with increasing depth and lake size faster than their importance in providing structured habitats. This implies that, by providing structure, macrophytes may still be important for biotic interactions in situations where they may have no significant effect on water-quality, nutrient cycling, or as a source of organic matter. Most researchers agree that a PVI (percentage volume infested by plants) exceeding 40% is required for macrophytes to influence water quality (Canfield & Jones, 1984) and have a major influence on the entire lake ecosystem (Gasith & Hoyer, 1998).

4.1.1.2. Bottom sediment and water movement

The substrate preferences of macrophytes are mainly related to granulometric composition, nutrient and organic matter content of sediments (Lachavanne, 1985; Barko & Smart, 1986; James & Barko, 1990; Barko et al, 1991; Schmieder, 1995; Sand-Jensen, 1998, Boedeltje et al., 2001). Hydrologic and hydrodynamic conditions affect macrophytes mainly in two ways: by the fluctuating water level (Spence, 1982; Best et al, 1984; Coops et al, 1996; Schwarz & Hawes, 1997; Fernández-Aláez et al, 1999) and by mechanical stress caused by waves and water flow (Spence, 1982; Idestam-Almquist & Kautsky, 1995; Coops & Velde, 1996; Rea et al, 1998). Wave-induced turbulent forces on the bottom have been shown to increase with decreased water depth (Sand-Jensen, 1989). The helophyte zone and, especially, the zone of floating-leaved plants decrease with the increasing lake area due to wind stress related to the height and strength of waves (Spence, 1982). The wind fetch exceeding 500-800 m has a significant influence on distribution of macrophytes (Rea et al, 1998). Among submerged plants, the water dynamics has a strong influence on the length and branching of shoots. Plants that grow in sheltered places are taller, have a longer distance of internodes and are more branched compared to plants growing in areas opened to wave action (Idestam-Almquist & Kautsky, 1995).

As a structuring part in lake ecosystems, aquatic macrophytes reduce sediment resuspension and erosion smothering and altering the water flow (Fonseca et al., 1982; Gregg & Rose, 1982; Madsen & Wrancke, 1983). In shallow lakes macrophytes produce a remarkable amount of organic matter increasing the sedimentation and creating favourable conditions for sediment accumulation (Barko & James, 1998). Depending on wind stress, erosion and sedimentation shores can be distinguished

(James & Barko, 1990), the formers characterized by a small sediment thickness, low concentration of organic matter and nutrients, in contrary to sedimentation shores.

4.1.1.3. Light conditions

Generally, submerged macrophytes grow to a depth of two to three times the Secchi depth (Chambers & Kalff, 1985). Climatic differences associated with geographic latitude appear to have a strong influence on the relationship between water transparency and depth distribution of submerged plants (Duarte & Kalff, l987). At low latitudes, angiosperms colonize deeper and reach maximum biomass at greater depth than in lakes of similar transparency at higher latitudes because of warmer water, greater irradiance and longer vegetation period in the south. With some exceptions, a depth range between 10 and 15 m appears to be a limit for most angiosperms (Gasith & Hoyer, 1998). The growth of plants is dependent on minimum light requirement (Sand-Jensen & Madsen, 1991; Madsen & Sand-Jensen, 1994) and light use efficiency (Madsen & Brix, 1997). In most lakes, especially in eutrophic ones, plants are light-limited (Chambers & Kalff, 1987; Sand-Jensen & Madsen, 1991; Scheffer et al., 1992; Scheffer et al., 1993; Middleboe & Markager, 1997) and underwater light plays an important role in determining the depth distribution of different groups of aquatic macrophytes (Sculthorpe, 1971; Chambers & Kalff, 1985).

On the other hand, macrophytes are able to modify the underwater light climate. Dense reed stands, floating (*Lemna* spp., *Eichhornia crassipes* (Mart.) Solms) and floating-leaved plants (*Nuphar*, *Nymphaea*) modify habitat conditions for other species becoming the 'key-stone' species (US terminology), or 'edificator' species (*sensu* Braun-Blanquet, 1964, used mostly in Russian literature) in the ecosystem. Canopy-forming types or poorly rooted species creating dense shade affect their own light conditions by self-shading (Binzer & Sand-Jensen, 2006). Charophytes and elodeid species carpeting lake bottoms may contribute to water transparency by reducing water movement at the lake bottom and preventing resuspension of the sediments (Berg et al., 1997; Scheffer, 1998). The relationship between species-specific depth ranges and optical depth suggests that average light conditions over time play a major role in structuring not only the maximum depth to which charophytes can penetrate in a lake, but also the maximum depth of component species in a multi-species assemblage (Schwartz et al., 2002).

4.1.1.4. Temperature

The high specific heat content of water and the formation of ice on lake surfaces that prevent winter heat losses make lakes a thermally more stable environment compared to most of terrestrial surfaces. The rather small temperature variability worldwide makes freshwater systems particularly vulnerable to invasion (Shea & Chesson, 2002). Primarily aquatic or semi-aquatic grasses are globally among the most successful natural area invaders (Daehler, 1998). Temperature is a major factor that determines the rate of metabolic processes in plants (Berry & Bjørkman, 1980; Larcher, 1995). Physiological responses of plants to temperature differ among species as does the temperature dependence of growth. The temperature tolerance range of individual plant species is genetically fixed, although most species possess considerable phenotypic plasticity. Freshwater submerged macrophytes appear to be eurythermic and able to thrive within a wide range of temperatures (Madsen & Brix, 1997; Santamaria et al., 2003). In a close connection with temperature is the influence of ice. The major effects of lake ice on plants are expressed in casting shade, preventing access to the atmosphere, and scouring littoral habitats with ice-rafts during break-up (Wilcox & Meeker, 1991; Ormerod et al. 1994; Suren & Ormerod, 1998; Lacoul & Freedman, 2006). Also rapid increase of water level in winter may cause uprooting of plants from soft bottom by ice that can suppress emergent plants growth and expansion (Mäemets, 1973; Paper V).

4.1.2. Metabolic factors

The hydrochemical preferences of macrophytes are mostly related to nutrients and alkalinity (Figure 3) (Best et al., 1984; Graneli, 1985; Søndergaard, 1990; Rørslett, 1991; Kowalczewski & Ozimek, 1993; Scheffer, 1998). The abundance and productivity of macrophytes can vary within two orders of magnitude among lakes of different trophic levels. The maximum productivity of the biosphere occurs in the zone of emergent aquatic macrophytes (Westlake, 1963; Wetzel, 1990) and declines rapidly when submerged. The primary suppressing mechanisms are the exponentially attenuating light and the reduction of nutrient and gas exchange, especially for CO_2 which diffusion in the water is about 10^4 times slower than in the air (Raven, 1984). The most abundant and productive emergent, floating-leaved, and submerged aquatic macrophytes are herbaceous perennial plants that develop highly dissected foliage and are not the rapidly growing surface canopy-forming species under conditions of eutrophy. The continuous growth of perennials plants results in continuous turnover of organic matter with production of relatively resistant particulate organic matter in senescent tissues. Annual plants do not exhibit such continuous growth and biomass turnover (Wetzel & Søndergaard, 1998). Productivity of rosette perennials such as the isoetids and of most annual submerged plants is very much lower compared to the productivity of perennials with thin, finely divided, reticulated foliage that increases surface area, enhances gas exchange and light harvesting (Sculthorpe, 1971).

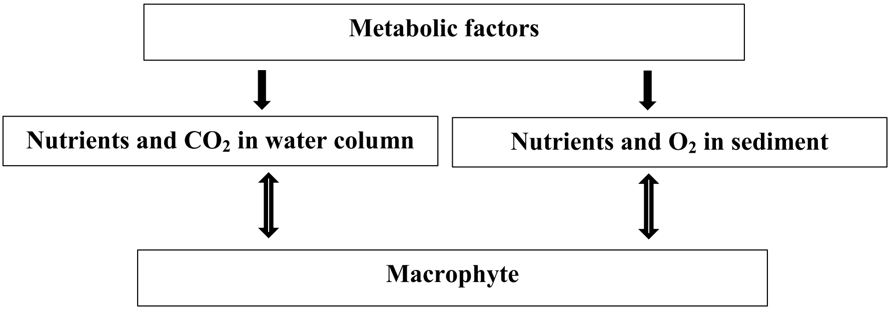

Figure 3. Metabolic factors affecting the distribution of macrophytes in lakes.

The growth of macrophytes is limited mostly by the availability of the sediment nitrogen (Anderson & Kalff, 1986; Barko et al., 1988, James & Barko, l99l; Rogers et al., 1995) however, in oligotrophic hardwater systems and systems with sandy sediments, phosphorus appears to be more important in limiting macrophyte growth. Also potassium and calcium are potentially important in affecting submerged macrophyte growth (Barko & James, 1998).

The trophic status of lakes is inversely related to mean depth (Vollenweider, 1975; Canfield & Bachmann, 1981). Deep lakes tend to be more oligotrophic and support lesser growth of aquatic macrophytes than shallow lakes. A study by Canfield and Hoyer (l992) showed that oligotrophic and mesotrophic lakes rarely have aquatic macrophyte abundance exceeding 20% PVI, whereas eutrophic and hypereutrophic lakes have the potential to reach 100% PVI. High turbidity may limit growth of submerged macrophytes in these lakes even though nutrients availability can support extensive growth (Gasith & Hoyer, 1998). Sediment related factors affecting the distribution of macrophytes are the high organic matter content that may have a toxic influence on macrophytes due to accumulation of phytotoxins (Drew & Lynch, 1980), poor oxygen availability that may disturb the metabolic processes in roots (Crawford, 1982; Lachavanne, 1985; Armstrong et al., 1999), and nutrient limitation due to complex formation (Sikora & Keeney, 1983).

Macrophytes themselves cause continuous changes in sediments by altering pH, redox conditions, and nutrient turnower (Jaynes & Carpenter, 1986) and having notable effects to water column nutrient status, resuspension of bottom material and water turbidity (James & Barko, 1990; Sand-Jensen & Borum, 1991; Horppila & Nurminen, 2001). Dense canopy-forming poorly rooted species (e.g. *Ceratophyllum demersum* L.) may create anoxic conditions in the bottom layers of lakes (Moss et al., 1986), thereby increasing the potential for phosphorus release from the sediment, particularly where the iron-bound and redox-sensitive phosphorus fractions constitute a significant part of the total phosphorous in the sediment (Moss et al., 1996). Similarly, elevated by high photosynthetic activity, pH may enhance phosphorus release from the sediment by affecting the phosphorus sorption mechanisms in the surface sediment (Søndergaard, 1988). Less dense macrophyte beds and macrophytes having a more developed root system (*Myriophyllum* spp., *Ranunculus* spp.) may diminish redox-sensitive phosphorus release rate by oxidizing the surface sediment (Andersen & Olsen, 1994; Flessa, 1994; Christensen & Andersen, 1996).

Results of experiments (Prentki, 1979; Trisal & Kaul, 1983; Carignan, 1985; Barko et al., 1988; Chen & Barko, 1988) indicate that rooted submerged macrophytes are capable of depleting sediment nutrient pools. Reductions of more than 90% of exchangeable N and more than 30% acid-extractable P from sediment by *Hydrilla verricillata* (L.f.) Royle were observed by Barko et al. (1988) in a 6-week experiment. Rooted macrophytes represent a direct link between the sediment and overlying water (Figure 4). Nutrients are mobilized from sediments directly via root uptake followed by subsequent release during seasonal senescence and decomposition. Because of this mechanism, some authors (Barko & Smart, 1980: Carpenter, 1980; Landers, 1982; Smith & Adams, 1986) consider littoral vegetation as a potential direct source of nutrients to the water column.

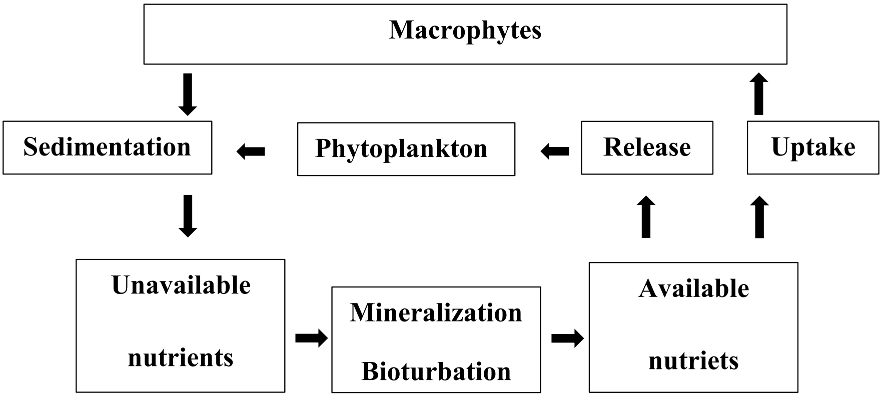

Figure 4. Sediment nutrients turnover and the role of macrophytes in releasing nutrients to the water column.

In fertile systems high productivity and biomass turnover of macrophytes contribute to high rates of nutrient mobilization from sediments, particularly with rapidly growing species such as *Myriophyllum spicatum* L. (Smith & Adams, 1986). In less fertile systems, however, the effects of macrophytes on nutrient budgets are probably less pronounced (Barko et al., 1991). Likewise, in large deep lakes, where macrophytes are less abundant relative to lake volume, effects on nutrient budgets are probably negligible (Gasith & Hoyer, 1998).

The final outcome for nutrient availability in macrophyte beds may therefore depend on macrophyte species and density and on the trophic status of the system. Although no final consensus exists, several authors (Carpenter & Lodge, 1986; Rørslett et al.. 1986; Jones, 1990) conclude that in general, submerged macrophytes may be regarded as nutrient sinks during their active growth and only as a potential nutrient source during the relatively short periods of their senescence.

4.1.3. Biotic factors

The lake biotic effects on macrophytes are very complicated and perform through the linkages with epiphytes, phyto- and zooplankton, fishes and herbivores (Figure 5). Because of complexities, interlacings and multiple levels of operation of biotic interactions, the overview on this subject is giving by organism groups in the lake. The more so that the biotic effects are mostly handled in the literature from active macrophytes point of view and resulting interactions are rather often lake and species specific.

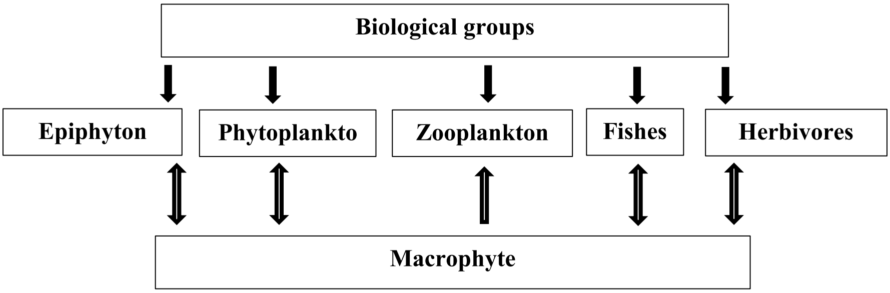

Figure 5. Interactions between macrophytes and other organism groups in lakes.

The surfaces of macrophytes, especially those of submerged plants are heavily colonized by highly productive epiphytic communities – algae, cyanobacteria and other microbes. Accompanying shading effect makes these communities recourse competitors and a key factor in the decline of submerged macrophytes (Silberstein et al., 1986; Brönmark & Weisner, 1992; Vierssen et al., 1994). Increase of trophic status is usually accompanied by a reduction of water transparency and, thereby, decrease of maximum colonization depth of submerged plants and a more intense competition (Sand-Jensen, 1997), which may end up with the replacement of submerged plants with phytoplankton or epiphytic algae (Scheffer, 1998). Therefor efficient removal of periphyton by different grazers may be a feedback mechanism to stabilize macrophyte dominance in lakes (Brönmark & Vermaat, 1998). Leaching nutrients from living and senescent macrophytes support large microbial communities. Productivity and nutrient recycling abilities are maximized by extensive development of both - submerged macrophytes and associated epiphytic microbiota (Wetzel & Søndergaard, 1998).

A negative effect of macrophytes on phytoplankton biomass is well known. Macrophytes and their associated epiphytes take up and store nutrients, which become unavailable for phytoplankton (Kufel & Ozimek, 1994; O'Dell et al., 1995). The response of phytoplankton is nonlinear along macrophyte density gradient with a threshold occurring at a macrophyte density of approximately 15-30% PVI. There are several macrophyte associated mechanisms that contribute to the maintenance of low phytoplankton biomass. The mechanisms can be divided into direct ones associated with the plants themselves (creation of a still water environment, poor light climate, and secretion of allelopathic substances) and indirect ones such as provision of refuges or habitat for grazers on algae, and modification of the ambient nutrient regime by the metabolic activity of plants. The complexity of such systems is illustrated also by the fact that in turn these mechanisms are affected by a second level of influences - predation of fishes on the grazers, imposition of nutrient loads from the catchments, and hydrodynamic conditions that determine the degree of water movement through the plant beds (Søndergaard & Moss, 1998).

Vegetated areas of lakes may function as a resource base and as refuge in fish-pray systems (Heck & Crowder, 1991; Mittelbach & Osenberg, 1993; Persson, 1993; Persson & Eklöv, 1995). In shallow lakes submerged macrophytes may alter the fish-zooplankton interaction strength because of large cover area. Zooplankton uses macrophytes as refuge against predation from fish. Large-sized pelagic zooplankters generally occur in greater numbers inside of or around macrophyte beds than outside, although this effect can be modified by fish. But again the interactions are complex, as the presence of macrophytes also influences the mutual interaction between piscivourus and prey fish (Jeppesen et al., 1998). Prey fish appear to use macrophyte beds as a daytime refuge against fish predates (Timms & Moss, 1984). Compared to lakes without macrophytes, a submerged plant cover of 3% in a lake is enough to increase the grazing potential of zooplankton in the open water by 100% (Lauridsen et al., 1996). Besides direct biotic influence on invertebrates submerged macrophytes have also indirect influence by affecting abiotic variables such as light, temperature and oxygen concentration and increase the diversity of habitats and thereby resources for macroinvertebrates (Carpenter & Lodge, 1986; Lillie & Budd, 1992; Kornijów, 1996; Kornijów & Kairesalo, 1994). Vegetation is associated with high densities of invertebrate prey affecting food consumption and growth of the fish (Crowder & Cooper, 1982; Heck & Crowder, 1991; Diehl, 1993; Persson, 1993). Also the physical structure of macrophytes has effects on competitive and predatory interactions between different species and size classes of fish (Winfield, 1986; Diehl, 1988; Persson, 1991). In this way macrophytes influence the relationships between macroinvertebrates and fish and reduce vulnerability of prey fish to piscivores (Diehl, 1988; Eklöv & Diehl, 1994).

Macrophytes in lakes serve also as a direct food resource. In terrestrial ecosystems herbivores are widely regarded as an important determinant of plant abundance and species composition and as an important selective force in the evolution (Rhoades, 1985; Rosenthal & Berenbaum, 1992). On the contrary, for decades the paradigm in limnology has considered live freshwater macrophytes to be of low nutritional quality, too tough for the mouthparts of aquatic herbivores, and therefore rarely consumed by herbivores (Lodge, 1991; Newman, 199l). The reason for that may be that about half of all studies on herbivory of macrophytes have been done on insects which have the smallest impact on macrophytes among the herbivore groups (insects, crayfish, fishes, birds, mammals). Data suggest that live macrophytes may be consumed far more than is often appreciated (Lodge, 199l). To be preferentially consumed, a macrophyte must have (1) a structure that makes it possible to bite, (2) lack of chemical deterrents, (3) a certain level of nutritiousness (Lodge et al., 1998). For fishes macrophytes and their associated epiphytic algae are a food resource (Prejs, 1984; Hansson et al., 1987) either directly or indirectly via other trophic components included in the food web (Persson & Crowder, 1998). After senescence and death, macrophytes become available as a food source to shredders and deposit feeders (Suren & Lake, 1989). Through these various pathways, submerged macrophytes have a strong, positive effect on the resource base of the benthic and epiphytic macroinvertebrates. As an example of complexities of these systems, Diehl & Kornijów (1998) showed that increasing densities of submerged vegetation enhance the densities of both macroinvertebrates and their fish predators.

4.2. SPATIAL AND TEMPORAL PATTERNS OF AQUATIC MACROPHYTES AND THEIR USE FOR INDICATIONAL PURPOSES

The structuring role of lake conditions to macrophytes may be described in a spatial and in a temporal aspect. It is obvious that space and time are inseparable and dividing them is just an abstraction. Spatial differences, which reflect the structure of a plant community at any moment of time, are like static snapshots. Moving from a closer to a more distant view, i.e. from the species level to the community level, spatial changes are reflected in species growth forms, architecture, depth distribution and zonation in any particular part of a lake, in differences between lake parts, and finally across lakes and lake types (Figure 6). Temporally macrophyte communities change from one season to another, from year to year and exhibit long-term changes related to the evolution of lake conditions (Figure 7). The possibility to decode these two aspects into growth conditions gives to macrophyte communities a strong indicator power for water quality in different types of lakes.

4.2.1. Formation of spatial differences

Lake conditions affect the spatial structure of macrophytes realized at species level as differences in growth form and architecture. The same species of plants can exhibit important morphological differences under different light and trophic conditions both in terrestrial (Kull, 1995; Möller & Cronka, 2001) and aquatic systems. The ecophysiological role of aquatic plants in lake processes depends on the distribution of their surface area and biomass (Gerber et al., 1994). Vertical distribution of leaf surface area and the surface area to biomass ratio within the water column characterizes light adaptation of macrophytes and can be used for describing growth conditions. The seasonality of growth rates and biomass development of submerged plants in shallow waters is often related to light conditions (Sand-Jensen & Madsen 1991; Hawes et al., 1999; Gevaert et al., 2002). Macrophytes are important producers in the littoral zone of shallow lakes contributing up to 84% of the daily summer primary production (Paper VII). Spatial differences in plant structures in a light-limited environment form the basis for differences in primary production within of one species and between species.

In shallow lakes rich in submerged macrophytes, epiphyton becomes an important component of primary productivity and a major regulator of nutrient fluxes (Jørgensen & Löffler, 1990; Wetzel, 1990). The architecture of macrophytes is very useful for describing relations between submerged macrophytes and epiphytic organisms (Cattaneo & Carigan, 1983; Galanti & Romo, 1997; Kelly & Hawes, 2005). As shown by Romo & Galanti (1998) *Myriophyllum spicatum* due to its larger leaf area supported higher epiphyte production compared to *Potamogeton perfoliatus* L. Our study on primary production of macrophytes and their epiphytes carried out in two large shallow lakes of Estonia, L. Peipsi and Lake Võrtsjärv (Paper VII), showed that production varied throughout the vegetation period for the same species in different lakes and for different species in same lake (Paper VII, Figure 1).

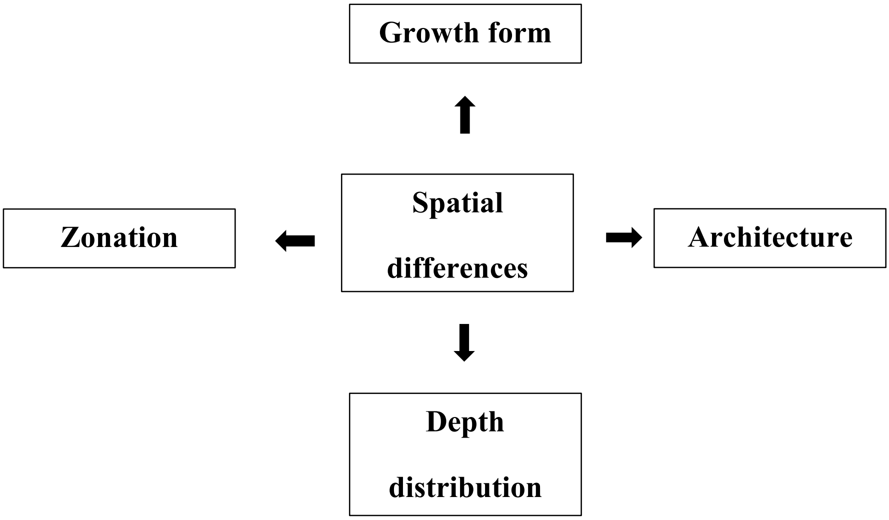

Figure 6. Expression of spatial differences in aquatic macrophyte communities.

Depending on the nutrient status, eutrophic shallow lakes can reach two alternative stable states: a vegetated state with clear water and a turbid state dominated by phytoplankton (Scheffer et al., 1993; Scheffer, 1998). Our data on the architectonics of *Potamogeton lucens* L. from two lakes of different light climate - the macrophyte dominated Lake Prossa and the phytoplankton dominated Lake Kaiavere (Paper VI) - showed that the total surface area of shoots and the surface area of leaves differed significantly between lakes. Also other size-related parameters of the plants tended to be larger in the macrophyte-dominated lake. The same pattern of seasonal changes of the area/dry weight ratio was characteristic of both lake types. In the beginning of the growing season, the maximum surface area of plants was located in the topmost sections and shifted to lower sections in the course of plant growth (Paper VI, Figure 2). In the macrophyte-dominated lake, the improvement of light conditions in summer likely stimulated further ramification on plants and the formation of a more uniform vertical distribution of plant surfaces.

The second important group of phenomena in which lake conditions occur as a structuring force for macropytes, is the formation of macrophyte communities and zones based on evolutionally and adaptationally different depth distribution of species. In shallow lakes the littoral zone constitutes a large part of the lake's area. This area is characterized by a wide spectrum of environmental conditions, which were comprehensively summed up by Spence (1982): velocity of water flow, composition of bottom sediments, hydrostatic pressure (unimportant in shallow lakes), underwater light climate, and nutrient conditions. Species of aquatic macrophytes as sessile and relatively long-living organisms are differently adapted to environmental conditions. These adaptations are expressed not only in the presence or absence of certain species but also in their life form, length of shoots and colonization depth. On a plant association level, differences in environmental stress are expressed primarily in spatial variation of species diversity. Combinations of factors in different lake parts or in different lakes are revealed in the patterns of macrophyte distribution. The domination of certain species depends on the environmental factors as well as on the historical development of the vegetation (Sculthorpe, 1971). A good example showing how differences in environmental conditions affect macrophyte distribution and diversity in the littoral zone is provided by our studies carried out in the large and shallow Lake Võrtsjärv (Papers III & V). Among the 114 species found in Lake Võrtsjärv (Mäemets, 2002), 32 species may be considered common species. *Phragmites australis* (Cav.) Trin ex Steud. was the most frequent species in the helophyte zone, while among floating-leaved and submerged plants *Nuphar lutea* (L.) Sm. and *M. spicatum* were, correspondingly, the most frequent species, the latter occurring in all parts of the lake. According to the dominating westerly and south-westerly wind directions, the northern and eastern shores were most wind exposed while the most sheltered reaches were located in the south. The northern shore was characterized by the coarsest sediments while the shores as well as the open water in the southernmost end of the lake were dominated by fine sapropel sediments. Most of the bigger inflows enter the lake from the south and from the west causing spatially different nutrient availability in the lake. This is reflected in the average shoot numbers of *N. lutea* and *P. australis*, which is higher near the inflows. Also the shoots of *P.australis* were longer near the inflows while those of *Typha angustifolia* L. and *Schoenoplectus lacustris* (L.) Palla were longer in the areas between the inflows (Paper III). The littoral area of Lake Võrtsjärv mostly has a very gentle slope but especially in the north where the shallow zone is significantly broader than in other parts of the lake. Generally, the width of the helophyte zone tended to increase in reaches with a gentler slope. Differences of environmental conditions create a large diversity of macrophyte distribution patterns in different parts of the lake. The described spatial gradients in nutrient availability, sediment type, wind stress, and bottom slope were important for the number of species, which decreased in the south–north and west–east directions. Also the maximum colonisation depth of *P. australis* and the relative abundances of *P. australis* and *M. spicatum* increased in same direction (Paper III). Differences in species frequency were reflected in the hyperbolic shape of the frequency curve (Paper III, Figure 2). At one end the frequency distribution we can find species with a large distribution are and at the other end - species with a small distribution area (Paper III). According to depth distribution, *P. australis* reached the widest range of colonisation depth (1.9 m) among species. In the zone of floating-leaved plants, the colonisation range of *N. lutea* was 1.3 m. The dominating submerged plant, *M. spicatum*, colonised the deepest areas up to 3 m (Papers III & V). The relative abundance of the two most common species, *P. australis* and *M. spicatum*, tended to increase with increasing depth (Paper V, Figure 2). The average width of the helophyte zone in the lake was 95 m, varying from 0 to 480 m. It was the narrowest along the southern and eastern shores, and the widest but most variable along the northern shore of the lake. In this part both the mean width of the reed belt and its variability were significantly higher than in other areas. According to the bathymetry of the lake and the ranges of colonization depth, macrophytes could potentially colonize 95% of lake area, but in reality they colonized only 19% of it. This difference shows clearly that other factors besides depth were strongly limiting the depth distribution of plants. Most suppressed were the floating-leaved plants, which colonized only 6% of areas within their suitable depth range. Helophytes were able to colonize 19% and submerged plants 26% of their suitable depth ranges (Paper V).

The variability of macrophyte distribution patterns increases with lake size and development of the shoreline. In large lakes with a complex shoreline, variable local conditions combined with climatic variability create a wide range of habitat conditions for different macrophyte species. Sometimes it is even hard to indicate exactly the factors involved in the formation of a particular macrophyte distribution. A correlation analysis carried out between abiotic indices, plant variables and geographic co-ordinates in Lake Võrtsjärv (Paper V, Table 4) suggested several combinations of lake conditions to be responsible for creating differences in macrophyte parameters between different lake parts. Species richness increased from north to south while the relative abundance of the two dominants, *M. spicatum* and *P. australis,* decreased. The latter showed strong negative correlations with nutrients. The shoot density of *M. spicatum* increased with the wind exposure. The results of factor analysis (Paper V, Tables 3 & 5) showed a clear and strong polarization of environmental conditions and macrophyte indices in Lake Võrtsjärv. The first factor (Paper V, Table 3) described the gradients of environmental variables from north to south and the second from east to west. The wind influence decreased and the nutrient loadings increased from north to south. Sediment grain size increased from the windward western shore to the leeward eastern shore. A second analysis relating macrophytes indices with geographic co-ordinates (Paper V, Table 5) supported the idea of spatial gradients occurring in the macrophytes distribution. Important spatial gradients occurred in species richness, which decreased, and the maximum colonisation depth of *P. australis* and the relative abundances of *P. australi*s and *M. spicatum,* which increased towards north and towards east (Paper V). We distinguished three main reasons that created polarization in macrophyte distribution patterns in Lake Võrtsjärv. Firstly, the dominating westerly and south-westerly winds affecting the northern and eastern shores most, determine sediment composition and areas of mechanical stress for macrophytes. Secondly the irregular distribution of inflows with larger inflows entering the lake from the south and from the west causes an uneven nutrient availability in different parts of the lake. And thirdly, the combination of the elongated shape of lake in the north–south direction narrowing down towards south with the prevailing westerly wind directions generate a distinct contrast between the sheltered south western and exposed north eastern shores. The narrow southern part of the lake receiving heavier nutrient load represents a sheltered basin with distinctly different conditions for the macrophytes. These three factors together explain the spatial differences in species richness, abundance and colonization depth of macrophyte species in Lake Võrtsjärv (Paper III & V).

The complexity of relationships between lake conditions and macrophyte distribution can be most clearly followed across different lake types. The presence or absence of macrophytes is widely accepted as the main feature to distinguish between the two alternative stable states of lakes: the vegetated state with clear water, and the turbid state dominated by phytoplankton (Scheffer et al., 1993; Scheffer, 1998). In the vegetated type, contrarily to the phytoplankton-type, macrophytes have a direct influence to lake conditions by reducing water movement and preventing sediment resuspension (Scheffer, 1998) and an indirect influence via several mechanisms that suppress phytoplankton development. These mechanisms involve competition for nutrients and light, enhanced denitrification inside macrophyte beds, increased grazing on phytoplankton by plant-associated invertebrates, higher sinking losses of phytoplankton both by mechanically suppressed water turbulence and increased calcite incrustation of algae at higher pH, and, finally, the allelopathic influence of macrophytes (Jeppesen et al., 1998; Scheffer, 1998; Van den Berg, 1999; Meijer, 2000; Donk & Bund, 2002).

A comparison of two shallow lakes in Estonia (Paper II), the macrophyte dominated L. Prossa (33 ha), and the phytoplankton dominated L. Kaiavere (250 ha) showed that despite the different area, the nutrient dynamics was very similar in both lakes. After the vernal phytoplankton peak, the water became clear in the macrophyte-dominated lake but remained turbid in plankton-dominated lake. Similar nutrient and zooplankton dynamics occurred in both types of lakes, suggesting that an alternative mechanism may have accounted for the observed phytoplankton decline in the macrophyte lake. As carbonate alkalinity showed a clear difference between these two lakes increasing during spring in the plankton-dominated lake, while decreasing by nearly 50% in the macrophyte-lake, we suggested that co-sedimentation of phytoplankton with autochthonous calcite could have contributed to the shift to the clear water state. Such aggregation of algae and seston particles with autochthonous calcite crystals in hard-water lakes leading to increased sedimentation losses has been recurrently described by Koschel et al. (1983, 1990). The mechanism includes intense calcite formation due to an increase in pH provoked by the photosynthesis of dense macrophyte stands.

Another study involving additionally also the plankton-dominated Lake Võrtsjärv (Paper IV) revealed highest grazing rates of ciliates on small algae in the macrophyte-dominated lake suggesting that more intensive ciliate grazing could also be one factor causing a decrease in phytoplankton numbers in the macrophyte-dominated lake.

Jeppesen et al. (1994) estimated that at least 30% of a lake's bottom area must be covered by submerged vegetation to create stable clear water conditions. Although this does not give a clue to the mechanisms involved, it is in good agreement with our observations. The bottom of the macrophyte-dominated Lake Prossa was densely covered (PVI 40%) with charophytes, *Chara tomentosa* L. and *Nitellopsis obtuse* (Desv.) J.Groves, whereas the coverage by submerged plants was much smaller (PVI 6%) in Lake Kaiavere and even less (PVI 1.7%) in Lake Võrtsjärv. The reduced sediment resuspension and the possible allelopathic influence of charophytes on phytoplankton may also have contributed to the maintenance of the extensive clear-water period in the Lake Prossa (Papers II & IV).

4.2.2. Formation of temporal changes

Spatial patterns in macrophyte distribution created by differences in habitat conditions are not static but continuously changing with different rates. These changes are temporary or lasting, periodic or aperiodic. Formation of temporal changes can be described in three aspects – seasonal, year-to-year and in a long-term perspective (Figure 7). Weather conditions and changes in catchment management, which alter the otherwise regular seasonal cycle in macrophyte communities, may be seen as a trigger for the formation of lasting temporal differences. Despite large year to year variability, environmental pressures and natural evolution of in-lake conditions may create persistent trends and lead to long-term changes in macrophytes communities.

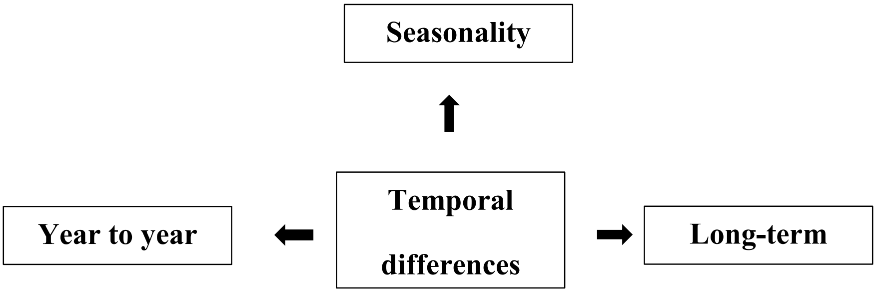

Figure 7. Expression of temporal differences in aquatic macrophyte communities.

Seasonality of conditions during the vegetation period is a universal factor creating changes in temperate zone ecosystems. Seasonality expressed in variations of biomass and growth rates of submerged plants is often related to light conditions (Sand-Jensen & Madsen 1991, Hawes et al. 1999, Gevaert et al., 2002). Our studies showed that the importance of internal and external processes affecting seasonal development of macrophytes depends largely on lake size. In small lakes seasonal changes are more affected by internal processes within lake ecosystems themselves because the role of macrophytes there is much bigger than in large lakes (Papers II & IV). The effect of lake size on macrophyte growth was more clearly expressed in the comparative study of two drumlin lake (Paper II). These lakes situated rather close to each-other in the same landscape were both shallow and had similar nutrient dynamics, however, after the vernal phytoplankton peak one lake became clear and macrophyte-dominated, whereas the other remained turbid because of plankton dominance. The most important difference between the lakes was the size, the macrophyte lake having seven times smaller surface area than the plankton lake. We suggested the longer wind fetch to be the main reason for the scarcity of submerged macrophytes in the bigger lake where the distribution of macrophytes is strongly physically controlled by water turbulence and higher turbidity (Papers IV & V). Besides lesser water movement and reduced bottom sediment resuspension in the smaller lake, mechanisms supporting clear-water period, such as zooplankton grazing pressure on phytoplankton, sinking losses of non-motile algae, aggregation of algae and seston particles with autochthonous calcite crystals (Papers II & IV), were more effective because of the edificatory role of macrophytes in the ecosystem.

Often clear temporal differences in macrophyte communities can be seen between years and arising changes may perpetuate if conditions (e.g. climatic, anthropogenic) have a clear tendency. A good example of such changes is the strongly physically driven Lake Võrtsjärv (Papers III & V) where various trends in the macrophyte community have been revealed. Climatic conditions create the background which, in combination with the morphometric features of the lake, determines locally the habitat conditions for macrophytes (transparency, hydrodynamics, sediment transport, fluctuations in water levels). Depending on the water level and transparency, the aphotic bottom area may extend from 30 to 90% of the total lake area (Nõges, 2000). This complex of conditions divides Lake Võrtsjärv into two different parts – a small and narrow southern part and a large northern part where the effect of winds increases with the broadening of the lake. Dominating winds, in turn, create differences in sediment composition and divide the northern part of the lake into eastern and western parts (Paper III). Each of those lake parts exhibit distinct macrophyte seasonality and different long-term trends.

Like in a movie where single static pictures in a sequence create a dynamic picture, long-term changes in macrophyte communities demonstrate how temporal and spatial changes are connected. Comparing data from the pristine period (so-called reference condition) with nowadays situation, in the context of environmental changes, gives us an idea how the lake ecosystem reacts. Certainly it needs good and reliable data to follow these changes. In case of Lake Võrtsjärv the reference status at the beginning of the 20th century has been described by Mühlen & Schneider (1920) who recorded the status of the lake in detail during the complex expedition carried out in 1911-13. We developed a special similarity index (Nõges & Feldmann, 1999) in order to compare the historical list of species with nowadays data. We found changes in the lake ecosystem in all aspects including macrophytes, which showed a strong deviation of the distribution patterns from the reference. The index showed clear trends of decreasing species diversity and changes of dominating species in time (Paper I). The former dominant at the beginning of the 20th century, *Elodea canadensis* Michx. (Mühlen & Schneider, 1920), has by now been replaced by *M. spicatum* and partly by *C. demersum*. Disappearance of charophytes, the increasing importance of *M. spicatum*, expansion of reeds, and overgrowing of the southern part of the lake by floating-leaved plants are the main trends characterising long-term temporal changes in Lake Võrtsjärv macrophyte communities (Paper III). These shifts in the community structure are similar to the changes described by Kowalczewski & Ozimek (1993) as a transition from the *Charophytes-Potamogeton* spp. type to the *Myriophyllum-Potamogeton* spp. type. The main reason for these changes is the increasing anthropogenic eutrophication pressure. Recent decades give evidence of a remarkable change in land management and land use intensity in Central and Eastern European countries (Liira et al., 2008). This has caused changes in the environment and in the state of natural habitats including shallow lake ecosystems. The already occurring long-term changes are closely connected to the spatial aspect of macrophytes distribution. The zone of emergent macrophytes is most suitable for long term observation and assessing community changes because of its "accessibility" by remote sensing techniques (Paper VIII). Many studies have demonstrated continuously increasing overgrowth of coastal zones by aquatic macrophytes and mostly by common reed (*P. australis*), in several European large boreal and northern temperate lakes (Andersson, 2001; Partanen & Luoto, 2006; Paper III). The expansion of tall macrophytes causes biodiversity loss and the reduction of ecosystem services from the recreational point of view (Rørslett, 1991; Güsewell & Klötzli, 1998; Lenssen et al., 2000; Andersson, 2001; Rannap et al., 2007; Daniel & Rydin, 2008). According to literature, the expansion of reed could be attributed mostly to eutrophication (Andersson, 2001; Partanen & Hellsten, 2005; Zeng et al., 2009; Mäemets et al., 2010). Analyses showed that in Lake Võrtsjärv large inflows had the strongest positive effect on the expansion of macrophytes (Paper VIII). Catchments of the six major inflows of the lake cover 80% of the lake's total drainage basin and account for 80% of the total phosphorus and nitrogen loadings (Järvet & Nõges, 1994; Nõges et al., 1999). Agricultural activities and point source loadings from the towns of Valga (population 14,000) and Viljandi (population 21,000) provide the main source of these nutrients (Pettersson et al., 2010; Paper VIII). The positive effect of large inflows is reflected also in the spatial distribution of shoot density and length of *P. australis* with longer and denser communities located near these inflows (Papers III & V).

4.2.3. Macrophytes as lake status indicators

Lake morphometry, water chemistry, and biotic interactions are the main groups of factors affecting macrophytes (Carpenter & Lodge, 1986; Lacoul & Freedman, 2006), hence, we can argue that their community composition as well as spatial and temporal distribution are results of the structuring role of lake conditions. The possibility to decode these aspects into growth conditions gives to macrophyte communities a strong indicator power for water quality in lakes. Macrophytes have long been used in lake typology (Spence, 1967; Rørslett, 1991; Palmer et al., 1992; Vestergaard & Sand-Jensen, 2000) and for assessing anthropogenic influence (Hofmann, 1994; Tremp & Kohler, 1995; Melzer, 1999; Stelzer et al., 2005). Simultaneously, the discriminating power of macrophytes along lake size and depth gradients is more complicated and less straight forward (Gasith & Hoyer, 1998, Nurminen, 2003).

4.2.3.1. Presence / absence

The role of macrophytes in the foodweb and their ability to reflect changes is dependent on their diversity, abundance, and composition (Olson et al., 1998; Cheruvelil et al., 2001). As a community, macrophytes respond to environmental changes by modifying their taxonomic composition and/or increasing or decreasing plant abundance (Schaumburg et al., 2004). Close contact of macrophytes with the lake environment through the root-system and, especially through the leaves, which are surrounded by water or floating, raise expectation of macrophytes characteristics reflecting environmental conditions. In order to exploit the indicator abilities of macrophytes, three main aspects need to be taken into account. The first two are connected with the presence and environmental demands of macrophytes, and the third important aspect is, similarly to most sessile organisms, their cumulative long-term reaction to changes in environmental conditions (Arts et al., 1990; Melzer, 1999; Nurminen, 2003). Self-evidently, indication with aquatic macrophytes is restricted to sites with sufficient macrophyte cover and therefore fails to indicate extreme eutrophication leading to depopulation of submerged macrophytes (Schaumburg et al., 2004). Submerged macrophytes are good indicators in shallow lakes or in shallow areas of deep lakes where most of the lake bottom can potentially be covered by vegetation (Søndergaard et al., 2010).

Authors of a new theory (Pärtel et al., 2011) consider the absent species in nature as important as the existing ones and call species in the region that are absent, but that could potentially inhabit those particular ecological conditions, ‘dark diversity’. Based on patterns of species co-existence, a potential “species pool” can be defined for any habitat and the deviation of the community composition found from this pool (ie. the ‘dark diversity’) refers to a shift in environmental conditions. To a certain extent, this concept is related to the reference conditions approach in the absence of historical data.

4.2.3.2. Interference of environmental factors

The presence or absences of different species reflect different environmental conditions, for example, many of them are indicators of eutrophication (Naumenko et al., 2000; Egertson et al., 2004; Jupp & Spence, 1977; Lachavanne et al., 1992), and others are sensitive to acidification (Roelofs, 1983) or salinization (Schutten et al., 1994; Schaumburg et al., 2004). It is important to consider that different physical factors influence vegetation simultaneously and that in each occasion some of these factors play the leading role that may interfere the use of macrophytes as indicators for a particular factor. For example, in wind-exposed areas where hydrodynamics is the leading factor for macrophytes, there usability for assessing eutrophication is limited

(Paper V). The major factors the effect of which needs to be taken into consideration regarding boreal lakes are the water level (Toivonen & Nybom, 1989; Rørslett, 1991; Partanen & Hellsten, 2005), the exposure to waves and wind (Segal, 1971; Keddy, 1983; Weisner, 1991; Riis & Hawes, 2003), the shore slope (Duarte & Kalff, 1986) and the bottom quality (Barko & Smart, 1983). In these regards macrophytes, similarly to other species in ecosystems, can be divided into two large groups – generalists and specialists. Species in the first group occur in most samples and are thus recorded in the widest range of environmental conditions. Species in the second group, in the opposite, characterise narrow ranges of environmental conditions, which correspond to their narrow requirements (Brown, 1984; Hengeveld, 1990, 1993; Gaston, 1994; Heegaard et al., 2001).

4.2.3.3. Indicative power of macrophyte metrics

Traditional macrophyte based assessment methods for lakes focus on the presence of indicator species, which are often derived based on expert judgement (Duigan et al., 2007; Schneider, 2007). As good indicators need to have narrow distribution ranges, such methods involve the risk of creating a "rarity" index instead of a "pressure" index, and some species may be classified differently in different countries when empirical relations are analysed (Penning et al., 2008). It is also important to take into account that the occurrence of species is more likely determined by biological and stochastic factors than by simple environmental determinism (Moss, 2007; Søndergaard et al., 2010). One solution of the problem is to use general quantitative macrophyte metrics, for example, the per cent coverage or the colonisation depth, instead of species specific characteristics. These metrics are well defined and more objective but have been given less attention and are less frequently included as standards in lake monitoring programmes (Cheruvelil & Soranno, 2008). These simple quantitative macrophyte metrics respond sensitively to increasing TP and Chla and therefore can be considered as potential indicators of eutrophication (Søndergaard et al., 2010).

Different ecological groups of macrophytes have different indicative power that determines their use in assessment schemes. In short term, the indicative power of helophytes is quite poor because of their relative independence from the conditions in the aquatic environment (Penning et al., 2008) and strong dependence on the geomorphological conditions in any given reach of the shore that in places determines their high diversity. For example, the number on hydrophytes and amphibious species in Lake Võrtsjärv is 40 among the total of 114 registered species (Paper III). However, because the helophyte zone width reacts slowly but steadily to the evolution of lake conditions, it seems to be a very good long-term indicator for monitoring using, for example, remote sensing (Paper VIII). In the opposite, submerged macrophytes are good indicators of lake chemical and physical conditions in a shorter term while their composition and abundance can change from year to year and reflect the conditions of the growing season (Søndergaard et al., 2010).

4.2.3.4. Eutrophication

The main aim of using macrophytes as indicators is to assess human impact and, first of all, eutrophication in lakes ecosystems. The question is how to assess realistically the current status and occurring changes. The chemical environment of many lakes has changed due to intensified agricultural land use, urban expansion, as well as atmospheric and water pollution (Wallsten, 1981; Lougheed et al., 2001; Partanen et al., 2009). The anthropogenic landscape features may override patterns in natural landscape or local features and are important in predicting present-day macrophytes in lakes (Cheruvelil & Soranno, 2008). Changes along the eutrophication gradient strongly affect the abundance and species diversity of aquatic vegetation (Kurimo, 1970; Uotila, 1971; Churski, 1983; Pieczyn´ska et al., 1988; Naumenko et al., 2000; Egertson et al., 2004; Jupp & Spence, 1977; Lachavanne et. Al., 1992; Sand-Jensen et al., 2000; Hilt et al., 2006; Søndergaard et al., 2010). The abundance and diversity of macrophytes follows the bell-shape function and reach their maxima in mesotrophic or eutrophic range of the scale. At the lower end of the scale, the answer to the increasing nutrients concentrations is dense growth of submerged and emergent macrophytes (e.g. Birks et al., 1976; Moss, 1979), but with more extreme nutrient levels, diversity and growth decline (e.g. Moss, 1979; Phillips et al., 1978; Heegaard et al 2001). In Lake Võrtsjärv the main quantitative changes are the steady increase in the importance of *M. spicatum* in the whole lake (which repleaced the earlier dominant *P. perfoliatus*), the expansion of reeds, and the fast overgrowing of the southern part with emergent and floating-leaved plants (Papers III & V). Several studies have suggested that eutrophication is one of the main factors behind the expansion of *P.*

australis (Andersson, 2001; Mäemets & Freiberg, 2004; Hellsten et al., 2006, Engloner, 2009) which is the dominant emergent species In Lake Võrtsjärv (Papers III & V). A study of 300 Danish lakes (Søndergaard et al., 2010) showed that despite the clear response of macrophytes to eutrophication, only few species were found to be good indicators of either low or high nutrient concentrations. Therefore, the use of changes in macrophyte species abundances as indicators of variable nutrient loading is limited (Chambers & Calff, 1985; Nurminen, 2003). This was affirmed also by data from the REBECCA project (http://www.rbm-toolbox.net/rebecca/), which showed the existence of general trends among aquatic vegetation in response to eutrophication pressure, but high variation of responses of individual species over European lake types (Penning et al., 2008). Moreover, taking account of the often delayed response of macrophyte communities (Søndergaard et al., 2010), using them as indicators needs profound ecological knowledge.

One output of using macrophytes as indicators is the European Water Framework Directive (WFD), which main purpose is to achieve good ecological status of all waters by 2015. Studies connected with WFD have also focused on how submerged macrophytes can be used for assessing lake water quality (Coops et al., 2007; Penning et al., 2008). The more so submerged macrophytes are one of the four key biological quality elements to be used to describe the ecological quality of lakes (European Commission, 2000; Søndergaard et al., 2010). It is therefore often suggested that macrophytes can be used as indicators for pressures such as eutrophication.

4.2.3.5. Reference conditions

In the most simplistic sense, certain macrophyte species are present in waters of good status and absent in bad status (Moss et al., 2003; Birk et al., 2006; Penning et al., 2008). As lakes are naturally different, the hardest question is how to determine the reference conditions or the high status baseline. In Estonia most lakes in rural areas were in pristine status before the onset of industrial methods in agriculture and application of artificial fertilizers, i.e. at least until the 1930s. Thus the results of early complex investigations of lakes carried out during the first decades of the 20th century (e.g. Mühlen & Schneider, 1920 in Lake Võrtsjärv) obtain a totally new value. According to these data, biggest changes in Lake Võrtsjärv over all biotic groups from phytoplankton to waterfowl have taken place among aquatic macrophytes (Paper I). Six of the disappeared species (2 species of *Chara*, *Ranunculus trichophyllus* Chaix (s.l.), *E. canadensis*, *Potamogeton pectinatus* L., *P. pusillus* L.) belong to submerged macrophytes that colonized mainly the sheltered narrow southern end of the lake. Obviously, the increased nutrient load has favoured phytoplankton development in this area, which in its turn has suppressed shorter macrophytes growing on lake bottom. Instead of them *M. spicatum*, a taller plant able to reach the euphotic layer, has enlarged its distribution and tends to overgrow open-water areas in the southern part of the lake. Also *C. demersum*, not mentioned earlier, occurs now often in masses carpeting the bottom.

5. MAIN CONCLUSIONS BASED ON ORIGINAL PAPERS

Based on Võrtsjärv studies, the following four conclusions can be drawn regarding the formation of macrophyte distribution patterns, their long-term changes and controlling factors in a large shallow lake:

1. Environmental differences between lake parts in the large and shallow Lake Võrtsjärv are expressed in the variable number of macrophyte species, their different distribution patterns and morphological differences (Paper III).
2. Three main factors cause polarized distribution of macrophytes in Võrtsjärv: (i) the dominating westerly and south-westerly winds affecting the northern and eastern shores determine sediment composition and areas of mechanical stress for macrophytes; (ii) the irregular distribution of inflows with larger inflows entering the lake from the south and from the west causes an uneven nutrient availability in different parts of the lake; (iii) the combination of the elongated shape of lake in the north–south direction narrowing down towards south with the prevailing westerly wind directions generate a distinct contrast between the sheltered south western and exposed north eastern shores (Paper V).
3. Retrospective studies based on satellite image analysis revealed that large inflows had a strong positive effect on the expansion of macrophytes in Võrtsjärv (Paper VIII) showing that eutrophication has been obviously the strongest factor modifying the plant community of the lake. The zone of emergent macrophytes proved suitable for long-term observation and assessing community changes by remote sensing techniques. Since the beginning of the 20th century, Võrtsjärv macrophytes have a clear decreasing trend in species diversity and several dominant species have changed over time. Among all organisms groups, macrophytes are the most altered group in the lake (Paper I).Long-term temporal changes in Lake Võrtsjärv macrophyte communities characterise the shifts in the community structure from the *Charophytes-Potamogeton* spp. type to the *Myriophyllum-Potamogeton* spp. type (Paper III).

4. A study including also the largest lake in Estonia, Lake Peipsi, showed that macrophytes are important producer in shallow lake littoral zones contributing up to 84% of the daily summer primary production. Macrophyte production varied through the vegetation period, for same species in different lakes and for different species in same lake (Paper VII).

On our small lake studies, the following three conclusions can be drawn which characterize the mutual relationships between aquatic plants and their environment in lakes of alternative stable states:

1. The active role of macrophytes in transforming the lake environment increases with decreasing lake size and seasonal changes in small lakes are more affected by in-lake ecosystem processes compared to big lakes, which tend to be more externally controlled (Paper II). In a comparison of two adjacent lakes of similar trophic state, the different size and especially, the longer wind fetch in the bigger lake was the main reason for the scarcity of submerged macrophytes. This study showed the strong physical control of the distribution of macrophytes by a combination of meteorological conditions and lake morphometry (Paper IV).

2. In macrophyte-dominated hard-water lakes, sedimentation of phytoplankton with autochthonous calcite can contribute to the shift to a clear water state, which is supported by higher pH provoked by the photosynthesis of dense macrophyte stands (Paper II). The reduced sediment resuspension, the possible allelopathic influence of charophytes on phytoplankton (Paper II), and high grazing rates of ciliates on small algae (Paper IV) can also cause a decrease in phytoplankton numbers and contribute to the maintenance of the clear-water periods in macrophyte-dominated lakes.

3. Prevailing conditions in a macrophyte-dominated lake and a plankton-dominated lake had specific impact on the growth form of plants. In case of *Potamogeton lucens* two architectonic plant parameters, the total surface area of shoots and the surface area of leaves, differed significantly between the lakes of alternative stable states (Paper VI). Still the area/dry weight ratio of *P. lucens*

had a similar seasonal dynamics in both lakes. In the beginning of the growing season, the maximum surface area of plants was located in the topmost sections and shifted to lower sections in the course of plant growth.

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SUMMARY

Macrophytes play an important role in lake ecosystems, which provisionally can be divided into an active role consisting of modifying in-lake processes and creating habitat for other groups of biota, and a passive role where macrophytes themselves are subjected to forcing factors within lake environments. The active role of macrofytes as providers of food, shelter and habitat is predominant in small and shallow lakes where the littoral area colonized by plants constitutes a large part of the lake's total area. With increasing lake area and depth, the active role is gradually declining and replaced by a more passive role in large lakes in which macrophyte distribution and composition are strongly controlled by lake morphometry and meteorological factors. As small and shallow lakes form the majority in the world's lake population, research has paid more attention to studying the active role of macrophytes. The present thesis, however, has put the emphasis on the opposite aspects – the questions how the in-lake conditions affect the distribution of species, plant architecture and community composition, and how these parameters can be used in lake status assessment.

The materials for the present thesis have been collected during 14 years from 9 Estonian lakes, but the bulk of the data originates from Võrtsjärv and two smaller lakes, Prossa and Kaiavere, located in the Vooremaa drumlin area. The spectrum of macrophyte related topics analysed and discussed in the original publications is wide ranging from eco-physiological aspects and aspects of autecology to population ecology and synecology. Given the broad thematic spread of the underlying papers, the synthesis part of the thesis follows the format of a review paper in which the original papers are integraded by references. This format was selected to avoid unnecessary repetition of what was already written in the papers and to enable a more complete overview of the various aspects of the topic, including those not directly covered by the original papers.

The complex of factors in lakes can be divided into three major groups – physical, chemical and biological, which have, correspondingly, limnological, metabolic and biotic effects on macrophytes. Limnological effects on macrophytes are expressed through physical parameters of water and sediments, water movements, and conditions of light and temperature, metabolic effects are related to nutrient cycles and production of organic matter, whereas biotic effects are the result of mutual relationships within the plant community or between plants and other groups of biota. These groups of factors form a complex structure which influences on aquatic macrophytes are reviewed in the synthesis part of the thesis in both spatial and temporal scales. The sensitivity of macrophytes to environmental conditions is the basis for their indicator power enabling to use plant community metrics for assessing the ecological status and its trends in water bodies.

One of the major results of the studies was the finding out of the complex of factors determining the structure and distribution of macrophytes in Lake Võrtsjärv. Nutrient availability and the effect of prevailing winds play the leading roles in this lake, which owing to the shape of the lake create a distinctive polarization of the littoral vegetation both in a north-south and a west-east gradient. A comparison with historical data from the beginning of the 20th century showed the change in the community composition of macrophytes being the largest among all biotic groups of the lake. Eutrophication resulting from riverine nutrient loadings was proved as the major cause of these changes. A retrospective analysis of satellite images for the last 20 years showed that the changes continue as evidenced by the rapid expansion of the reed belt with an average annual rate of 2.2 m and especially pronounced around the mouths of inflowing rivers. The contribution of macrophyte production to the total primary production over the vegetation period reached 35.5% in Lake Võrtsjärv but was only 10% in the deeper Lake Peipsi.

Studies of the two lakes in Vooremaa revealed that the lake size dependent wind impact supports the shift of the balance from the macrophyte dominance to phytoplankton dominance and showed how the resulting differences in light climate change the architecture of submerged plants.

SUMMARY IN ESTONIAN

Järvedes valitsevad tingimused veetaimestiku kujundajatena

Järve ökosüsteemis on veetaimestikul väga oluline roll, mida võib tinglikult jagada aktiivseks, kus veetaimed mõjutavad järves toimuvaid protsesse ja kujundavad elutingimusi teistele järve asukatele ning passiivseks, kus veetaimed on ise mõjutatud järves toimuvatest protsessidest. Väikestes ja madalates järvedes, kus taimedega asustatud litoraal moodustab suure osa järve kogupindalast, on ülekaalus taimede aktiivne funktsioon nii toidu tootja, varje pakkuja kui elupaiga loojana, kuid enamasti see ülekaal kahaneb nii järve pindala ja sügavuse kasvades ning suurtes järvedes on taimestik enam allutatud ilmastikust ja järvenõo kujust sõltuvatele teguritele. Kuna suurem osa järvi maailmas on väikese pindalaga ning madalad, on suurem rõhuasetus veekogude taimestiku uuringutes langenud veetaimestiku aktiivse rolli selgitamisele veekogus. Käesolev töö keskendub vastupidisele aspektile – küsimustele, kuidas mõjutavad järves valitsevad tingimused taimeliikide levikut, nende morfomeetrilisi näitajaid ja taimekoosluste struktuuri ja kuidas neid näitajaid saab kasutada järves valitsevate tingimuste hindamisel.

Käesoleva töö materjal on kogutud 14 aasta jooksul kokku üheksast Eesti järvest, kuid peamine andmestik pärineb Võrtsjärvest ja kahest Vooremaa järvest, Prossast ja Kaiaverest. Töös kirjeldatud teemade ring on lai, hõlmates öko-füsioloogilisi, autökoloogilisi, dem-ökoloogilisi ja sün-ökoloogilisi aspekte. Tööde laia temaatilist ulatust arvestades on dissertatsiooni sünteesiv osa koostatud erinevaid uurimusi ühendava ülevaateartikli vormis, millesse üksikartiklite tulemused on lõimitud viidete abil. Töö selline ülesehitus vähendab artiklites esitatu asjatut kordamist ning võimaldab käsitletavast teemast anda oluliselt laiema ja terviklikuma ülevaate, kattes ka neid aspekte, mida töö aluseks olevad artiklid otseselt ei käsitle.

Järves valitsevaid tingimusi võib tinglikult jagada kolme suurte rühma – füüsikalised, keemilised ja bioloogilised, mis mõjutavad veetaimestikku limnoloogiliselt, metaboolselt ning biootiliselt. Järve limnoloogiline mõju avaldub läbi vee ja setete füüsikaliste parameetrite, vee liikumise, valgustingimuste ja temperatuuri. Metaboolne mõju on seotud toiteainete ringetega ja orgaanilise aine produktsiooniga ning biootiline mõju on seotud mitmesuguste veekogu organismirühmade ja veetaimestiku vaheliste suhete ning koosluste struktuuriga. Nimetatud tegurite rühmad moodustavad keeruka kompleksi, mille mõju avaldumist veetaimestikule on ülevaates käsitletud nii ajalises kui ruumilises skaalas. Veetaimede tundlikkusel veekogudes valitsevate tingimuste suhtes põhineb nende indikaatorväärtus, mis annab veetaimestiku uuringutele olulise rakendusliku aspekti, võimaldades taimekoosluste järgi hinnate veekogu seisundit ja selles toimuvaid muutusi.

Tehtud uuringute ühe peamise tulemustena selgitati välja Võrtsjärve taimekoosluste jaotumist ja struktuuri mõjutav tegurite kompleks, milles juhtival kohal on toiteainete kättesaadavus ja valitsevate tuulte mõju, mis Võrtsjärve spetsiifilise kuju tõttu tekitavad taimestiku omapärase polariseerumise nii põhja-lõuna kui ida-lääne suunas. Võrdlus 20. sajandi algusest pärinevate ajalooliste andmetega näitas, et Võrtsjärve veetaimestiku liigiline koosseis on kõigist elustikurühmadest kõige enam muutunud. Muutuste peamiseks põhjuseks on eutrofeerumine jõgede kaudu järve jõudvate toiteainete mõjul. Viimase 20 aasta satelliidifotodelt nähtub, et muutused jätkuvad, mille üheks ilminguks on roostike kiire laienemine keskmise kiirusega 2.2 m aastas, mis on eriti markantne jõesuudmete ümbruses. Suurtaimede produktsioon moodustas Võrtsjärves 35,5% järve suvisest koguproduktsioonist, sügavamas Peipsis, kus litoraali osakaal järve kogupindalas on väiksem, oli see näitaja 10%.

Kahe Vooremaa järve uuringud selgitasid, kuidas järve suurusega kasvav tuule mõju aitab kaasa tasakaalu nihkumisele suurtaimede valitsemiselt fütoplanktoni valitsemisele ja kuidas sel moel kujunevad erinevad valgustingimused muudavad taimede arhitektuuri.

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I

ORIGINAL PUBLICATIONS

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Deviation of Lake Võrtsjärv from its pristine status documented 90 years ago

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Most lakes in rural areas of Estonia were in pristine status before the onset of industrial methods in agriculture and application of artificial fertilizers, i.e. at least until the 1930s. For L. Võrtsjärv (270 km^2, mean depth 2.8 m) this status was recorded by the complex expedition carried out in 1911-13. The monograph on the biota and fisheries (Mühlen & Schneider, 1920) described seasonal occurrence and abundance of 498 species from cyanobacteria to mammals. Our aim was to compare the early biological data with the present status of the lake using expert opinions and a special similarity index for interpreting historical data. The biggest deviation (25%) from the pristine status was revealed for macrophytes, the composition of all planktonic groups differed from the high quality status equally by about 20%. Changes in groups belonging to higher trophic levels were smaller: 11% for waterfowl and 4% for fishes. No changes in fish parasite fauna could be proved . Some methodological problems arisen in this work are discussed in the paper.

long-term changes, similarity index, shallow lake, community structure

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The EU Water Framework Directive requires member states to distinguish ecological status of their waters compared with high quality sites. It also requires that all lakes be brought into at least 'good' state compared with high quality reference areas. As lakes are naturally different, the hardest question is how to determine the high status baseline for a certain lake(type). Most lakes in rural areas of Estonia were in pristine status before the onset of industrial methods in agriculture and application of artificial fertilizers, i.e. at least until the 1930s. One way to measure the degree of change from these times is to use paleoecological methods and reconstruct the community structure on the basis of sub-fossil assemblages. However, only few biological groups can be identified in sediment samples. In this context the results of early complex investigations of lakes carried out during the first decades of the 20th century obtain a totally new value. In 1911-1913 the Lake Commission of the Naturalists' Society at Tartu University led by Max von zur Mühlen investigated L. Võrtsjärv (270 km^2, mean depth 2.8 m), the second largest lake in Baltic countries. The results were published in two monographs: the first summarising geological and hydrological investigations (Mühlen, 1918) and the second biological investigations (Mühlen & Schneider, 1920). The latter described seasonal occurrence and abundance of 498 species from cyanobacteria to mammals. Our aim was to compare the early biological data with the present status of the lake. Preliminary results of this comparison as well as methodological problems arisen in this work are discussed below.

The nowadays database used for the comparison was collected during last 35 years but as possible, the latest data were considered. Expert opinion was used as the basic method. Each expert familiar with some certain biological group was asked to assess the degree of coincidence of the status described by Mühlen & Schneider with present status. Experts had to decide

1) whether the species mentioned in the early list still exist in the lake or not. In general, species and groups not investigated later (some groups of insects less related with water) were excluded from the further analysis. However, in some cases in addition to the decisions 'exists'=1 and 'does not exist'=0, the probability assessments 'probably exists'=0.8 and 'practically vanished'=0.2 were applied. The former was used for species that are generally common (e.g. seen as adults), but the potential aquatic habitats of which have not been specially studied. In contrast the second decision 'practically vanished' was used for species belonging to well investigated groups if they had not been found for a long time and the probability of their occurrence in less studied habitats was considered low.
2) whether there have emerged species which at their present abundance, if it would have been unchanged, could not have been missed by earlier investigators. In other words, new invaders and species that have become considerably more abundant.

A special similarity index K_N (Nõges & Feldmann, 1999) was used to compare the historical list of species with nowadays data:

$$K_N = \textit{number of common species in two lists / number of species in the shorter list}$$

This similarity index can obtain values from 0 to 1 similarly to the well-known indexes of Jaccard (K_J) and S✱rensen (K_S), but is especially suitable for comparing historical data as it does not require equal elaboration level of both list compared. Groups which have not been investigated later, e.g. Collembola, were omitted as well as those hundreds of species which are known now, but were not mentioned by Mühlen & Schneider. As only exception the new dominants – very abundant species at present but not even mentioned by Myhlen & Schneider – were included in the analysis. Altogether 371 species about which new information was available, formed the final list used for analysing the occurrence. Species originally arranged by their taxonomy by Mühlen & Schneider were divided into ecological groups (Table 1).

The biggest changes have taken place among aquatic macrophytes. We could state the present certain occurrence of only 33 species of the 44 included in the analysis (similarity index 75%). Six of the disappeared species (2 species of Chara, *Ranunculus trichophyllus* Chaix, *Elodea canadensis* Michx., *Potamogeton pectinatus*

L., *P. pusillus* L.) belong to submerged macrophytes that colonized mainly the sheltered narrow southern end of the lake. Earlier *E. canadensis* has developed in masses (Table 2) preventing seine catching of fishes in long shore regions. It is mentioned by Mühlen (1918) that the water transparency in the lake ranged generally from ¾ to 1 m, but the water was 'rather clear' in the southern part. Now this difference has almost disappeared. Macrophytes and phytoplankton compete for light but the switches between the plant-dominated and phytoplankton-dominated states are affected by nutrient thresholds (Scheffer, 1998). Obviously, the increased nutrient load has favoured phytoplankton development in this area, which in its turn has suppressed shorter macrophytes growing on lake bottom. Instead of them *Myriophyllum spicatum* L. a taller plant able to reach the euphotic layer has enlarged its distribution and tends to overgrow open-water areas in the southern part of the lake. Also *Ceratophyllum demersum* L., not mentioned earlier, occurs now often in masses carpeting the bottom.

Table 1. Similarity between species composition registered in L. Võrtsjärv in 1911-13 by Mühlen & Schneider (1920) and at present

Ecological group	Number of analysed species	Present occurrence	Similarity index K_N %
Macrophytes	44	33.2	75
Phytoplankton	40	31.8	80
Neustonic animals	3	2.4	80
Metazooplankton	47	38.2	81
Benthic animals	133	108.6	82
Protozooplankton	11	9	82
Waterfowl	32	28.6	89
Terrestrial animals	3	2.8	93
Fishes	27	26	96
Semiaquatic animals	10	9.8	98
Parasites	21	21	100
Total	371	312.4	84

The composition of all planktonic groups deviated equally by about 20% from the pristine status. Several changes have taken place among the dominants (Table 2). Probably two species *Planktolyngbya limnetica* (Lemm.) Kom.-Legn. and *Limnothrix planctonica* (Wolosz.) Meffert were described as narrow straight blue-green filaments by Mühlen & Schneider under the name of *Lyngbya limnetica* Lemm. In the 1960s *Limnothrix redekei* (van Goor) Meffert appeared in plankton and became a subdominant since the 1970s. Earlier dominants *Bothryococcus braunii* Kütz. and *Anabaena hassallii* var. *macrospora* (Wittr.) Lemm. have not been met during last decades. *A. lemmermanni* P. Richt., which bloom was described in the lake in June 1912 has become quite rare. The third subdominant among cyanobacteria named by Mühlen & Schneider (1920) was *Aphanizomenon flos-aquae* Allm. (probably *A. skujae* Kom.-Legn. & Cronb. a species described later). The domination of three N-fixing species refers to low N/P ratio in the lake. The years 1911-13 belonged to the period of low water level. Latest investigations (Nõges & Nõges, 1999) have demonstrated the relationship between the water level and N/P ratio: at lower water level more phosphorus is washed out from the sediment while denitrification is intensified resulting in a decrease of the N/P ratio.

Obviously, as a result of eutrophication, earlier dominating rotifer species *Conochilus unicornis* Rouss. and *Kellicottia longispina* Kellicot preferring lower trophic state have disappeared. Also *Asplanchna herricki* Guerne mentioned by Mühlen & Schneider (1920) has been found for the last time in the 1960s. Instead of them an indicator of eutrophic waters *Anuraeopsis fissa* (Gosse) has emerged and often become a dominant in summer zooplankton.

Table 2. Changes in dominating species in L. Võrtsjärv during 90 years

Ecological group	Dominants in 1911-13, which later have disappeared	Present dominants not mentioned in 1911-13
Aquatic macrophytes	*Elodea canadensis* Michx.	*Ceratophyllum demersum* L.
Phytoplankton	*Bothryococcus braunii Kütz.* *Anabaena hassallii* var. *macrospora* (Wittr.) Lemm.	*Limnothrix redekei* (van Goor) Meffert
Metazooplankton	*Conochilus unicornis* Rouss. *Kellicottia longispina* Kellicot	*Anuraeopsis fissa* Gosse

Compared to 1911, the abundance of the phytophilous isopod *Asellus aquaticus* has increased. Meanwhile several new species have spread/introduced to the lake. The zebra mussel *Dreissena polymorpha* (Pallas) was introduced around 1950 probably with fishing-gare, its initial outburst has receded by now. The giant oligochaete *Tubifex newaensis* (Mich.) introduced in 1965 has become abundant in places.

All the fish species mentioned by Mühlen & Schneider still occur in the lake. Some new species found like *Phoxinus phoxinus* L., *Leucaspius delineatus* (Heckel) and *Cobitis taenia* L. are rare and could easily be missed in earlier studies. Only *Osmerus eperlanus* L. introduced probably with fishing-gare in the 1850s from L. Peipsi, was temporarily so rare that it was not cought during the 1911-13 field-works. No changes in fish parasite fauna could be proved .

Several problems arose in the course of interpreting the historical data. The first one we met was due to changes in taxonomy. 145 species of the 498 mentioned by Mühlen & Schneider (1920) had been renamed. It is rather easy to find synonymic names (still 6 names we have not found yet), but much more trouble is caused by taxa not identified to species level and with taxa, which have been splitted into several species later. Usually an expert can guess what species has been seen, especially if its seasonal occurrence or habitat have been described.

It does not need any competence to compare formally two lists of and to mark the common and specific species. A totally different task is to find out real changes in community structure. The main problem is connected with the extremely different weight of positive and negative decisions regarding the occurrence of species. Only one scientifically sound record would prove the existence of the Loch Ness monster, but tens of expeditions can not finally prove the opposite. Only a good specialist can decide with a high probability about the absence of a particular species if it has not been met in its typical habitat for a reasonably long period.

Another problem in handling historical data is related with sampling methods. For example, most of the insects described by Mühlen & Schneider (1920) were cought as adults. Later only the benthic larval fauna has been studied. The historical plankton samples were taken with a plankton net of unknown mesh size. That explains the relatively high abundance of larger forms like *Ceratium hirundinella* O.F.M. in phytoplankton while some small-sized species could be totally missed.

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THE ROLE OF CHAROPHYTES IN KEEPING
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The role of charophytes in increasing water transparency: a case study of two shallow lakes in Estonia

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Key words: Chara, clear water, shallow lake, zooplankton grazing, calcite precipitation

Abstract

The hydrochemical regime and the biota in two lakes of Vooremaa landscape protection area, Central Estonia, were studied in 2000–2001 within the frames of the EC project ECOFRAME aimed to work out water quality criteria for shallow lakes in Europe. Lake Prossa is a macrophyte-dominated lake with an area of 33 ha and a mean depth of 2.2 m. Most of the bottom in this lake is covered by a thick mat of charophytes all the year round. Lake Kaiavere located at a distance of 10 km from the former is a much larger (250 ha, mean depth 2.8 m) plankton-dominated lake. Despite the different area and the *Chara* meadows in Lake Prossa, the nutrient dynamics were very similar in both lakes. The first vernal phytoplankton peak was expressed in reduced Secchi depth in both lakes. After that peak, the water became clear in L. Prossa but remained turbid in Lake Kaiavere. In the *Chara*-lake the mean individual weight of zooplankton reached its maximum in both years in June. In the year 2000 it coincided with the peak of the zooplankton/phytoplankton ratio and with the minimum of soluble reactive phosphorus both contributing to the initiation of the clear-water period. Towards autumn, the individual mean weight of zooplankton decreased in the *Chara*-lake and remained smaller than in the plankton-dominated lake. Hence, zooplankton grazing could initiate the clear-water phase in the *Chara*-lake but other factors were needed for its maintenance. Another parameter that showed a clear difference between these two lakes was the carbonate alkalinity. It was rather stable or even increasing during spring in the plankton-dominated lake, while it decreased by nearly 50% between April and July in the *Chara*-lake. The calculated saturation level of calcite remained still lower in the *Chara*-lake showing that the co-precipitation of algae with autochthonous calcite could not explain the observed increase in water transparency above *Chara* meadows. The reduced sediment resuspension and the possible allelopathic influence of charophytes on phytoplankton remain the main explanations for the maitenance of the extensive clear-water period in the *Chara*-lake.

Introduction

The role of macrophytes, especially charophytes, in keeping lake water clear is widely recognized. Dense mats of charophytes strongly reduce water movement at the lake bottom preventing resuspension of the sediments (Scheffer, 1998). Besides the simple mechanical effect of macrophytes on the amount of suspended solids, the turbidity is reduced also by a weaker development of phytoplankton in macrophyte-rich lakes. As pointed out in recent reviews by Jeppesen et al. (1998), Scheffer (1998), Van den Berg (1999), Meijer (2000), and Van Donk & Van de Bund (2002) and Søndergaard et al. (2003), the observed negative relationship between macrophytes and phytoplankton may include several mechanisms. For example, competition for nutrients and light, stimulated denitrification inside macrophyte beds (Ruggiero et al., 2003), increased grazing by zooplankton and plant-associated invertebrates hiding themselves from predators in dense macrophyte stands, higher sinking losses of phytoplankton both by mechanically supressed water turbulence (Pluntke & Kozerski, 2003) and increased calcite incrustation of algae at higher pH, and, finally, the allelopathic influence of macrophytes on phytoplankton (Gross et al., 2003). Due to a similar outcome of these complex interactions, it is often hard to decide which of those mechanisms play the leading role in a particular case. Depending on the trophic state, species composition, climatic and seasonal conditions, some of the mechanisms may have no effect or the effect may be even opposite. For example, in Veluwemeer no significant differences of dissolved phosphorus or nitrogen could be found in- and outside *Chara*-beds (Van den Berg et al., 1998). Rooted macrophytes may even increase phosphorus release from the sediment (Søndergaard, 1988; Moss et al., 1996). In five shallow mesotrophic to eutrophic lakes in Sweden and Latvia, dense vegetation stands and clear water coincided with a low abundance of crustacean plankton during summer (Blindow et al., 2000). The authors showed that also the plant-associated zooplankton had no major influence on the maintenance of water clarity outside the vegetation.

In the present paper we analyse the differences found in the dynamics of nutrients, pH, carbonates, suspended solids, phyto- and zooplankton between two eutrophic shallow lakes in Estonia. One of these lakes had a dense *Chara*-bed and became clear in summer while the other was phytoplankton-dominated during the whole ice-free period.

Description of the study site

The studied lakes Prossa and Kaiavere are two of the eleven drumlin lakes in the Vooremaa landscape protection area, Central Estonia. The relief in this area was formed by moving continental ice-sheet during the last glaciation and is dominated by elongated moraine drumlins. The drumlins orientated from SE to NW are 2–5 km long, 0.5–0.8 km wide and have a relative height of 20–40 (60) m. Most of the drumlin area is cultivated. The calcareous eutrophic shallow lakes are located in the valleys between drumlins and have the same elongated shape as the moraine drumlins. The two lakes studied were in alternative stable states because of the differences in wind fetch and, perhaps also differences in nutrient loading (Kisand & Nõges, 2003). The bottom of the 33-ha Lake Prossa (further referred to as the *Chara*-lake) was densely covered with charophytes, *Chara tomentosa* up to a depth of three metres and *Nitellopsis obtusa* in deeper parts. After a vernal phytoplankton peak, the water in this lake remained clear during summer. Lake Kaiavere, the plankton-dominated lake used as a reference, had a comparable depth but was larger (Table 1). It remained turbid during summer. The coverage by submerged plants in Lake Kaiavere was much smaller and consisted mainly of sparsely distributed *Potamogeton* spp.

Materials and methods

The lakes were sampled monthly from April to October 2000 and weekly from April until the middle of June 2001. Thereafter the lakes were sampled again monthly until September 2001. For hydrochemical and plankton analyses depth- and area-integrated samples were taken from the central part of the lakes. The sampling was carried out with a Ruttner sampler at 1-m depth intervals from surface to the lake sediment. Samples were taken randomly from five stations in the lake and pooled. For pelagic zooplankton 10 l of this pooled water was filtered through a 48 μm mesh and preserved with Lugol's solution. The plant- and sediment-associated chydoride assemblages (PA, SA) were studied once, in August 2000, in both lakes. Therefore two-metre sweep samples in five replicates were taken from the vegetation-free zone (depth 0.5–1 m) and from the macrophytes zone (depth 1 m) using a 100-μm mesh net (with a 5-mm mesh pre-screen). These samples were also fixed with Lugol's solution. Due to large variability, all replicate samples were counted thoroughly. The biovolume of phytoplankton was measured using Utermöhl (1958) technique. Zooplankton was counted in Bogorov's chambers.

Hydrochemical analyses were performed using standard methods (Grasshoff et al., 1982). The saturation level (*S*) of calcite was calculated from its solubility:

$$S_{CaCO3} = \frac{[Ca^{2+}] * [CO_3^{2-}]}{SP}, \qquad (1)$$

where in brackets are the molar concentrations of Ca^{2+} and $CO_3{}^{2-}$ ions, SP is the solubility product of $CaCO_3$ ($10^{-8.39}$ at 20 °C).

We calculated the concentration of Ca^{2+} from a regression between Ca^{2+} and $HCO_3{}^-$ ions for Estonian calcareous lakes (Simm, 1975) and the concentration of carbonate ions from the dissociation reaction of

Table 1. General morphological and hydrological *Chara*cteristics of the lakes studied

*Chara*cteristic	L. Prossa (*Chara*-lake)	L. Kaiavere (plankton-dominated lake)
Length, km	1.6	3.6
Maximum width, km	0.3	0.9
Area, km^2	0.33	2.51
Mean (max.) depth, m	2.2 (4.2)	2.8 (5.0)
Water retention time, y	0.56	0.33
PVI of submerged plants,%	40	6

hydrocarbonates:

$$[CO_3^{2-}] = \frac{K_2 * [HCO_3^-]}{[H^+]} \qquad (2)$$

where K_2 is the dissociation coefficient ($10^{-10.38}$), [H$^+$] is the molar concentration of hydrogen ions (10^{-pH}).

The share of the calcite crust and periphyton in the dry weight of plants was measured in two series of samples in five replicates consisting of equal amounts (100 g) of fresh plant material. The first series of samples was dried at 105 °C and the total dry weight was measured while in the second series the calcite was dissolved in 1 M HCl before drying. The loose particulate material was filtered on Whatman GF-C filters and weighed after drying at 105 °C.

Results

Plankton abundance

After a similar spring peak of phytoplankton in both lakes, the plankton biomass decreased and the water became clear in the *Chara*-lake (Fig. 1A) but the turbidity increased in the other one together with the plankton biomass and the amount of suspended solids (Fig. 1B). In both lakes the spring peak of phytoplankton was caused by a mixed community consisting of diatoms, chlorophytes, chrysophytes, cryptophytes and dinophytes (not shown in figures). In the plankton-dominated lake diatoms (*Aulacoseira granulata* var. *angustissima, Asterionella formosa*) dominated in May (2001) or May and June (2000) followed by continuously increasing share of cyanobacteria (*Microcystis pulverea, Aphanizomenon skujae, Anabaena* sp.) towards the end of the growing season. The total phytoplankton biomass reached its maximum in autumn. In the *Chara*-lake the phytoplankton biomass declined, while the species composition in summer was dominated by motile forms of crypto-, chryso- and dinophytes.

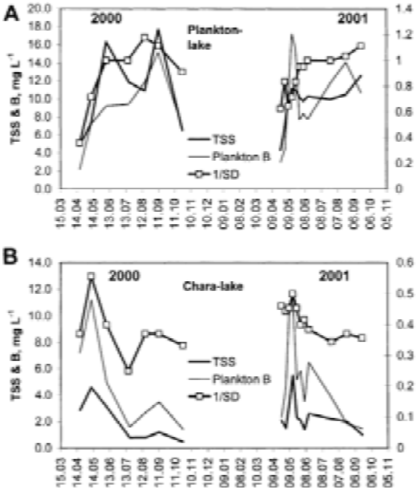

Figure 1. Seasonal dynamics of total suspended solids, total phyto- and zooplankton biomass and the reciprocal of the Secchi depth in the plankton-dominated lake (A) and in the *Chara*-lake (B).

The biomass of the pelagic zooplankton in the *Chara*-lake (Fig. 2E) was almost always smaller than in the plankton-dominated lake. Also the abundance of macrophyte-associated (MA) and sediment-associated hydorids (SA) studied in August 2000 were higher in the plankton-dominated lake (MA, correspondingly, 384 vs. 224 ind. and SA 271 vs. 25 ind. per 2-m sweep sample). In the *Chara*-lake MA was dominated by *Pleuroxus truncatus* and SA by *Acroperus harpae*

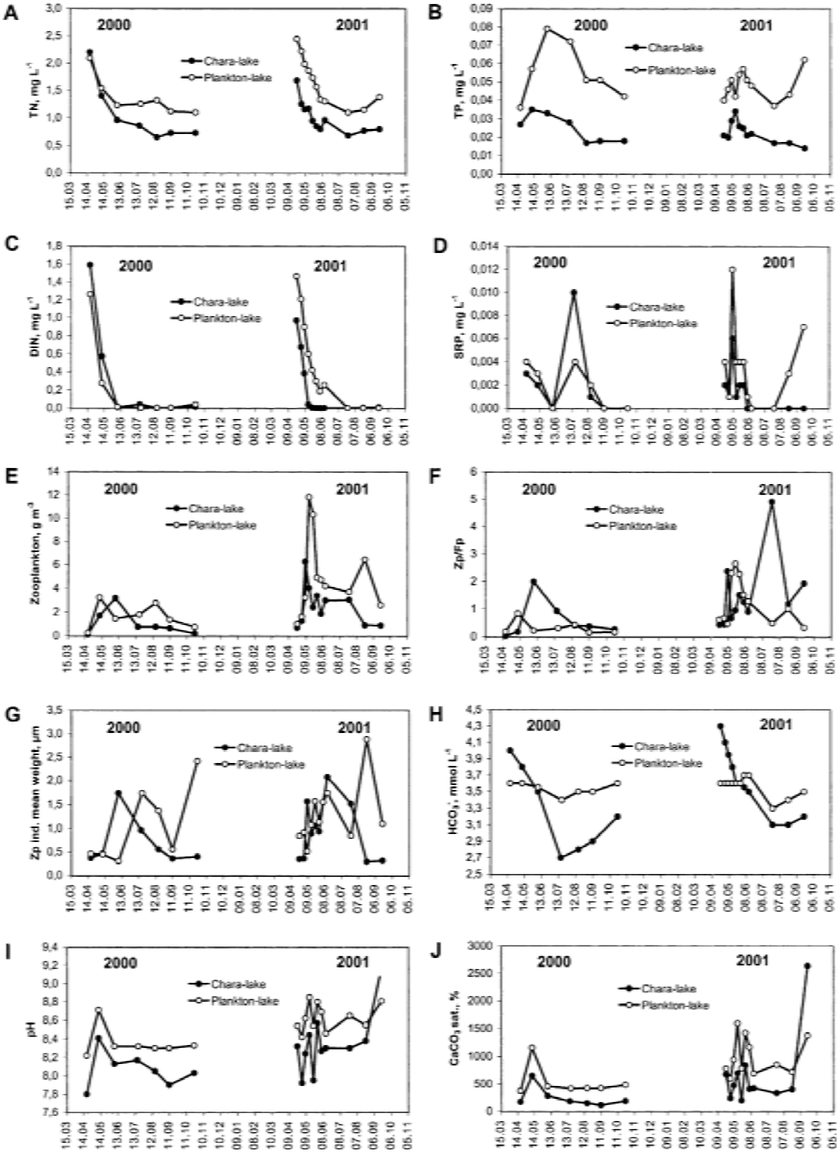

Figure 2. Seasonal dynamics of some chemical and biological parameters in the lakes studied. A – total nitrogen, B – total phosphorus, C – dissolved inorganic nitrogen, D – soluble reactive phosphorus, E – zooplankton biomass, F – zooplankton/phytoplankton biomass ratio, G – the mean individual weight of zooplankton, H – hydrocarbonate concentration, I – pH, J – calcite saturation level.

while *Chydorus sphaericus* was most numerous in both habitats in the plankton-dominated lake.

In both years, the zoo- to phytoplankton ratio (Zp/Fp) reached higher values in the *Chara*-lake compared to the plankton-dominated lake (Fig. 2F). The individual mean weight of zooplankton peaked in the *Chara*-lake in June (caused by *Bosmina longirostris*) but in the plankton-dominated lake in autumn (Fig. 2G).

Nutrients

Regarding the concentrations of total nutrients, the *Chara*-lake proved to be less eutrophic (Fig. 2A,B). In April 2000, the nutrient concentrations were almost equal in both lakes but the differences increased during summer. The dynamics of inorganic nutrients were rather similar in both lakes, however, the peak of soluble reactive phosphorus (SRP) in the *Chara*-lake in July 2000 was nearly twice as high as the peak in the plankton-dominated lake (Fig. 2C,D).

The carbonate system

After the disappearance of the ice cover, the concentration of HCO_3^- decreased rapidly in the *Chara*-lake while the changes were much smaller in the plankton-dominated lake (Fig. 2H). The pH showed similar dynamics in both lakes but it was nearly always higher in the plankton-dominated lake (Fig. 2I). The calculated calcite concentration mostly showed a less than fivefold supersaturation in the *Chara*-lake and a more than fivefold supersaturation in the plankton-dominated lake (Fig. 2J). The saturation dynamics followed the changes in the pH. As measured in autumn 2001, the calcite crust formed 39% and periphyton 21% of the total dry weight of the *Chara* plants.

Discussion

Increased resuspension due to the scarcity of submerged macrophytes and the longer wind fetch in the larger plankton-dominated lake resulted in generally higher concentrations of total nutrients and suspended solids in this lake. However, only the inorganic nutrients let us judge upon the possible nutrient limitation. In July and August 2000, SRP occurred in both lakes in measurable amounts that excludes P-limitation to phytoplankton at least in this particular summer. The peak of soluble reactive phosphorus in the *Chara*-lake was even higher than in the plankton-dominated lake which could probably be attributed to a release from redox-sensitive fractions in anoxic conditions often formed on the sediment surface beneath dense *Chara* beds (Pokorny et al., 1984; Moss et al., 1986; Kisand & Nõges, 2003). The inorganic nitrogen concentration dropped below the detection level in both lakes in summer. Low inorganic nitrogen levels alone commonly do not limit phytoplankton growth in freshwater systems but lead to a community dominated by N_2-fixing cyanobacteria. This clearly happened in the plankton-dominated lake where the role of *Aphanizomenon skujae* and*Anabaena* spp. continuously increased from May to September. The question remains, why could not cyanobacteria develop in the *Chara*-lake. In 2001 SRP decreased in both lakes below the detection level by the first half of June. Since the end of July it appeared again in measurable amounts in the plankton-dominated lake but remained low in the *Chara*-lake. In this hot and long summer, the competition for phosphorus between *Chara* and phytoplankton can not be excluded from the reasons for the clear-water period.

The increased grazing pressure on phytoplankton by pelagic zooplankton hiding in macrophytes during daytime (Timms & Moss, 1984; Søndergaard & Moss, 1998) as well as the grazing by macrophyte-associated zooplankton species (Irvine et al., 1989; Lauridsen et al., 1996) has often been considered to be one of the most important factors controlling phytoplankton biomass in macrophyte-dominated lakes. In both years the individual mean size of zooplankton in the *Chara*-lake reached its maximum in June during the domination of *Bosmina longirostris*, which as an efficient grazer could initiate the clear-water period in this lake. In June 2000 at the time of the minimum SRP concentration, zooplankton biomass was twice as high as that of the phytoplankton and indeed could control phytoplankton development. In 2001 the Zp/Fp ratio was generally higher in both lakes reaching even the value of five in the *Chara*-lake in July. Towards autumn the Zp/Fp ratio as well as the Zp individual mean weight declined and remained on the same level or even lower than in the plankton-dominated lake. Hence, zooplankton grazing was probably important in initiating the clear-water phase but could not be the main factor controlling phytoplankton biomass during the whole vegetation period.

The dominance of flagellated algae in summer phytoplankton in the *Chara*-lake was consistent with the findings by Balls et al. (1989) and Van den Berg et al. (1998) and could be attributed to larger sinking losses of non-motile algae in conditions of reduced turbulence. However, it can not fully explain the biomass decline.

Koschel et al. (1983, 1990) have demonstrated that the aggregation of algae and seston particles with autochthonous calcite crystals in hard-water lakes may increase their sedimentation. Calcite formation is provoked by an increased pH due to the photosynthetic uptake of CO_2 and HCO_3^- by phytoplankton and macrophytes. Calcite has a low solubility but it can form a stable solution, which tolerates a 10 – 15-fold supersaturation before crystal formation begins (Starast & Simm, 1973). The continuous decline of the HCO_3^- concentration from April to July in the *Chara*-lake was probably caused by uptake by charophytes, however, it seemed that the pH was much more affected by the short-time phytoplankton development in spring. Both the pH and the calcite saturation level were almost always lower in the *Chara*-lake. Hence, the pH and calcite concentration could not enhance the sedimentation of phytoplankton. The small influence of charophytes on the pH of the water column can probably be explained by the localization of the buffering reactions on the adaxial surfaces of the plants (Wetzel, 1960). Thus, the calcite covering the plants is formed immediately within a thin water layer surrounding the plants and not settled from longer distances where it could influence the sedimentation of algae.

We found that the increase in water transparency in the *Chara*-dominated lake in summer was a complex phenomenon. It could be initiated by the grazing pressure of cladocerans in June at the time when SRP was depleted and when the Zp/Fp ratio reached its maximum. Later in summer when the SRP availability improved and the grazing pressure by zooplankton decreased, other factors should have overtaken the control over phytoplankton. Perhaps it could be partly attributed to larger sinking losses of non-motile algae in conditions of reduced turbulence and partly to the possible allelopathic influence of charophytes on phytoplankton that we did not investigate in our study.

Acknowledgements

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III

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Macrophytes

Tõnu Feldmann and Helle Mäemets

HISTORICAL BACKGROUND

Already in the 19th century data about the macrophyte vegetation of Lake Võrtsjärv supported the formulation of Klinge's law on the faster overgrowing of the wind protected lakeshores (Klinge, 1890). In 1911–1912 comprehensive investigation of the lake included also description of the macroflora (Mühlen & Schneider, 1920). In the 1930s the eastern shore was studied by Pastak (1936) and the western shore by Eichwald (1939). In the 1950s botanical data were collected by H. Tuvikene (unpublished) and were supplemented by researchers of the benthos (Ristkok & Ruse, 1962). A thorough overview of the macrophyte vegetation completed by A. Mäemets in 1965–1967 was published in the first monograph on Lake Võrtsjärv (1973), but her later data about the fast changing southern part, collected in 1985–1986, remained in the manuscript form. A thesis on the factors determining the distribution of macrophytes in Lake Võrtsjärv was compiled by Feldmann (2000) on the basis of quantitative analysis of the sampling quadrats on 45 transects in 1997. The floristic data were summarized by H. Mäemets (2002). The results of all these investigations were included in the second Estonian-language monograph on Lake Võrtsjärv (Feldmann & Mäemets, 2003).

MATERIAL AND METHODS

Floristic data were collected on boat and shore expeditions. The most thorough recent quantitative data were collected in August 1997 using a combined transect and sampling quadrate method (1 × 1 or 2 ×2 m depending on the vegetation type). To use geobotanical methods, the growth area of macrophytes was divided into nine subareas including a more or less equal number of sampling quadrates – seven shore areas, one open water area (between the islands of Ainsaar and Tondisaar) and an area surrounding Tondisaar Island (Fig. 1). In community analysis the following indicators and indices were used: **frequency of species (*F*)** ($F = N_i \times 100/N$, where N_i is the number of areas in which species i was found; N is the total number of areas); relative **abundance** **(A)** ($A(\%) = n_i \times 100/n$, where n_i is the total number of shoots for a particular species in all quadrates of one area and n is the total number of shoots for all species in all quadrates of one area) and the **index of Shannon–Weaver (H_S)** (1949) ($H_S = -\Sigma(N_i \times \ln N_i)$, where N_i is the relative abundance of species i). For the ecological factors, the following indices were used: **wind index (W)** (original index, $W = \Sigma(S_i \times T_i)/n$, where S_i is the frequency (%) of the wind from direction i; T_i is the fetch of the wind (km) from direction i and n is the number of wind directions); **sediment index (G)** (original index, $G = \Sigma$(the number of a sediment fraction × coverage (%) in the growth area of macrophytes/100). The calculations were based on a map of bottom deposits (Raukas & Mäemets, 1995) and the result for a corresponding area was the weighted average of the number of a sediment fraction. To calculate the **nutrient load index (L_N, L_P)**, the nutrient loads from the rivers in t y^{-1}, discharging into each shore area, were summed up. The estimation of the **influence of rivers** was based on two indicators: the number of shoots per square metre and the length of shoots. The data of the macrophyte species growing in a river mouth (found at least in two areas) were compared with the corresponding data of the species growing between the river mouths. The rivers were grouped as follows (Fig. 1): the northern coast – the Tänassilma River; the southern coast – the Väike Emajõgi and the Rõngu rivers; the western coast – the Õhne and the Tarvastu rivers; the eastern coast – the Konguta River. In the statistical analysis of the data correlation, regression and factor analyses were used.

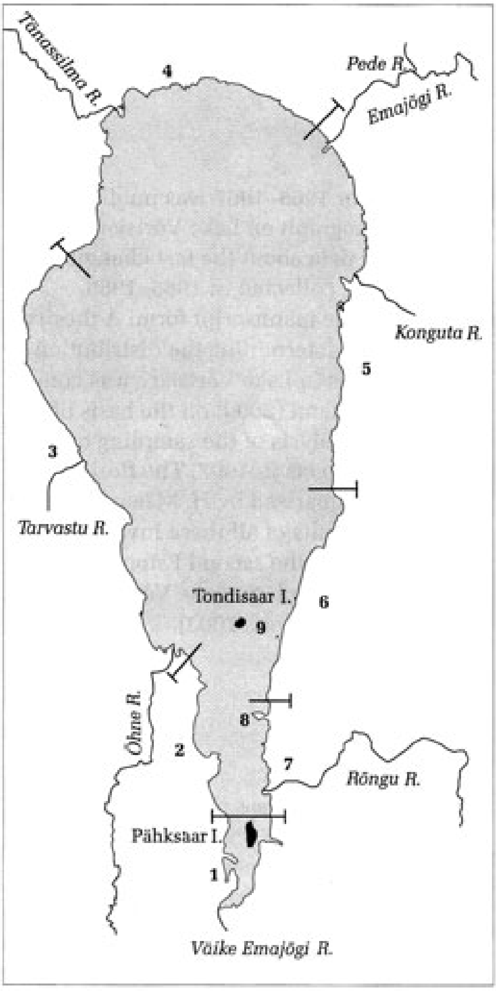


Figure 1. Location of the investigated macrophyte subareas of Lake Võrtsjärv.

FACTORS DETERMINING THE DISTRIBUTION OF MACROPHYTES

Macrophytes as resident and relatively long-living organisms store information about the environment, which is reflected in the presence or absence of certain species, but also in their life form, length of shoots and colonization depth. On the association level the differences in environmental stress are expressed primarily in the spatial changes of species diversity. Combinations of factors for a lake or for different lake parts are revealed in the patterns of macrophyte distribution. In shallow lakes the littoral zone constitutes a large part of the lake's area. The gradient of the factors usually forms a clear zonation in the macrophyte distribution of this area. The distribution factors were comprehensively summed up by Spence (1982): velocity of water flow, composition of bottom sediments, hydrostatic pressure (unimportant in shallow lakes) and light and nutrient conditions. Domination of species depends on the environmental factors as well as on the historical development of the vegetation (Sculthorpe, 1967; Åkland, 1974). As most studies on the macrophytes of Lake Võrtsjärv have been descriptive, the reasons for such a distribution have rarely been a subject of discussion.

Table 1. Frequency (*F*), average abundance (*A*), depth range, average number of shoots per square metre and shoot length of common macrophyte species in Lake Võrtsjärv

Species or ecological group	*F* (%)	*A* (%)	Colonization interval (m)	Number of shoots (m^{-2})	Shoot length (m)
Helophytes					
Sium latifolium L.	11.11	0.04	–	1	
Oenanthe aquatica (L.) Poir.	11.11	0.04	0–0.8	1	
Rorippa amphibia (L.) Besser	33.33	0.85	0–0.8	3.7	
Rumex maritimus L.	22.22	0.27	–	1	
Butomus umbellatus L.	22.22	34.51	0–0.8	104.5	
Schoenoplectus lacustris (L.) Palla	55.56	28.75	0–1.7	74.8	2.4
Eleocharis palustris (L) Roem. et Schult.	11.11	1.85	0–0.6	43	
Phalaris arundinacea L.	11.11	2.15	0.5–0.7	5	
Agrostis stolonifera L.	11.11	3.10	0–0.6	72	
Phragmites australis (Cav.) Trin. ex Steud.	88.89	43.46	0–1.9	33	2.9
Sparganium microcarpum (Neum.) Ĕelak.	11.11	9.52	–	110.5	
S. emersum Rehm.	11.11	9.35	–	108.5	
Typha angustifolia L.	33.33	6.03	0–1.3	12.4	2.9
Floating-leaved plants					
Nymphaea alba L.	22.22	3.61	0.6–1.7	13.4	
Nuphar lutea (L.) Sm.	44.44	21.14	0.5–1.8	25.8	
Polygonum amphibium L.	11.11	2.41	0–0.6	8	
Alisma plantago-aquatica L.	11.11	4.39	0–0.8	51	
Sagittaria sagittifolia L.	11.11	0.09	–	2	
Potamogeton natans L.	11.11	0.42	–	1.9	
P. gramineus L.	11.11	13.15	0.1–1.2	19.2	
Submerged plants					
Ranunculus circinatus Sibth.	11.11	0.04	–	1	
Ceratophyllum demersum L.	11.11	7.24	–	168	
Myriophyllum verticillatum L.	11.11	0.22	–	5	
M. spicatum L.	100	16.34	1.5–3	4.8	
Potamogeton pectinatus L.	11.11	2.74	–	12	
P. compressus L.	11.11	0.43	–	0.3	
P. lucens L.	22.22	1.39	0.6–2.8	1.4	
P. perfoliatus L.	44.44	4.88	0.4–2.2	7.5	

Polygonum amphibium. Photo by N. Laanetu.

FREQUENCY AND ABUNDANCE OF SPECIES

In 1997, 32 of the 114 known species (Mäemets, 2002) were found, 28 of them falling in the sampling quadrates (Table 1). The most frequent species was spiked water milfoil (*Myriophyllum spicatum*) (Fig. 2) and the most abundant species was common reed (*Phragmites australis*) (Fig. 3). The high abundance of flowering rush (*Butomus umbellatus*), simple bur reed (*Sparganium emersum*) and branched bur reed (*S. microcarpum*) and their low or medium frequency are related to the growth

Table 2. Shannon-Weaver index (H_s), number of species (*NS*), width of the helophyte zone (*B*), slope of the helophyte zone (*D*), area without helophytes (*E*), wind index (*W*), sediment index (*G*) and index of nutrient loading (L_N, L_P)

Area No.	H_s	*NS*	*B* (m)	*D* (m)	*E* (%)	*W*	*G*	L_N (t y^{-1})	L_P (t y^{-1})
1	2.4	21	93	160	42	43.4	9	1654	35.2
2	0.6	6	100	162	38	35.1	5	1654	35.2
3	1.6	8	148	152	3	59.2	6.7	564	6.7
4	1.4	5	249	322	23	81.1	3.9	538	15.8
5	1.3	6	171	316	46	80.9	5.1	175	4.9
6	1.0	3	125	171	27	61.4	5.7	–	–
7	1.4	7	200	250	20	29.3	4.5	1654	35.2
8	–	1	–	–	–	57.4	9	1654	35.2
9	0.7	2	74	350	79	75.7	4.5	–	–
Average	1.1	6.6	162	233	31	58.2	5.9	877.0	18.7

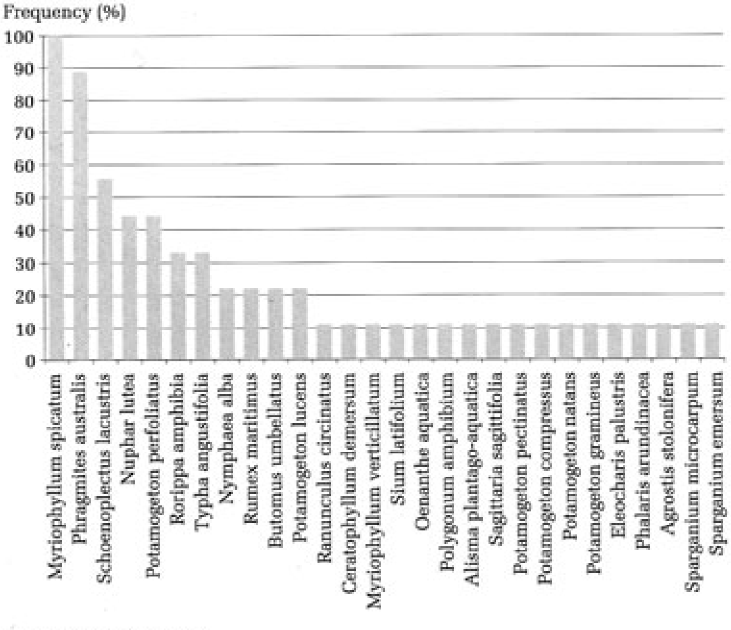


Figure 2. Frequency of the macrophyte species in Lake Võrtsjärv.

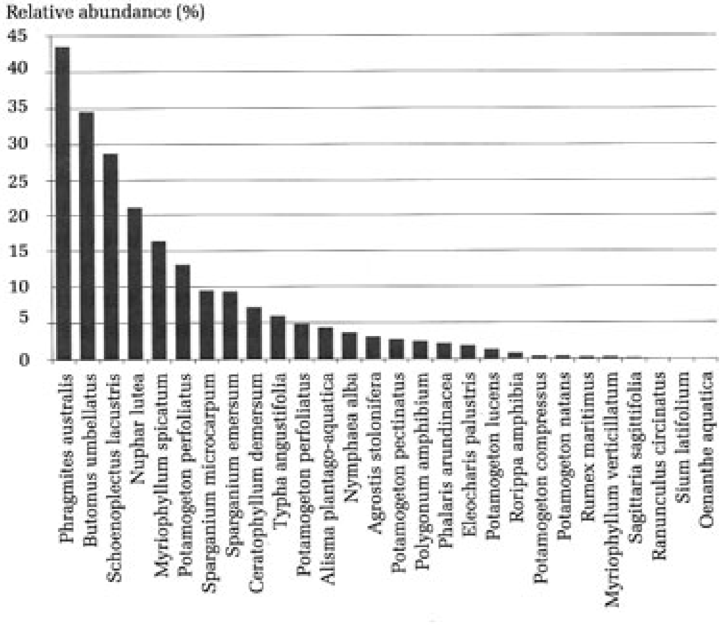


Figure 3. Average relative abundance of the macrophyte species in Lake Võrtsjärv.

form: thick monodominant clumps are present mostly in the southern part of the lake. The highest density among the macrophytes was reached by lake hornwort (*Ceratophyllum demersum* L.), which covered large bottom areas. As the water level in August 1997 was about 40 cm below long-term average, the boundary of most helophytes coincided with the water's edge. The average length of the shoots of reed and narrow-leaved cattail (*Typha angustifolia*) was similar, while the shoots of bulrush (*Schoenoplectus lacustris*) were about half a metre shorter.

Phragmites australis. Photo by M. Pedaste.

INDICES CHARACTERIZING DIFFERENT DISTRIBUTION AREAS OF MACROPHYTES

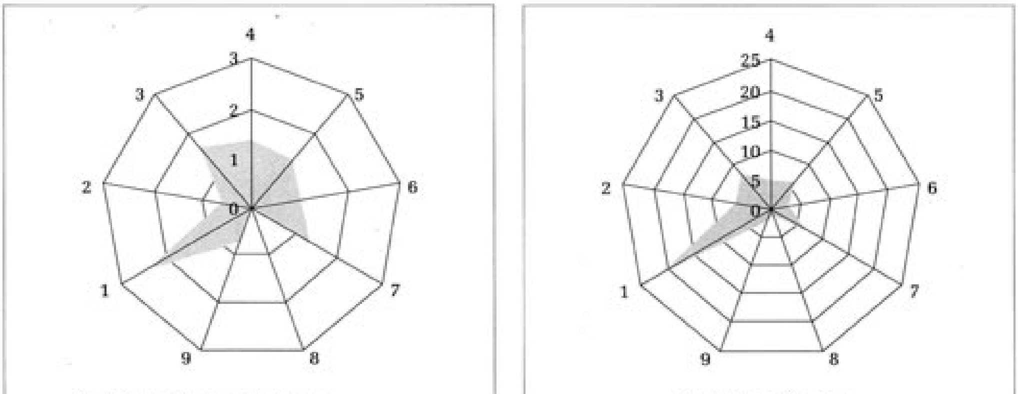
For a better characterization of the biological and ecological characteristics, we present, beside the table, also a figure (Table 2, Fig. 4, A–H) corresponding to the approximate geographic location of the areas. Among the indices of nutrient loading only the phosphorus loading index is shown graphically as it is similar to that of nitrogen index.

Typha angustifolia. Photo by H. Timm.

The index of species diversity varied from 0 (open water area, 8, where only spiked water milfoil was found) to 2.4 (southernmost area in Fig. 1) (Fig. 4A). In the helophyte zone in the western, northern, eastern and southeastern parts (corresponding areas 3, 4, 5 and 7 in Fig. 1) of the lake, the reed thicket was wider than in some other places (Fig. 4C). Comparison of the slope (distance from the water's edge to the 1 m isobath, Fig. 4D) and width of the helophyte belt enables to calculate the area devoid of helophytes (Fig. 4E). The distribution of plants is most inhibited in the southwestern and northeastern parts of the lake and near Tondisaar Island (corresponding areas 1, 2,

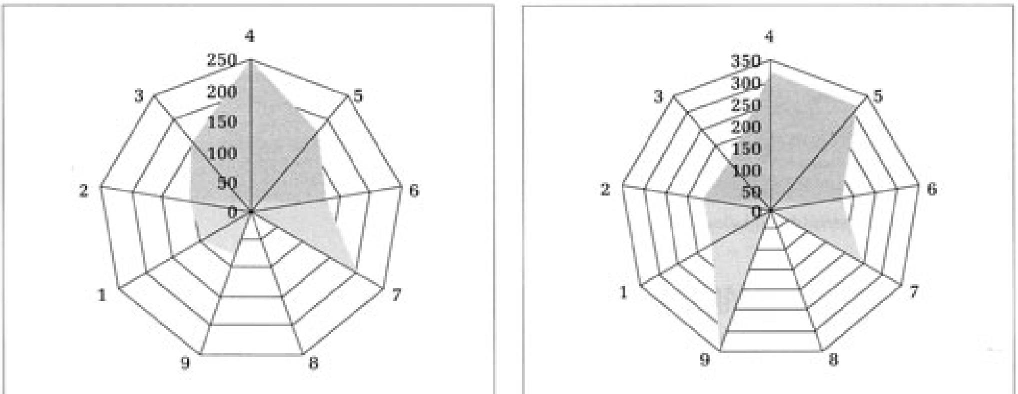
Schoenoplectus lacustris (detail below) and *Nyphar lutea*. *Photo by M. Pedaste.*

5, 6 and 9). The index of nutrient loading is the highest for the southern part of the lake (Fig. 4F). As the prevailing directions of the wind in Lake Võrtsjärv are southern, southwestern and western, the winds affect mostly the shores in the north and east (Fig. 4G). The most widespread sediment types (constituting more than 40% of all sediment types in the area) were sapropel, silt, sand and sandy silt, silty sand, gravelly sand and till (Fig. 4H, Table 2). According to the bathymetry of the lake and the range of colonization depth, macrophytes could occupy 94.5% (25 503 ha) of the lake's area. In fact, they colonize only 18.8% (5070 ha). Submerged plants covered the largest area (3520 ha), followed by helophytes (1230 ha) and floating-leaved plants (320 ha) (Fig. 5). Floating-leaved plants are the most stressed species; they grow mainly in the southern and western sheltered lake parts.



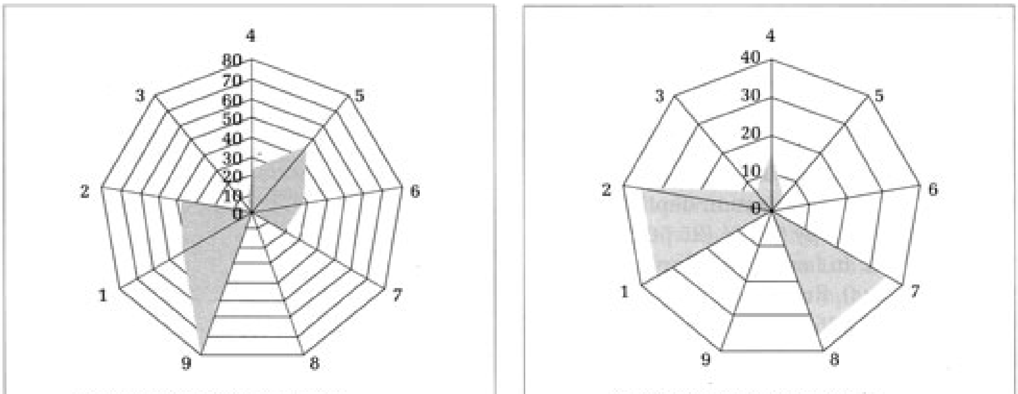
A. Index of Shannon-Weaver

B. Number of species



C. Width of the helophyte zone (m)

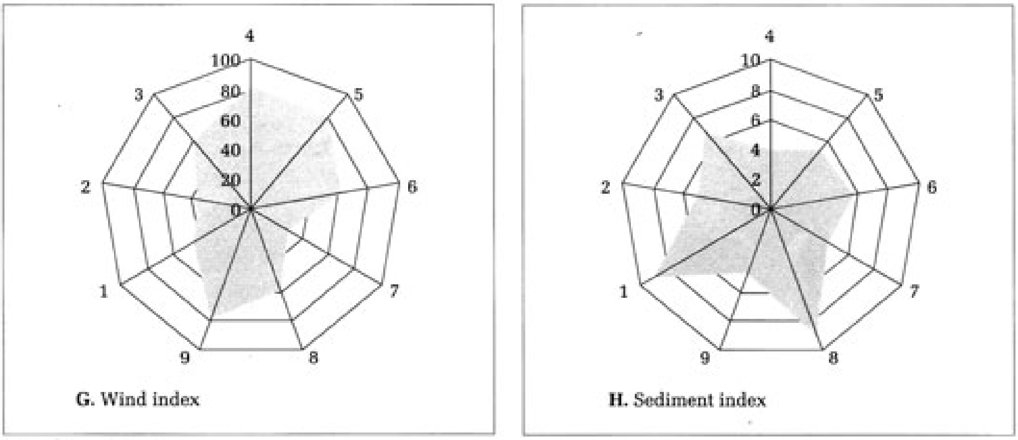
D. Slope of the helophyte zone (m)



E. Area without helophytes (%)

F. Phosphorus load index (t y^{-1})

Figure 4. Biological and ecological characteristics and indices of the macrophyte subareas in Lake Võrtsjärv.



G. Wind index

H. Sediment index

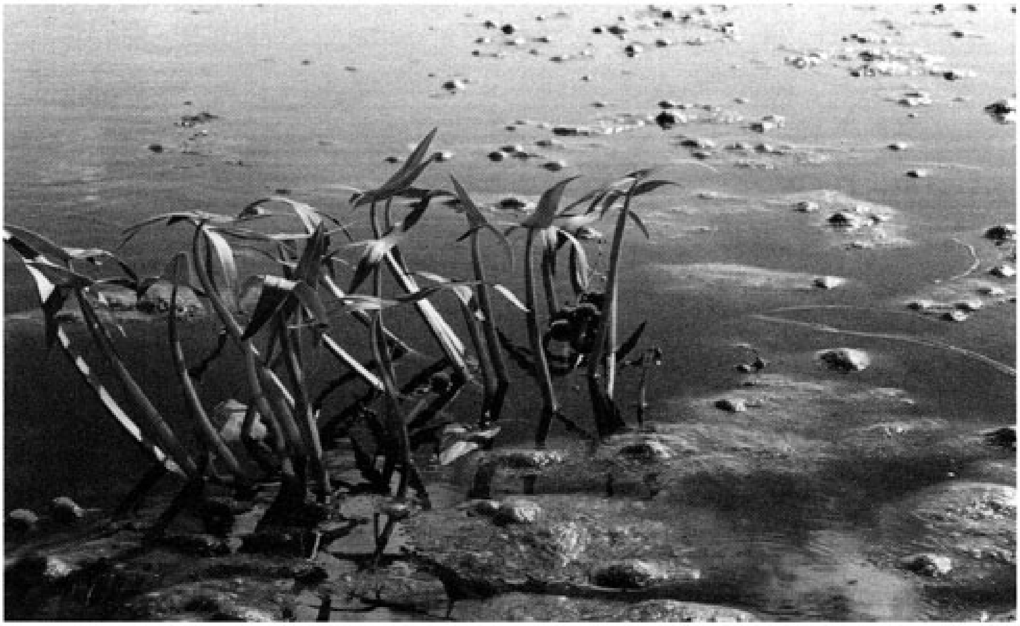
Figure 4 *continued.*

EFFECT OF INFLOWS

The determination of the effect of the inflows was based on the assumption that nutrient dynamics (N and P) depends mostly on the river's loading (Nõges et al., 1998). The calculations are based on the balance compiled for 1988–1991 (Järvet & Nõges, 1994). The six major inflows selected for evaluation – Väike Emajõgi, Õhne, Tarvastu, Tänassilma, Rõngu and Konguta – accounted for 80% of the catchment area and also 80% of the total

Table 3. The average number (shoots m^{-2}) and length (m) of shoots near and between the inflows. The numerator denotes the value for the area near the inflows and the denominator denotes the value for the area between the inflows in Lake Võrtsjärv. The third number shows statistical significance; the values $p<0.05$ are in bold

Species	Number of shoots					Length of shoots				
	Whole lake	N	S	E	W	Whole lake	N	S	E	W
Nuphar lutea	$\frac{27.6}{17.8}$ 0.193		$\frac{27.8}{16}$ 0.188		$\frac{34.7}{20.6}$ 0.159					
Myriophyllum spicatum	$\frac{3.6}{5.9}$ 0.141		$\frac{3.8}{2.8}$ 0.535	$\frac{3.4}{6.3}$ 0.407	$\frac{5.3}{6.8}$ 0.751					
Potamogeton perfoliatus	$\frac{6.3}{8.5}$ 0.568									
Schoenoplectus lacustris	$\frac{72.2}{88}$ 0.649		$\frac{65.8}{88}$ 0.529			$\frac{2.2}{2.3}$ 0.598		$\frac{2.3}{2.3}$ 0.913	$\frac{2.2}{2.3}$ 0.054	$\frac{2.2}{2.3}$ 0.800
Phragmites australis	$\frac{35.3}{31}$ 0.388	$\frac{46.6}{30.7}$ 0.110	$\frac{25.5}{25.8}$ 0.971	$\frac{52.5}{30.2}$ **0.028**	$\frac{34}{30.7}$ 0.607	$\frac{3}{2.9}$ 0.075	$\frac{3}{2.7}$ **0.019**	$\frac{3}{2.8}$ **0.031**	$\frac{2.7}{2.9}$ 0.196	$\frac{3.3}{3}$ **0.001**
Typha angustifolia	$\frac{11.7}{14.3}$ 0.227		$\frac{11.7}{14}$ 0.348		$\frac{7}{14.3}$ **0.018**	$\frac{2.7}{2.9}$ **0.054**		$\frac{2.7}{2.9}$ 0.163		$\frac{3.3}{3}$ **0.008**

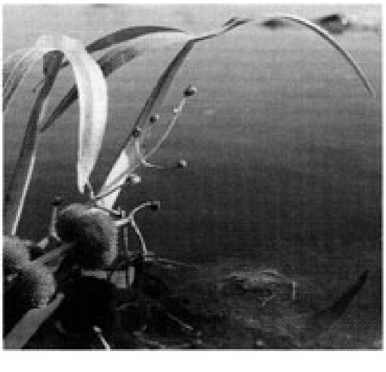


Sagittaria sagittifolia (detail below). *Photo by N. Laanetu.*

phosphorus and nitrogen loading (Järvet & Nõges, 1994). The average shoot number for yellow water lily (*Nuphar lutea* (L.) Sm.) and common reed was higher near the inflows, while the stands of the other species were denser in the areas between the inflows (Table 3). The shoots of common reed were longer near the inflows; the shoots of narrow-leaved cattail and bulrush were longer in the areas between the inflows.

SIGNIFICANT FACTORS

The statistical processing of the data showed that the relative abundance of reed depends on the index of nitrogen loading and the shoot number of spiked water milfoil depends on wind index. The corresponding models are the following:



Relative abundance of reed = –0.000374 N loading index + 0.763 ($R^2 = 0.88$; $p = 0.0006$),

Shoot number of spiked water milfoil = 0.120 wind index –1.79 ($R^2 = 0.71$; $p = 0.005$).

Nitrogen loading reduces the relative abundance of reed in the western and southern parts of the lake where nutrient loading is high, and increases it in the northern and eastern parts where the loading is low. High

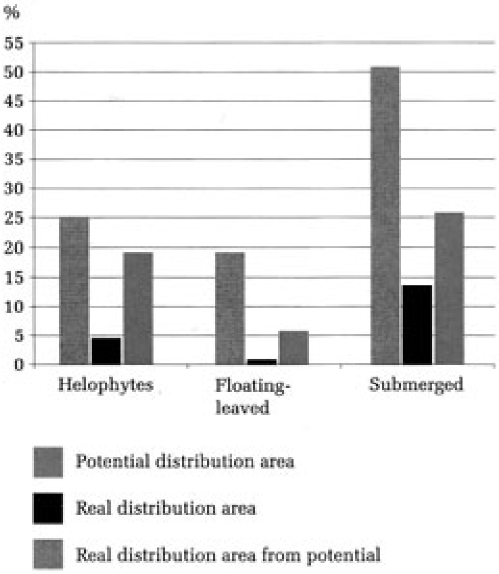


Figure 5. Potential and actual distribution areas of macrophyte vegetation in Lake Võrtsjärv, August 1997.

Table 4. Average values of factor 1 for the eastern (areas 5 and 6) and western (area 3) parts of Lake Võrtsjärv

Characteristic	Eastern shore	Western shore
Sediment index	5.4	6.7
Wind index	71	59
L_N	88	564
L_P	2.5	6.7

Table 5. Average values of factor 2 for the northern (area 4) and southern (areas 1, 2 and 7) parts of Lake Võrtsjärv

Characteristic	Southern shore	Northern shore
Number of species	12	5
Index of Shannon-Weaver	1.5	1.4
Abundance of *Phragmites australis*	26	42
Abundance of *Myriophyllum spicatum*	2.0	7.1

amounts of nitrogen cause also the loss of less tolerant species. In the northern and northwestern lake parts, the lower amount of nutrients, the larger width of the lake basin and frequent southwestern winds create unfavourable conditions for macrophytes; only a few species, mostly spiked water milfoil, are able to grow there. The number of shoots per square metre for this species is positively correlated with the wind index.

Factorial analysis classified the biological and ecological indicators under two factors and described 64% of the changeability inherent in the data. Factor 1 was considered the factor describing the changes occurring in the west–east direction in the lake (Table 4). The eastern shore is open to the prevailing winds and is subjected to strong erosion. As a result, finer sediments are carried away and sedimentation takes place in sheltered places including the western shore. The nutrient loading is also different on the eastern and western shores. Two small inflows, the Rõngu and Konguta rivers, discharge into the lake in the east, while two large inflows, the Õhne and Tarvastu rivers, contribute to the high loading in the west.

Factor 2 describes the changes occurring in the north–south direction (Table 5). That is why latitude is included in the significant variables in this analysis. The number of species decreases from south to north and only a few species tolerate the low nutrient loading and the strong effect of the wind. The decrease in the number of species reduces species diversity and results in an increase in the relative abundance of the most tolerant species, spiked water milfoil and reed, in the northern part of the lake.

Potamogeton natans. Photo by M. Pedaste.

Potamogeton lucens. Photo by H. Timm.

DIVISION OF THE LAKE ON THE BASIS OF GROWTH CONDITIONS

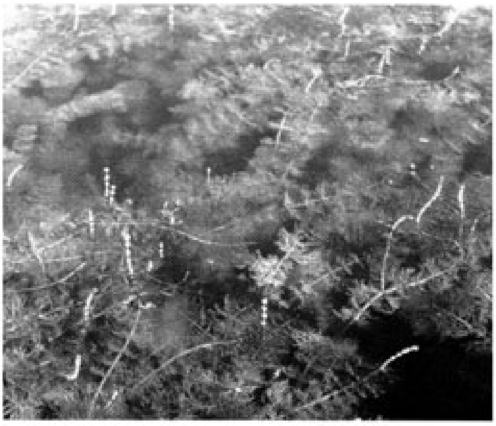
There are three main reasons for the strongly polarized conditions in Lake Võrtsjärv.

1. Main directions of the wind. The length of the fetch that influences macrophytes is >500–800 m (Rea et al., 1998). In the northern and eastern parts of Lake Võrtsjärv the fetch is in places more than ten times as long. This area is more often affected by the waves and the erosion of sediments. The western shore, on the contrary, is more sheltered and dominated by sedimentation processes. As a result, there occur grain-size differences in the sediments: the texture is coarse on the eastern shore and fine on the western shore. In the sheltered parts accumulation and decomposition of organic matter take place at production sites, while in places open to the wind the produced organic matter is transported away. In this way sediments of different composition are formed, which in turn is the reason for the differences in species composition (Schmieder, 1995). Thus in Lake Võrtsjärv the main directions of the wind exert both a direct influence (mechanical effect) and an indirect influence (composition of sediments) on the distribution of macrophytes. This process is clearly evident in the sheltered southern part of the lake where only the fairway is free of macrophytes.

2. Irregular distribution of the inflows. The large inflows (the Väike Emajõgi, Rõngu, Õhne, Tarvastu and Tänassilma rivers) enter the lake in the south and the east causing accumulation of nutrients in these areas.

3. Shape of the lake basin. Lake Võrtsjärv has an elongated shape in the north–south direction, narrowing towards the south. The lake can be divided into two different parts – the relatively small and sheltered southern part and the large northern part (with a conventional boundary near Tondisaar Island) where the effect of the winds increases with the broadening of the lake. Organic-rich sediments have accumulated in the most wind-protected part of the lake. Rare storms with the northern winds may relocate large amounts of sediments and bury young shoots of macrophytes (Nõges et al., 1999). Owing to the abundance of organic-rich sediments, the helophyte belts are narrow in the southern areas 1 and 2 (Fig. 4C). The influence of the dominating winds and the differences in sediment composition divide the northern lake part in turn into the eastern and western parts. Thus Lake Võrtsjärv can be divided into three parts on the basis of the distribution and growth conditions of macrophytes. Differences in species frequency are reflected in the hyperbolic shape of the frequency

Potamogeton perfoliatus. Photo by H. Timm.



Myriophyllum spicatum. Photo by H. Timm.

curve (Fig. 2). At one end are species with a large distribution range and at the other end are species with a small distribution range, typical of only one area.

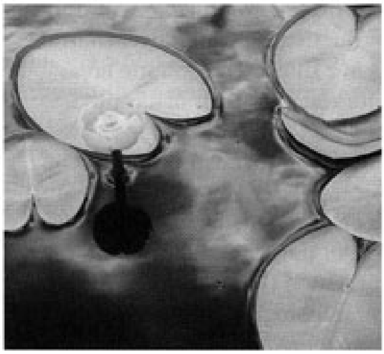
Besides the above factors, water transparency and fluctuations in water level have a general effect on the distribution of aquatic macrophytes. The floristic list contains many amphibious species specific of lakes with gentle slopes. The large distribution area of spiked water milfoil can probably be explained, apart from eutrophication, also by its tolerance of fluctuating water level (Barrat-Segretain et al., 1999). The aphotic area, unsuitable for the growth of macrophytes, ranges from 30% to 90% of the lake's area depending on water level and transparency. The basic optically active components are phytoplankton and detritus, whose amount is the highest in the second half of the year, before ice formation (Nõges, 2000). The existence of several biological and ecological factors has prevented and/or slowed down the distribution of macrophytes in Lake Võrtsjärv. The balanced distribution patterns and the consequent diversity of macrophytes are based on the stability of conditions here. Tondisaar Island can be regarded as some kind of a boundary point south of which the growth conditions are more favourable.

Sparganium microcarpum. Photo by H. Timm.

FLORISTIC COMPOSITION

The list of macrophyte taxa for the whole investigation period contains altogether 114 species and is presented in Table 6. The number of hydrophytes and amphibious

Nuphar lutea. Photos by M. Pedaste and A. Ader.



plant species is 40. The floristic composition is characteristic of eutrophic lakes, especially that of the southern and western parts. In shallow areas of the northern and eastern parts this type of flora is supplemented by amphibious species in places where the process of overgrowing with taller emergent plants is suppressed for the reasons explained above. *Potamogeton gramineus* is dominating, *Ranunculus reptans* is quite common, while the occurrence of *Eleocharis acicularis* has declined in recent decades. *Polygonum amphibium* is more frequent in the southern part of the lake. The other characteristic species in shallow sandy areas are *Potamogeton perfoliatus, P. pectinatus, Juncus articulatus, J. nodulosus, Eleocharis uniglumis, E. palustris, Agrostis stolonifera* and *Carex* spp. Alkaliphilous *Potamogeton filiformis* (Samuelsson, 1934; Preston & Croft, 1997) grows on the stony shallows of the northern part. It is quite rare in Estonian lakes.

Myriophyllum spicatum, dominating in the whole lake, has replaced the earlier dominants *Potamogeton perfoliatus* in the northern part and *P. lucens* in the southern part. Its dominance is more pronounced in the southern part, where sparse stands of *M. spicatum* grow over the whole lake (Fig. 6). According to the descriptions by von zur Mühlen & Schneider (1920) as well as by Mäemets (1973), these areas were occupied earlier by beds of *Elodea canadensis* and charophytes *(Nitellopsis obtusa, Chara contraria)*. In the southern and western parts *Phragmites australis* is accompanied with *Schoenoplectus lacustris, Typha angustifolia* and *Sagittaria sagittifolia* as well as with characteristic species of larger eutrophic lakes – *Butomus umbellatus, Sium latifolium, Oenanthe aquatica, Rorippa amphibia*, etc. In sheltered habitats opulent stands of *Nuphar lutea* and *Nymphaea alba* occur.

Nymphaea alba. Photos by M. Pedaste and A. Ader.

CHANGES IN THE COURSE OF EUTROPHICATION

Comparison of the data from the early 20th century with those from the 1960s does not reveal essential differences in the composition of the macrophyte vegetation. The most significant changes took place later and especially in the southern part of the lake (Table 6). At the beginning of the 20th century masses of *Elodea canadensis* hindered fishing there (von zur Mühlen & Schneider, 1920). At present *Elodea* is quite rare and has been replaced by masses of *Myriophyllum spicatum*, partly also by *Ceratophyllum demersum*. Charophytes disappeared between the 1960s and the 1980s, probably owing to the increased phosphorus loading (Sviridenko, 2000). Also *Stratiotes aloides* has markedly declined. Presumably, the sediments in its former growth areas in the southern and southwestern lake parts have become anaerobic and poorer in iron at the expense of the reduction of sulphates into toxic sulphides. Unfavourable factors are also the mobilization of phosphorus and high content of ammonium ions (Smolders et al., 1996). Beginning from the 1980s *Myriophyllum verticillatum* has occurred quite often in the southern part. The main quantitative changes are the steady increase in the importance of *Myriophyllum spicatum* in the whole lake, the expansion of reeds and the fast overgrowing of the southern part with emergent and floating-leaved plants (Fig. 6). The expansion of reeds is supported also by low water periods. The domination of *Phragmites* and *Myriophyllum* is levelling out the differences between the lake parts.

The change in the lake type, based on the dominating species, is similar to the

Table 6. List of the macrophyte taxa of Lake Võrtsjärv and the occurrence of species in different periods (according to Mühlen & Schneider, 1920; Mäemets, 1973 and the authors) (x – rare; xx – occasional; xxx – frequent; xxxx – very frequent; o – frequency unknown; N, S etc., – points of compass; p – part; Rl – rivulet; I – Island; B – bay)

Taxa	1912	1965–1966	1995–2001	Comments
SUBMERGED PLANTS				
Chara spp.	xx	xx	x	Earlier frequent in S p
Chara contraria A. Br.		xxx		Earlier everywhere, especially in S p
Nitellopsis obtusa (Desv. in Lois.) Gr.		xx		In 1960s abundant in S p
Drepanocladus aduncus (Hedw.) Moenkem.		x		At Vaibla Rl
Fontinalis antipyretica DC.				1986 at Pähksaar I
Ranunculus trichophyllus Chaix (s.l.)	o		x	2001 in Jõesuu
R. circinatus Sibth.		xx	x	Mainly in S p
Ceratophyllum demersum L.		x	xx	In S p, at present abundant
Myriophyllum spp.	xx			
M. verticillatum L.			xx	Mainly in S p
M. spicatum L.		xx	xxxx	Dominating in the whole lake
Callitriche hermaphroditica Jusl.		x		At Pähksaar I
Hottonia palustris L.		x	x	In S p & at Rl-s, rarely
Utricularia vulgaris L.		x	xx	Scattered
Elodea canadensis Michx.	xx	xxx	x	Earlier in masses in S p, now scattered
Stratiotes aloides L.		xx	x	In S p, at present rarely
Potamogeton compressus L.	o	x	x	In S p
P. alpinus Balb.				In 1930s in S p
P. crispus L.		x		More frequent in 1930s, in S and W p
P. filiformis Pers.		x	x	On stony shallows of N and NE p
P. friesii Rupr.		x		Scattered
P. gramineus L.	xxx	xxx	xxx	Frequent at N and E shore
P. perfoliatus L.	xxx	xxxx	xxx	Earlier dominant, now frequently
P. pectinatus L.	o	xxx	xx	In N, E and W p, decreased
P. lucens L.	xx	xxx	xxx	Abundant in S, SE and W p, earlier codominant
P. obtusifolius Mert. et Koch		x	x	Rare
P. praelongus Wulf.		x		Rare
P. pusillus L.	o			
P. × nitens Weber				In 1980s in S p
Zannichellia palustris L.				In 1930s at E shore
FLOATING AND FLOATING-LEAVED PLANTS				
Hydrocharis morsus-ranae L.	o	x	xx	Mainly in S p
Lemna trisulca L.	o	x	xx	In canals and sheltered creeks
L. minor L.	o	x	x	Rare
Spirodela polyrrhiza (L.) Schleid.		x	xx	In canals and sheltered creeks

Taxa	1912	1965–1966	1995–2001	Comments
Nuphar lutea (L.) Sm.	xxx	xxx	xxxx	Dominant, masses in S end
Nymphaea alba L.	xx	xx	xxx	In S and W p frequent
N. candida C. Presl				In 1950s
Polygonum amphibium L.	xx	xx	xx	Frequent in S p
Potamogeton natans L.	xx	xx	xx	Frequent in W p, earlier more frequent in S p
Sparganium emersum Rehm.		xx	x	In S p and at inflows
EMERGENT PLANTS				
Equisetum × litorale Kühlew. ex Rupr.			x	At Vaibla 2001
E. fluviatile L. em. Ehrh.		xx	xx	In S and SE p
E. sylvaticum L.			x	In places in supralittoral
Thelypteris palustris Schott		x		In S p
Caltha palustris L.		x	xx	Scattered
Ranunculus reptans L.	o	xxx	xx	At N and E shore
R. sceleratus L.			x	Scattered
R. lingua L.	xx	x		Scattered
Potentilla palustris (L.) Scop.	o	x		Scattered
P. anserina L.		xx	xx	In supralittoral of N and E shore
Lathyrus palustris L.			x	At Pähksaar
Lythrum salicaria L.		xx	xxx	In places frequent
Sium latifolium L.	xx	xx	xx	Frequent in S p, scattered elsewhere
Oenanthe aquatica (L.) Poir.	o	xx	xx	Frequent in S p, scattered elsewhere
Cicuta virosa L.	o	x	xx	Mainly in S p
Galium palustre L.		xx	xx	
Menyanthes trifoliata L.	o	xx		Mainly in S p
Myosotis scorpioides L.	o	x	xx	
Symphytum officinale L.			xx	In places, abundant at Pähklisaar I
Solanum dulcamara L.			xx	In places, in shore side of reeds
Scutellaria galericulata L.			xx	Scattered
Lycopus europaeus L.		xx	xx	
Mentha aquatica L.		x	xx	In places
Stachys palustris L.			xxx	In places frequent
Hippuris vulgaris L.		x	xx	Scattered
Rorippa amphibia (L.) Bess.	o	xx	xxx	Frequent in S p, elsewhere in sheltered places
Achillea salicifolia Bess.			xx	More frequent on E shore
A. ptarmica L.			xx	Scattered
Bidens tripartitus L.			xx	In places
B. cernua L.			x	Rare
Cirsium arvense (L.) Scop.			xx	In places
Tussilago farfara L.			xx	Abundant in low-water periods
Senecio paludosus L.			xx	Scattered
Rumex hydrolapathum Huds.		x		In S p

Taxa	1912	1965–1966	1995–2001	Comments
R. maritimus L.			xx	On E shore, in places
Lysimachia vulgaris L.			xxx	
L. nummularia L.		x	xx	Scattered
L. thyrsiflora L.		x	x	In S p, scattered
Alisma plantago-aquatica L.	xx	x	xxx	Scattered, in masses in Maapera B
Sagittaria sagittifolia L.	xx	xxx	xxx	Masses in S end, frequent at inflows and W p
Iris pseudacorus L.	xx	x	xx	Scattered
Butomus umbellatus L.	xx	xxx	xxx	Frequent at inflows and in S and W p
Juncus ranarius Song. et Perr.			x	
J. compressus Jacq.				
J. articulatus L.	xxx	xxx	xx	
J. nodulosus Wahlenb.		xx	xx	
Eleocharis acicularis Roem. et Schult.	xx	xxx	xx	Mainly at NE shore
E. palustris (L.) Brown em. Roem. et Schult.	xx	xx	xxx	N and E shore
E. uniglumis (Link.) Schult.	xxx	xxx	xx	N and E shore
Eriophorum angustifolium Honck	xx			90 years ago abundant on N and NE shore
Schoenoplectus lacustris (L.) Palla	xxx	xxx	xxx	Abundant in S p, elsewhere scattered
Scirpus sylvaticus L.			xx	In places
Carex nigra (L.) Reichard			o	
C. hirta L.			x	
C. elata Bell.	o			In 1930s frequent on NE shore
C. viridula Michx.			xx	
C. vesicaria L.			o	
C. acuta L.			xxx	In supralittoral
C. acutiformis Ehrh.			xx	In places
Agrostis stolonifera L.	xxx	xxx	xxx	In shallow water & flooded zone, frequent in N and E p
Calamagrostis stricta (Timm) Koeler			xx	Wet meadows
C. canescens (Weber) Roth			xx	S p, in places
Glyceria fluitans (L.) R. Brown		x		
G. maxima (Hartm.) Holmb.		x	xx	In places
Phalaris arundinacea L.		xx	xxx	Mainly at inflows
Phragmites australis (Cav.) Trin ex Steud.	xxx	xxxx	xxxx	Dominant, remarkably increased
Scolochloa festucacea (Willd.) Link.		x	xx	Scattered
Acorus calamus L.		x	xx	Scattered
Sparganium microcarpum (Neuman) Eelak		xx	xxx	Frequent at inflows and in S p
Typha angustifolia L.		xxx	xxx	In S and SE p, increased
T. latifolia L.		x	xx	Scattered

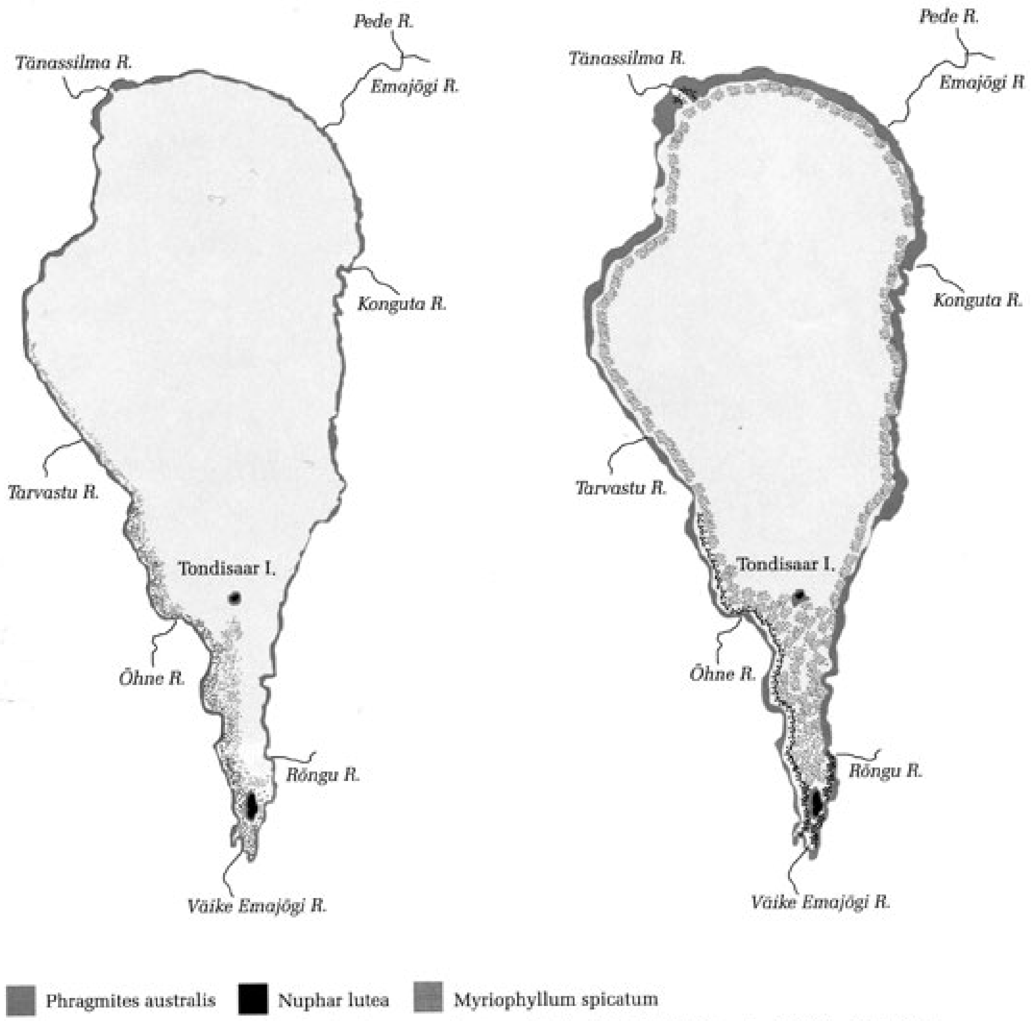


Figure 6. Distribution areas of the dominating macrophyte species in 1965–1966 (Mäemets, 1973) and in 1997 (Feldmann, 2000).

transition described by Kowalczewski & Ozimek (1993): Charophytes → *Potamogeton* spp. → *Myriophyllum–Potamogeton* spp.

Aknowledgements

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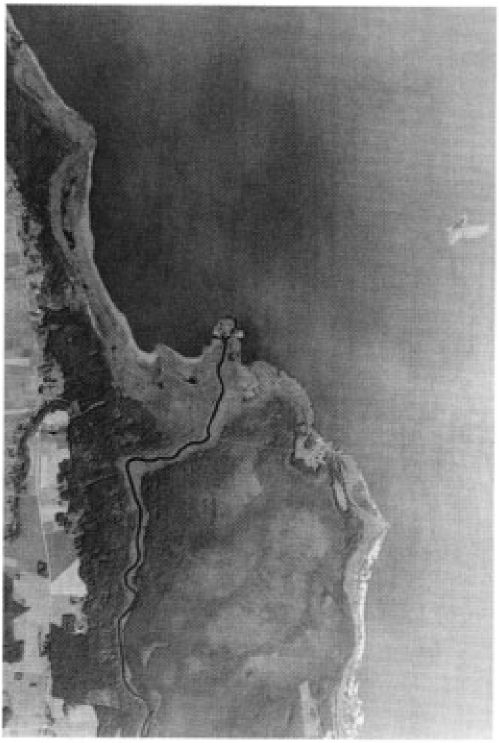
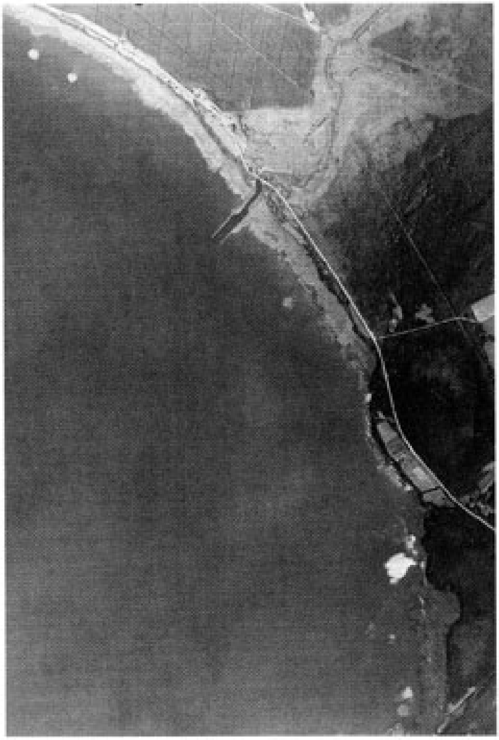
Thick stands of yellow and white water lilies in the mouth of the Väike Emajõgi River in the southern end of Lake Võrtsjärv give evidence of favourable conditions for floating-leaved plants.



Mouth of the Õhne River, also Tondisaar Island is visible.

The mouth of the Tänassilma River. The impact of nutrient-rich river water during decades has caused opulent growth of the emergent plants – mainly common reed and common club-rush.



The outflow, the Emajõgi River, starts from the north-eastern corner of Lake Võrtsjärv. Peculiar round stands of reed can be seen.

The aerophotos were made with support from the Finnish Ministry of the Environment.

IV

Zingel, P., Nõges, P., Tuvikene, L., **Feldmann, T.**, Järvalt, A., Tõnno, I., Agasild, H., Tammert, H., Luup, H., Salujõe, J. and T. Nõges. 2006
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Ecological processes in macrophyte- and phytoplankton-dominated shallow lakes

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Abstract. Stratified lakes often receive more attention from limnologists although most of the world's lakes are indeed shallow. This study describes ecological processes in three shallow lakes, one dominated by macrophytes, one by phytoplankton, and one with both of them. Investigations focused on abiotic (water chemistry) as well as biotic factors such as phytoplankton, bacteria, zooplankton, and macrophytes. The macrophyte- and plankton-dominated lakes differed clearly in water transparency, which was far greater in macrophyte-dominated lakes due to phytoplankton setback in summer. Similar nutrient and zooplankton dynamics occurred in both types of lakes, suggesting that an alternative mechanism may account for the observed phytoplankton decline in macrophyte lakes. In contrast, herbivorous ciliates dominated only in the macrophyte lake. More intensive ciliate grazing could be one factor causing a decrease in phytoplankton numbers. In the plankton-dominated lake bacteria were mostly related to phytoplankton production but that was not the case in the macrophyte-dominated lake. In the plankton-dominated lake the grazing rate of ciliates on bacteria was higher than in the macrophyte-dominated one. However, when grazing on small algae was considered, the highest grazing rates were found in the macrophyte-dominated lake. This suggests that the microbial loop was weaker in the macrophyte-dominated lake than in the plankton-dominated lake.

Key words: shallow lakes, aquatic food webs, macrophyte-dominated lake, phytoplankton-dominated lake.

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INTRODUCTION

The most classical fundamental studies on lake ecology have been done in relatively deep lakes, which are in summer subject to thermal and chemical stratification (e.g. Hutchinson, 1957, 1967). Thermal stratification largely isolates the upper water layer (epilimnion) from the colder deep water (hypolimnion) and from interaction with the accumulation sediment during summer. So the hypolimnion is usually cold, dark, and rich in nutrients (nitrogen and phosphorus) but unproductive. In such lakes the impact of macrophytes on the community is relatively small, as plant growth is restricted to a narrow marginal zone. A large number of lakes that do not undergo stratification also exist. In these lakes, the entire water column is frequently mixed (polymictic) and kept in contact with sediments. The functioning of that kind of ecosystem differs completely from the "classical" lake type and deserves also a completely different theoretical approach (Scheffer, 1998). Comprehensive theoretical studies about shallow lake ecosystems started to emerge only in the last decade (Kufel et al., 1997; Moss et al., 1997; Scheffer, 1998; Jeppesen et al., 1998) and their authors agree that there is still much unknown.

The clear-water, macrophyte-dominated state is considered the pristine condition in shallow lakes (Scheffer, 1998). Nutrient loading has caused the water to turn turbid and with the increase in turbidity, submerged plants have largely disappeared. The macrophytes seem to have the key position in the development of the ecological state in shallow lakes (Jeppesen et al., 1998). Lakes with a low nutrient content have usually a vegetation dominated by relatively small plants. With moderate nutrient loading, the biomass and proportion of aquatic macrophytes increase and plants can fill the entire water column. However, with further eutrophication phytoplankton can gain the upper hand. Disappearance of macrophytes changes the lake ecosystem so drastically that the new phytoplankton-dominated system can be regarded as a new stable state. By the state-of-art theory, two alternative stable states exist for shallow lakes (Scheffer, 1998) – the vegetation-dominated clear state and the turbid phytoplankton-dominated state. Switches between the two stable states can be abrupt; the ecosystem's response to increasing eutrophication is not linear but follows the sigmoidal hysteresis curve (Scheffer, 1998). When the nutrient loading to a macrophyte-dominated lake first increases, the low phytoplankton biomass and low turbidity can still prevail for quite a long time. Macrophytes can prevent wave resuspension, affect nutrient availability in the water column, influence algal growth through allelopathic exudates, and harbour high densities of phytoplankton eating cladocerans. When these stabilizing mechanisms are suddenly somehow eliminated (e.g destruction of vegetation by human or introduced bird or fish species, water-level changes, changes in salinity, destruction by predatory fish, etc.) the ecosystem will switch to a new stable state with turbid water and phytoplankton dominance. It can happen also when nutrient loading increases to such a level that phytoplankton grows so fast in spring that they inhibit macrophyte growth by shading and light limitation. When macrophytes are gone, increased wave resuspension will act as a positive feedback from the increased turbidity and sediment nutrient release. The macrophytes cannot return now even when the amount of nutrients decreases. So, a switch back to the clear water state can only occur in circumstances when the nutrient concentrations are significantly lower than those when switching to the turbid state occurred.

Still we are a long way from a full comprehension of the shallow lakes ecosystem, which includes a full set of physical-chemical (bottom-up) and biological (top-down) interactions (Jensen et al., 1994; Jeppesen et al., 1998). When a lake has a low nutrient content, phytoplankon cannot achieve enough biomass to hinder macrophyte growth. However, with increased nutrient loading, these responses are less predictable. We may get an algae-dominated lake where the only limiting factor for phytoplankton growth is their own density. On the other hand, we have evidence from lakes where nutrient concentrations are very high but zooplankton suppress algal biomass, water is clear, and macrophytes are strongly present.

Because of insufficient knowledge about the shallow lake ecosystems we cannot adequately predict their future in the rapidly changing global environment. Also the results of different restoration methods remain incalculable. The aim of this study was to describe some key ecological processes and communities in three macrophyte- and/or phytoplankton-dominated shallow lakes focusing on phytoplankton, bacteria, and meta- and protozooplankton.

MATERIAL AND METHODS

In 2000 we sampled seasonally three shallow lakes of varying ecological status: L. Kaiavere – a eutrophic plankton-dominated lake, L. Prossa – a eutrophic macrophyte-dominated lake, L. Võrtsjärv – a eutrophic lake, the central part of which was studied separately as a plankton-dominated lake and the southern part as a macrophyte-dominated one. To obtain a wide range of background data, in July and August we sampled three additional shallow lakes: dyseutrophic L. Valguta Mustjärv (henceforth L. Mustjärv) semidystrophic L. Uljaste, and halotrophic L. Mullutu Suurlaht (L. Suurlaht) (Tables 1 and 2).

The studied lakes Prossa and Kaiavere are calcareous eutrophic shallow lakes. The bottom of L. Prossa is carpeted with a dense macrophyte cover dominated by *Chara* spp. Lake Kaiavere has a comparable depth but is larger and the coverage by submerged plants was much smaller and consisted mainly of *Potamogeton* spp. Võrtsjärv is a large and shallow eutrophic lake. During the vegetation period, Secchi depth usually does not exceed 1 m in the central parts of the lake and water blooms are a common phenomenon. Besides this, the shallowness of the lake and the wave-induced resuspension of bottom sediments contribute to the formation of a high seston concentration and high turbidity during summer. The southern part is more

Table 1. Some background information on the studied shallow lakes

Lake	Average depth, m	Max depth, m	Area, ha	Geology	Type
Prossa	2.2	4.2	33	Calc/rock	Eutrophic–macrophyte
Kaiavere	2.8	5	251	Calc/rock	Eutrophic–plankton
Võrtsjärv	2.8	6	27 000	Calc/rock	Eutrophic–plankton
Harku	1.6	2.5	164	Calc/rock	Eutrophic–plankton
Maardu	1.6	3.2	170	Calc/rock	Dyseutrophic–macrophyte
Kirikumäe	2.8	3.5	64	Org/peat	Semidystrophic
Suurlaht	1.2	2.1	5 900	Calc/rock	Halotrophic
Uljaste	2	5.6	60	Org/peat	Semidystrophic
Mustjärv	0.8	1	23	Org/peat	Dyseutrophic

Table 2. Average annual values for some physico-chemical and biological parameters of the studied shallow lakes (Sec = Secchi depth, Chl a = chlorophyll *a*, TP = total phosphorous, TN = total nitrogen, PP = primary production, BA = bacterial abundance, PA = autotrophic picoplankton abundance, Phy B = phytoplankton biomass, CA = abundance of ciliates, CB = biomass of ciliates, MZP A = metazooplankton abundance, MZP B = metazooplankton biomass)

Lake	Sec, m	Chl a, mg m^{-3}	TP, mg L^{-1}	TN, mg L^{-1}	PP, mgC m^{-3} h^{-1}	BA, 10^6cell mL^{-1}	PA, 10^4cell mL^{-1}	Phy B, g m^{-3}	CA, ind. mL^{-1}	CB, µg L^{-1}	MZP A, ind. L^{-1}	MZP B, g m^{-3}
Harku	0.3	230.4	0.2	2.8				34.8			3064.9	1.5
Maardu	2.5	9.6	0.0	0.8				1.0			1000.2	1.1
Kirikumäe	1.2	9.0	0.0	0.7				3.2			390.3	1.0
Suurlaht	1.5	11.3	0.0	1.4	27.7	1.9	22.7	2.1	10.9	24.5	519.7	0.3
Uljaste	1.8	54.8	0.0	0.7	17.6	0.9	3.8	7.5	14.4	60.9	357.4	3.8
Mustjärv	0.6	17.0	0.0	1.1	32.0	1.8	1.5	1.5	19.1	122.6	2048.3	0.2

sheltered from the wave-induced disturbance than the northern part and is largely covered with submerged plants. During seasonal studies we gathered samples for water chemistry, phyto-, zoo-, and bacterioplankton, and measured primary and bacterial production, zooplankton filtering rate, and molecular nitrogen fixation. In July and August we measured in addition the number and species composition of macrophytes and the amount of periphyton on them and the quantity and species composition of chydorids and fishes.

In 2001 we sampled seasonally two shallow lakes: L. Kaiavere and L. Prossa. Starting from the end of April to the middle of June we sampled L. Prossa weekly to examine the development of macrophytes and the shift to a clear-water state. To widen the range of the study, we sampled in August three additional shallow lakes: L. Kirikumäe, L. Harku, and L. Maardu (Tables 1 and 2). During seasonal studies we gathered samples for water chemistry, phyto-, zoo-, and bacterioplankton, chydorids, and measured primary and bacterial production, zooplankton filtering rate, number and species composition of macrophytes, and the amount of epiphyton on them.

Water chemistry

Water temperature and the concentration of dissolved oxygen were monitored in the surface layer, at depths of 0.5 m and 1 m, and every metre down to the bottom using a Marvet Junior dissolved oxygen meter (Estonia, Tallinn). For other measurements, 2-litre water samples were taken from the above-mentioned depths with a Ruttner bathometer. These samples were mixed in a 30-litre container to get an average sample. Conductivity was measured with HACH conductivity/ TDS meter (model 44600; USA), and pH was estimated using WTW Universal Pocket Meter Multiline P4 (Wissenschaftlich-Technische Werkstätten GMBH, Weilhein, Germany). The concentrations of total phosphorus (TP), inorganic phosphate (PO_4-P), nitrates (NO_3-N), nitrites (NO_2-N), and ammonium nitrogen (NH_4-N) were estimated from unfiltered subsamples using standard methods described in (Grasshoff et al., 1999). The concentration of inorganic nitrogen forms (Nmin) was calculated as the sum of NO_3-N, NO_2-N, and NH_4-N. A spectrophotometer Spekol 11 (Carl Zeiss, Jena) was used for extinction measurements. Total nitrogen (TN) was determined by second-derivative UV spectroscopy (Crumpton et al., 1992), using an UV–visible scanning spectrophotometer Cecil 3000 (Cecil Instruments Ltd, Milton Technical Centre).

Phytoplankton, primary production, and molecular nitrogen fixation

Integral lake water (250 mL) was collected for phytoplankton (Phy) analyses and fixed with Lugol's solution (0.5% of final concentration). The samples were counted with an inverted microscope at ×400 magnification using the standard Utermöhl (1958) technique. The mean volume of each species was estimated in all samples by approximating the shape of species to the nearest simple geometric solid.

Chlorophyll *a* was extracted in 96% ethanol and analysed spectrophotometrically (Edler, 1979; Arvola, 1981). Primary production (PP) of Phy was estimated in situ using the $^{14}CO_2$ assimilation technique introduced first by Steeman-Nielsen (1952). Depth integrated water was poured to 24 mL glass scintillation vials, 50 μL of sterile $NaH^{14}CO_3$ (VKI, Denmark) solution (1.7 μCi per vial) was added to achieve final activity of 0.07 μCi mL^{-1}. Vials were incubated for 2 h at six depths in the lake. Then 6 mL of water from each sample was poured into a clean glass scintillation vial and acidified ($pH < 2$) by adding 150 μL of

0.5 N HCl. Inorganic ^{14}C was assumed to be removed during 24 h (Niemi et al., 1983; Hilmer & Bate, 1989; Lignell, 1992). Next, 5 mL subsamples were poured into new plastic vials. The radioactivity of water, filtrate, and filters was assessed by LSC RackBeta 1211 (Wallac, Finland) using external standardization for DPM calculations. Scintillation cocktail Ecoscint A was applied for water and filtrate, and toluol-POPOP-PPO cocktail for filters. Primary production of different fractions was calculated according to the standard formula (HELCOM, 1988). Non-photosynthetic carbon fixation was measured in dark vials and subtracted from light assimilation.

The acetylene reducion method (Stewart et al., 1967; Flett et al., 1976; Levine & Schindler, 1992; Présing et al., 1996) was used to measure the molecular nitrogen fixation (N_2fix) by cyanobacteria. Glass bottles of 60 mL were filled with lake water and exposed for 4 h in the incubator at constant illumination of 120 W m^{-2} and temperature adjusted to that of the lake surface. Measurements were made in the same days when water chemistry and Phy in the lakes were routinely monitored. In one measurement series three bottles were used. In one bottle 0.1 mL of 50% 3-chloro-acetic acid (TCA) solution was added as an inhibitor to detect possible nonbiotic N_2fix. Two parallels were used to measure biotic N_2fix by adding a gas phase (10.05 mL) consisting of 2 mL of air, 8 mL of argon, and 0.05 mL of acetylene into the bottles with 49.95 mL lake water. Reaction was stopped by adding 0.1 mL of 50% TCA solution. The N_2fix activity was determined by analysing 2 mL of gas from each bottle by a gas chromatograph “Chrom 5” (Czechoslovakia) with a flame ionization detector and 220 cm Porapak R 80/100 column (Ø 3 mm).

Bacterioplankton and picoplankton

The total number of bacteria (TNB) was determined by 4′,6′-diamidino-2-phenylindole (DAPI; Polysciences Inc; Porter & Feig, 1980). Formaldehyde preserved subsamples were incubated with DAPI (final concentration 10 μg mL^{-1}) for 5 min in the dark and filtered onto black 0.22-μm-pore-size polycarbonate filters (Osmonics Inc.). The abundance of autotrophic picoplankton (APP) was estimated by autofluorescence on the same filters as heterotrophic bacteria. All microscope observations were made at ×1000 magnification with an epifluorescence microscope Zeiss Axiovert S100 as soon as possible; slides were stored at –21 °C if necessary.

Bacterial production (BP) was estimated by the tritiated thymidine incorporation method. Five samples (+5 formaldehyde killed blanks), 10 mL each, were treated with different amounts of $[^3H]$ thymidine (20–900 nM: specific activity 5.0 Ci $mmol^{-1}$; Amersham). After 30 min incubation at in situ temperature cold base–acid–ethanol extraction was used for purification of DNA as described by Wicks & Robarts (1987). The cellulose acetate filters (pore size 0.22 μm; Millipore) were dissolved in Ecolume liquid scintillation cocktail, and radioactivity was measured by liquid scintillation counting (LSC RackBeta 1211, LKBWallac). The uptake of thymidine was converted to the number of produced cells by using the conversion factor 3.4 × 10^{18} (Kisand & Nõges, 1998).

Metazooplankton

All analyses were made from depth-integrated water taken from five sampling points from the lake centre to the shore and mixed together. Only in the central part of L. Võrtsjärv the sample was collected from a single sampling point. Metazooplankton (MZP) was collected by filtering 10 L integrated lake water through a plankton net (48 μm), fixed with Lugol's solution, and counted in three 2.5–5 mL subsamples. The samples were counted under a binocular microscope (MBC-9) in a Bogorov chamber and enumerated at ×32–56 magnification. The individual weights of zooplankters were estimated from average lengths according to Ruttner-Kolisko (1977) and Balushkina & Winberg (1979).

The samples of chydorids were collected from lakes Kaiavere, Suurlaht, Prossa, Uljaste, Mustjärv, and Võrtsjärv in August 2000. In 2001 the seasonal dynamics of chydorids of L. Prossa was studied. Five replicate samples were taken from the vegetation-free zone and from the zone with macrophytes. Samples were collected using a 100 μm mesh net. Due to great variability, all five replicate samples were counted.

The grazing of MZP was measured by in situ feeding experiments with two different methods using fluorescent microspheres (FMS) in lakes Kaiavere and Võrtsjärv in 2000 and ^{14}C-labelled Phy culture in L. Prossa in 2001. For grazing experiments with FMS the number of Phy cells (<31.0 μm), presumably edible for MZP, was counted separately. Size classes were split by the maximum linear length: 2.0–4.9 μm as the first, 5.0–14.9 μm as the second, and 15.0–31.0 μm as the third size class (SC1, SC2, and SC3, respectively). For bacteria FMS of 0.5 μm diameter (Fluoresbrite, Polysciences Inc.) and for Phy of 3 μm, 6 μm, and 24 μm diameter (Duke Scientific Corporation) were used. The tracer amount that did not exceed 10% of the density of the corresponding size groups in lake water was added to integrated lake water in a 3-litre incubation vessel. Incubations lasted for 7 min, after which the water was filtered through a plankton net (48 μm), anaesthetized with carbonated water, and fixed in 4% formaldehyde. For FMS counting, individual zooplankters were collected from the samples and filtered onto a polycarbonate filter of 10 μm pore size (Poretics). The number of FMS in the zooplankters' guts was counted at ×1000 using an epifluorescence microscope (Zeiss Axiovert S100). The filtration (FR; μL ind.$^{-1}$ h^{-1}) and ingestion (IR; bacteria ind.$^{-1}$ h^{-1}) rates for each taxon and community filtration (CFR; mL L^{-1} d^{-1}) and ingestion (CIR; cells L^{-1} h^{-1}) rates were calculated using standard equations. The individuals that had empty guts were included.

To assess zooplankton (ZP) community grazing by radioactively labelled Phy, 50 mL of *Scenedesmus brasiliensis* Bohlin monoculture (cell size 2.5–4 µm) was labelled with $NaH^{14}CO_3$ during 36 h at 120 W m^{-2}. Then cells were centrifuged at 3000 rpm, washed with filtered lake water (Whatman GF/C), and suspended in the same solution. The final amount of the algal suspension was 30 mL. Of this suspension 10 mL was added into 4 L of integral lake water and incubated in the lake for 7 min. In the experimental vessels the concentration of the labelled *S. brasiliensis* monoculture did not exceed 5–10% of the total suspended solid concentration of lake water (1.0–5.5 mg DW L^{-1}). After incubation, the water was filtered through a plankton net (mesh size 100 µm) to collect the ZP. The obtained filtrate was filtered through 48 µm mesh to obtain the fraction of smaller ZP (48–100 µm). The filtered ZP were anaesthetized with carbonated water and stored on ice. To measure the radioactivity of food, 30 mL of filtrate was retained on the GF/C filters. In laboratory ZP were washed from the net to the GF/C filters. The radioactivity of the filters with ZP and food particles was measured by a liquid scintillation counter RackBeta 1211 (LKB Wallac). One measurement series consisted of three replicates. The ZP community filtration rate (F, mL L^{-1} h^{-1}) was calculated according to the formulae developed by Lampert & Taylor (1985). Grazing rate (G, mg L^{-1} h^{-1}), relative grazing rate of Phy biomass (RGR_b, % d^{-1}), and relative grazing rate of primary production (RGR_{pp}, % d^{-1}) were calculated using standard equations.

Planktonic ciliates

For ciliate counts 250 mL of integral lake water was collected and fixed with Lugol's solution (0.5% of final concentration). The ciliates' biomass and community composition were determined using the Utermöhl (1958) technique. Ciliates were usually identified to genus by consulting several works (e.g. Patterson & Hedley, 1992; Foissner & Berger, 1996). Biovolumes of all taxa were estimated and the specific gravity was assumed to be 1.0 g mL^{-1} (Finlay, 1982), so the biomass was expressed as wet weight (WW). For grazing experiments FMS were used and the same methods were applied as described above under the metazooplankton section in lakes Kaiavere, Prossa, and Võrtsjärv in 2000. Incubations lasted for 7 min, after which the samples were fixed with buffered formalin (1% final concentration). The preserved samples were stained for 1–2 min with DAPI at a final concentration of 2 µg mL^{-1} and gently filtered through 0.8-µm pore-size black isopore (Poretics Inc.) filters. Protists and the contents of their food vacuoles were examined with an Olympus BX60 fluorescence microscope under ×1000 using blue light (470/505 nm, OG 515). As much as possible, the dominant taxa of fluorescently stained ciliates were identified based on knowledge on the composition of parallel Lugol fixed samples. To estimate the total ciliate grazing rate, their uptake rates were multiplied by their total in situ abundances.

Macrophytes

To estimate macrophyte abundances in lakes Kaiavere, Mustjärv, Prossa, Suurlaht, Uljaste, and Võrtsjärv the Percent Volume Infested (PVI) method (Canfield et al., 1984) was used. One radial transect per 100 m of lake shore up to a maximum of 20 transects per lake was selected. All species of submerged and floating-leaved plants were identified and distributed into the following categories: charophytes, isoetids, and floating-leaved and submerged macrophytes. In each sampling point the coverage of filamentous and thalloid algae was assessed using the following 3 categories: (a) very abundant (>50% coverage), (b) moderate (10–50% coverage), (c) rare (<10% coverage). In the case of emergent plants we determined the percentage of the lake colonized and identified the dominant species (>20% of the community). To assess macrophyte zones in lakes Mustjärv, Uljaste, and Võrtsjärv the weighting method was used – the different areas were copied to the map, cut out, and compared with the weight of the whole lake map. The macrophyte zones in the other lakes are relative.

Epiphyton

Five samples of dominant macrophytes and three samples of other plants were collected from all lakes. Plants were placed into glass vessels with 100 mL distilled water and shaken for 2 min. Water was filtered through a 94 µm net (2000) or sieved (2001) to avoid detritus from getting into the samples. Samples were preserved with Lugol's solution and algal communities were studied using an inverted microscope at ×400 (Utermöhl, 1958). For chlorophyll measurements the samples were filtered through GF/C filters and analysed as in Jeffrey et al. (1997). Plants, which were free of epiphyton, were dried for 24 h (at 100 °C) and then weighed. The chlorophyll amount was calculated for the dry weight of the plants. We compared epiphytic communities on dominant macrophytes and other plants in each lake. We also compared the epiphyton communities in similar plant species collected from the different lakes. The similarity of communities was assessed with Student's two-sided *t*-test.

Fish

The structure and relative composition of fish communities was investigated by Lundgren gillnets according to a protocol of fish of ECOFRAME program in August–September 2000. Each net was 42 m long, 1.5 m high, and consisted of 14 units of 3 m with different mesh sizes (from knot to knot) in the following order: 6.25, 8, 16.5, 75, 38, 25, 12.5, 33, 50, 22, 43, 30, 60, and 10 mm. In the littoral zone sinking nets and in the pelagial zone sinking and floating nets were used. The number of nets used depended on lake area. The sampling sites were selected randomly. The catch per unit effort (CPUE) per net for each species and two size groups (<10 cm and ≥10 cm) with 95% confidence limits was calculated. For most common species the length–weight relationship and also the average length and weight for fish <10 cm and ≥10 cm were determined. For each species the fork length (from nose tip to tail cleft) was measured to the nearest lower mm and weight in g with an accuracy of 0.1 g for fish smaller than 10 cm and with an accuracy of 1 g for fish over 10 cm was found. The abundance of fish in different lakes was compared on the basis of the mean CPUE either in weight or in the numbers of captured individuals. To calculate the mean yield of fish per the whole lake, the area of the littoral zone was taken into account as follows: Suurlaht 100%, Prossa 75%, Mustjärv 50%, Uljaste 25%, Kaiavere 25%, and Võrtsjärv 20%.

RESULTS

Water Chemistry, Secchi depth, chlorophyll, and primary production

In the central part of L. Võrtsjärv the PO_4-P concentrations were high (up to 0.03 mgP L^{-1}) in winter 2000, but stayed low in summer. The TP range was from 0.034 to 0.07 mg L^{-1}. The concentration of NH_4-N dropped below 0.03 mg L^{-1} by the end of April. The concentration of NO_2-N was 0.009–0.013 mgN L^{-1}, and from <0.002 to 0.004 mgN L^{-1} in summer. Also the concentrations of NO_3-N and TN were higher in winter than in summer.

In the southern part of L. Võrtsjärv the concentrations of PO_4-P and TP (0.007–0.027 and 0.073–0.12 mg L^{-1}, respectively) were higher than in the central part of L. Võrtsjärv as well as in other lakes during the ice-free period. Average concentrations of both NH_4-N and NO_2-N were low during the ice-free period (0.06 and 0.02 mg L^{-1}, respectively). The concentration of NO_3-N was still on its winter level (0.97 mgN L^{-1}) after ice break in April, but dropped quickly below 0.05 mg L^{-1} at the beginning of May. The TN values were 1.7 mg L^{-1} in April, but remained thereafter around 1 mg L^{-1}.

In L. Prossa TP was the lowest among the studied lakes: ≤0.035 mg L^{-1}. Its level decreased after May and remained low until September. In 2001 TP was lower than in the previous year, especially in the first part of summer. Concentrations of inorganic nitrogen compounds, mostly NO_3-N, were high in April, but decreased sharply at the beginning of June.

In L. Kaiavere the organic compounds of phosphorus dominated during the ice-free period while PO_4-P was usually lower than 0.005 mgP L^{-1} (<5% from TP). The average TP was slightly lower in 2001 than in the previous year (0.049 and 0.055 mg L^{-1}, respectively). The nitrogen dynamics (both TN and Nmin) of L. Kaiavere was similar to L. Prossa – a sharp decline occurred in May.

In both lakes Prossa and Kaiavere the Secchi depth (S) was quite high and chlorophyll *a* concentration (Chl a) and primary production (PP) were moderate in April after the ice break. From July L. Prossa developed into a typical clearwater macrophyte-dominated state (S ≤ 4 m) while L. Kaiavere remained turbid and plankton-dominated with the water transparency about 1 m (Fig. 1). In L. Kaiavere also a second boost in Chl and PP occurred in autumn 2001, which was not observed in 2000.

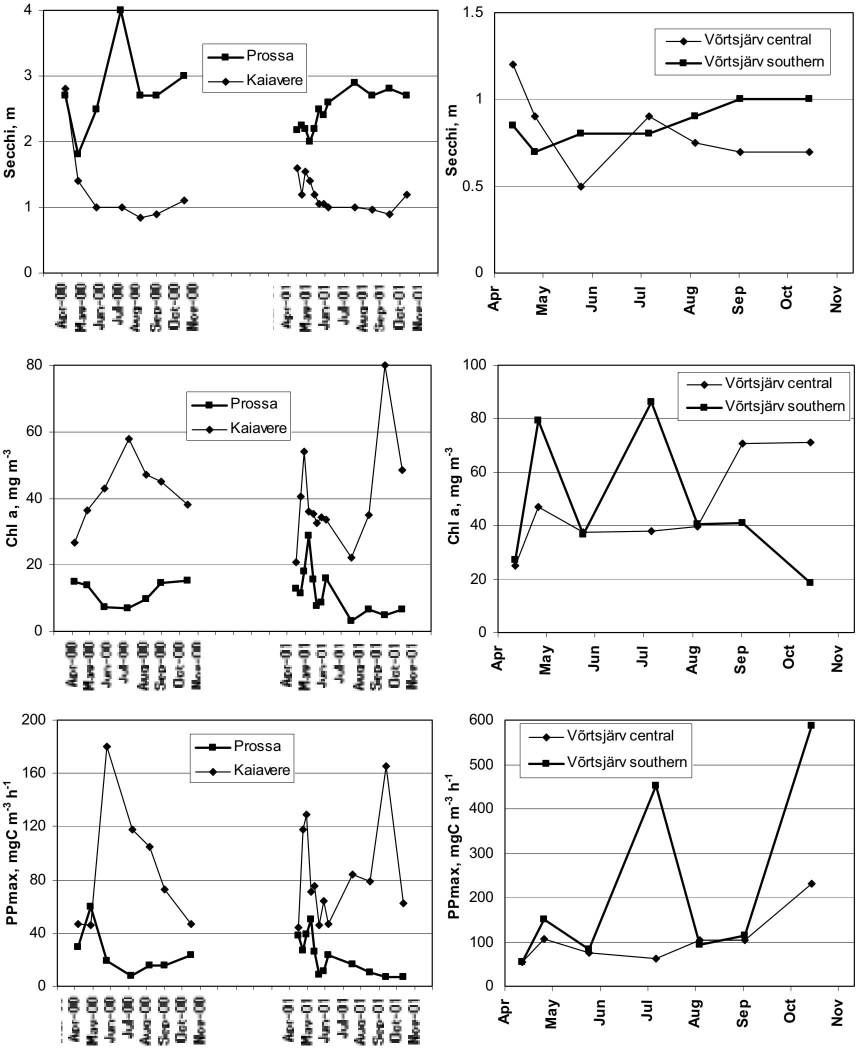

Fig. 1. Secchi depth, chlorophyll *a*, and primary production in lakes Kaiavere and Prossa (2000 and 2001) and in the central and southern parts of L. Võrtsjärv (2000).

The central part of L. Võrtsjärv acted like a typical plankton lake. The southern part of the lake did not develop to a typical clearwater macrophyte-dominated state and harboured an abundant Phy community also in summer.

Bacterioplankton and autotrophic picoplankton

The abundance of bacteria in L. Kaiavere was 0.4–7.5 × 10^6 cells mL^{-1} (median 3.0), being higher than in L. Prossa (0.7–4.1 × 10^6 cells mL^{-1}; median 2.0). In the central part of L. Võrtsjärv the abundance of bacteria (median 1.6 × 10^6 cells mL^{-1}) was lower than in its southern part (median 2.3 × 10^6 cells mL^{-1}). In L. Kaiavere and in the central part of L. Võrtsjärv the highest bacterial numbers were achieved in June. In L. Prossa and the southern part of L. Võrtsjärv the bacterial abundance peaked in July (in 2000) or May (in 2001 in L. Prossa). In the central part of L. Võrtsjärv (in 2000) the abundance of autotrophic picoplankton peaked in October, in its southern part in July and in L. Kaivere and in L. Prossa in June. Bacterial production (BP) rates were significantly higher in 2001 than in 2000. Also the difference in BP was more pronounced in L. Kaiavere and L. Prossa in 2001 than in 2000. In L. Kaiavere BP ranged during the study period from 3.5 to 254 × 10^6 cells L^{-1} h^{-1} (median 114) and in L. Prossa from 13 to 211 × 10^6 cells L^{-1} h^{-1} (median 103). In L. Kaiavere BP peaked in July in 2000 while in 2001 three BP peaks occurred, the highest at the end of May. In L. Prossa BP reached the highest values in July and August (in 2000 and 2001, respectively). In the central part of L. Võrtsjärv (in 2000) BP ranged from 3.8 to 165 × 10^6 cells L^{-1} h^{-1} (median 17) and in the southern part from 33 to 318 × 10^6 cells L^{-1} h^{-1} (median 94). During the study period, the highest production was measured in the central part of L. Võrtsjärv in June while the most pronounced maximum in the southern part was found in August.

Metazooplankton

In L. Prossa the MZP maximum was reached in May. The abundance and biomass were dominated by rotifers but in summer also cladocerans (*Bosmina longirostris*) and copepods (juveniles and *Mesocyclops* spp.) were abundant. The same pattern was observed in L. Kaiavere. From cladocerans *Bosmina longirostris*, *B. coregoni*, and *Chydorous sphaericus* were important in June and *Daphnia cucculata* in August. Copepods were dominated by *Mesocyclops leuckarti* and *M. oithonoides*. In L. Prossa the abundances of MZP were lower than in L. Kaiavere (Fig. 2). In L. Võrtsjärv's central part the zooplankton maximum was reached in July. The highest biomasses were measured at the end of May and in June. The abundance was dominated by rotifers (*Keratella tecta*, *Anuraeopsis fissa*) and the biomass by cladocerans (*Bosmina longirostris*, *Chydorous sphaericus*).

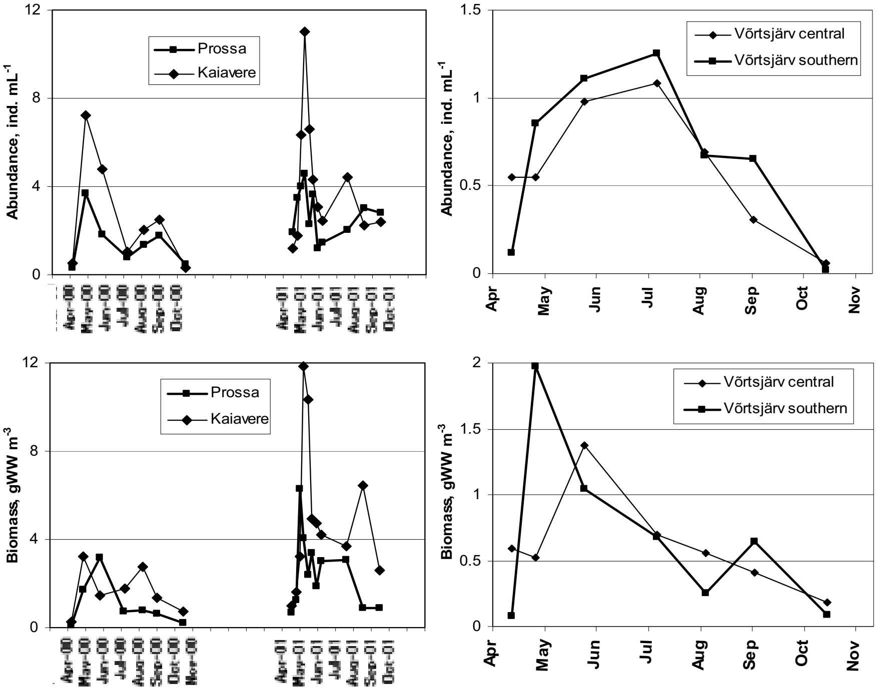

Fig. 2. Abundance and biomass of metazooplankton in lakes Kaiavere and Prossa (2000 and 2001) and in the central and southern parts of L. Võrtsjärv (2000).

Cladocerans peaked in June and copepods in May and July. During summer the number of small rotifers (*Anuraeopsis fissa*, *Keratella tecta*) increased. In L. Võrtsjärv's southern part the species composition, seasonal dynamics, and abundances were similar to those in the central part and the maximum abundance was reached in July (Fig. 2). Rotifers dominated both abundance and biomass. Cladocerans peaked in May and copepods in June.

In 2001 the abundance of chydorids in L. Prossa was low in April and May, but started to rise at the beginning of June and reached its maximum in July. Thereafter the abundance of chydorids dropped. The dominating chydorid species was *Chydorous sphaericus*.

Planktonic ciliates

In 2000 in L. Kaiavere the highest abundance and biomass of ciliates was achieved in late summer, while in 2001 the maximum biomass occurred during the spring peak of large-sized peritrichs, oligotrichs, and nassulids. In late summer the ciliate community was dominated by small-sized prostomatids but also scuticociliates and small oligotrichs (Fig. 3).

In 2001 in L. Prossa the highest abundance and biomass of ciliates was achieved in late spring, while in 2000 the biomass maximum occurred during late summer because of the occurrence of large-sized hymenostomatids. In spring the ciliate community was dominated mostly by large-sized oligotrichs. In summer these species were gradually replaced by small-sized prostomatids and oligotrichs but also the above-mentioned large hymenostomatids were important.

In L. Võrtsjärv's central part the ciliate abundance and biomass peaked in spring and in late summer. The highest abundance was achieved in July and the highest biomass in May. In L. Võrtsjärv's southern part the seasonal dynamics of ciliates was similar to that in the central part, but the maximum biomass coincided with the maximum abundance in July (Fig. 3). The main difference between the two sites was in the community structure. In both locations large-sized herbivorous

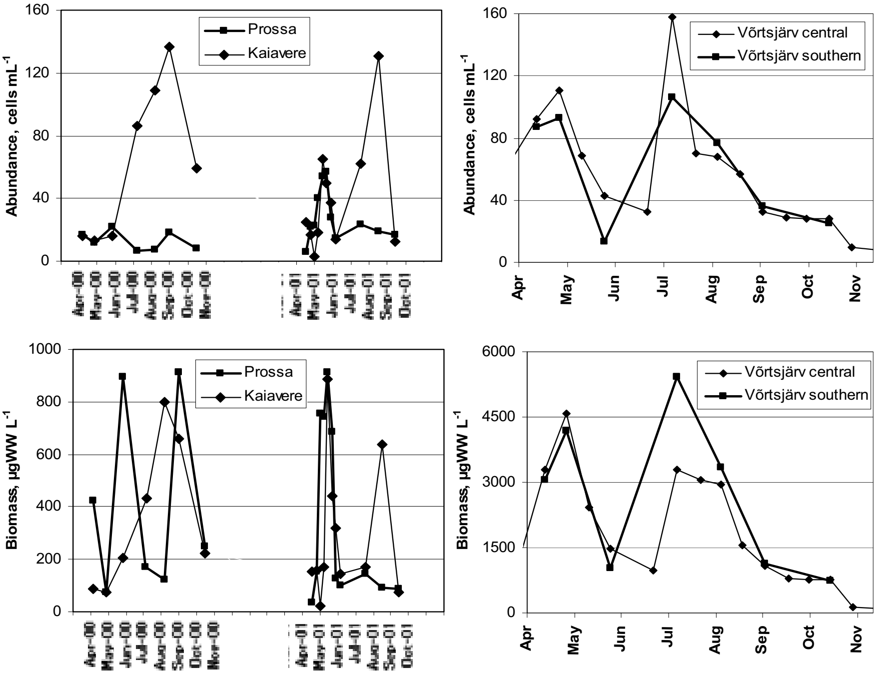

Fig. 3. Abundance and biomass of planktonic ciliates in lakes Kaiavere and Prossa (2000 and 2001) and in the central and southern parts of L. Võrtsjärv (2000).

oligotrichs made up the spring peak. The summer peak in the central part consisted mainly of small bacterivorous species but in the lake's southern part large-sized herbivores were still more numerous than small bacterivores.

Ciliate and metazooplankton grazing

Ciliate grazing rates upon bacteria were highest in L. Kaiavere (Table 3) and in the central part of L. Võrtsjärv (Fig. 4). Grazing rates upon algae were highest in L. Prossa and in L. Võrtsjärv's southern part. In all the studied lakes MZP showed the highest grazing rates on bacteria-sized FMS (Table 4). The highest grazing rates upon bacteria were found in June (Fig. 5). The most intense MZP grazing on algae was found in L. Kaiavere with the maximum in June. In L. Võrtsjärv the highest values were recorded in August (central part) and in May (southern) (Fig. 6).

The grazing experiments in 2001 in L. Prossa showed that zooplankters larger than 100 µm (cladocerans, copepods, and larger rotifers) achieved their maximum filtering rate of 12.7 mL L^{-1} h^{-1} in June (Fig. 7). The highest abundance of cladocerans, copepods, and large (>100 µm) rotifers occurred in May, but the filtering rate (6.6 mL L^{-1} h^{-1}) was not the highest at that time.

Table 3. The mean grazing rates of planktonic ciliates in the studied shallow lakes

Lake	Mean grazing rate	
	Bacteria (0.5 µm), mL^{-1} h^{-1}	Algae (3 µm), L^{-1} h^{-1}
Võrtsjärv central	20 334	50 996
Võrtsjärv southern	13 989	87 274
Kaiavere	27 850	18 633
Prossa 2000	8 226	145 849
Prossa 2001	8 105	186 388

Table 4. The mean grazing rates of metazooplankton in the studied shallow lakes

Lake	Mean grazing rate			
	Bacteria (0.5 µm), mL^{-1} h^{-1}	Algae (2–5 µm), L^{-1} h^{-1}	Algae (5–15 µm), L^{-1} h^{-1}	Algae (15–31 µm), L^{-1} h^{-1}
Võrtsjärv central	174	1151	541	–
Võrtsjärv southern	165	784	501	–
Kaiavere	907	9697	3400	89

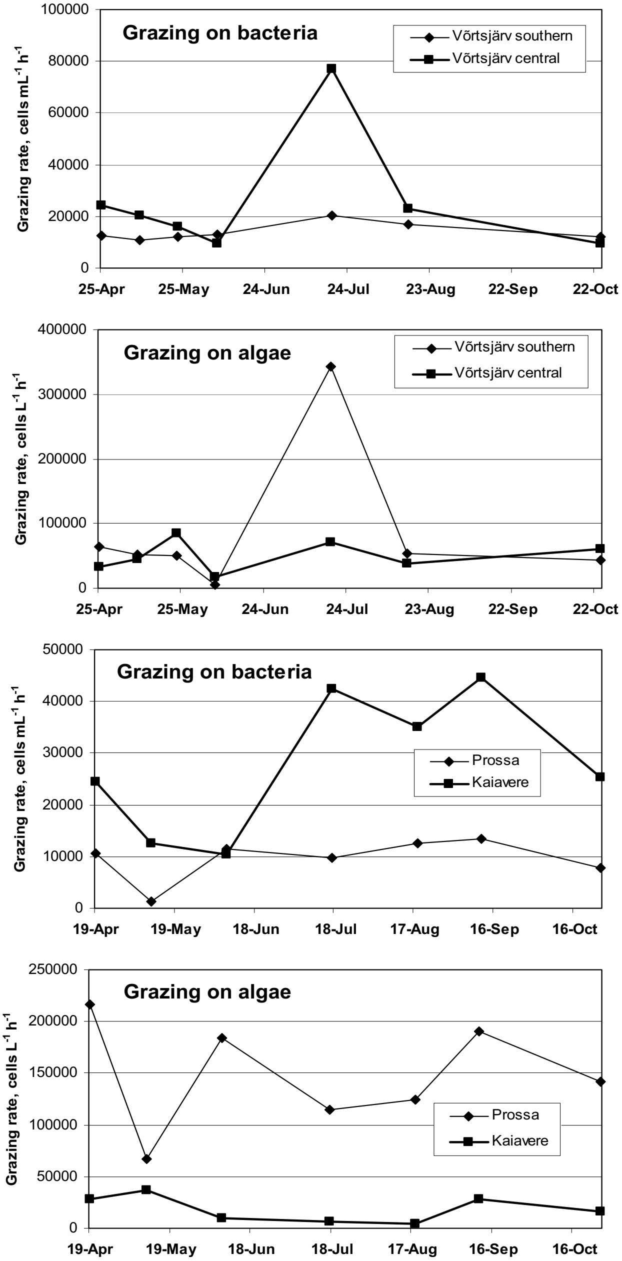

Fig. 4. Ciliate grazing on bacteria and algae in the central and southern parts of L. Võrtsjärv and in lakes Kaiavere and Prossa in 2000.

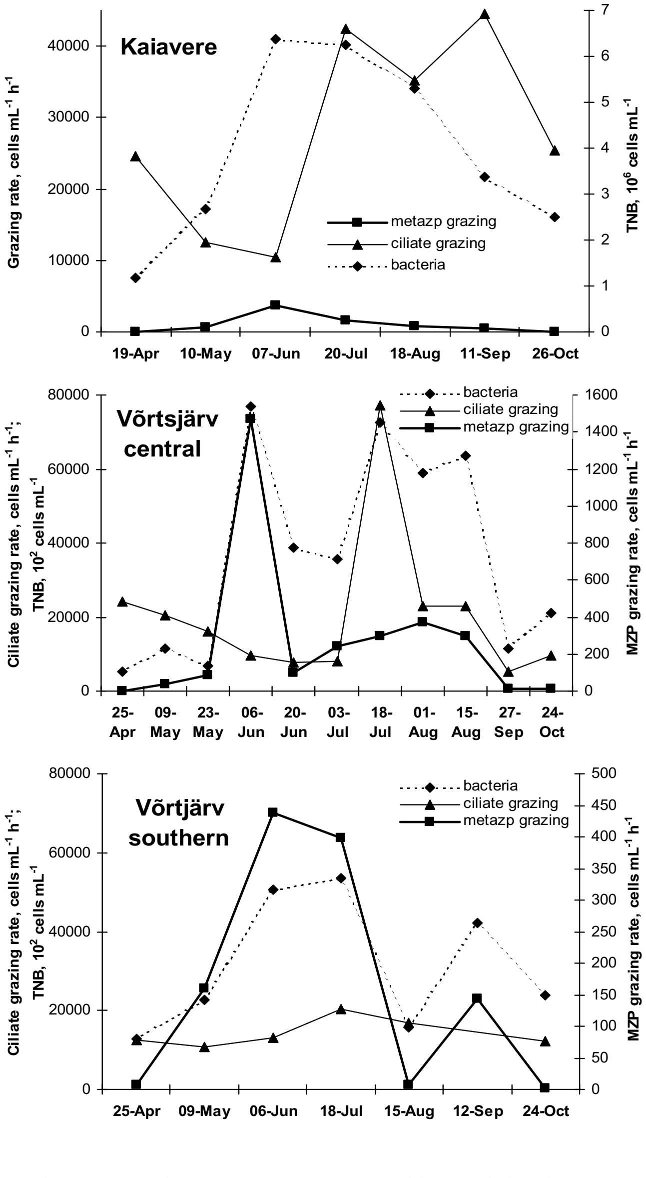

Fig. 5. Ciliate and metazooplankton grazing on bacteria and bacterial abundance in L. Kaiavere and in the central and southern parts of L. Võrtsjärv in 2000.

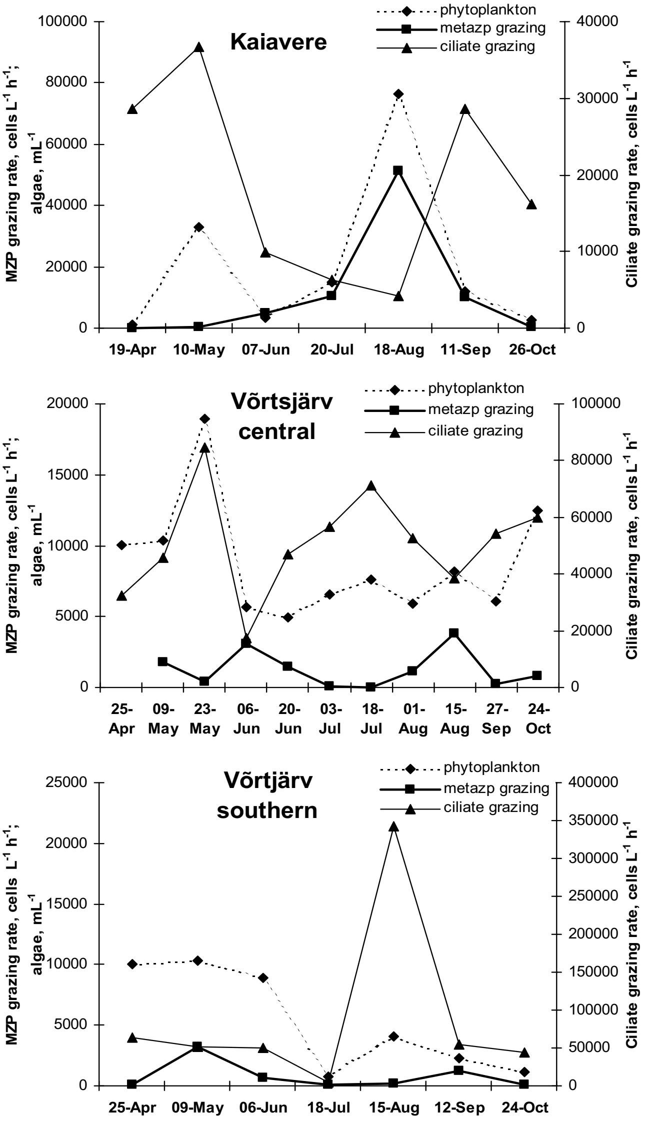

Fig. 6. Ciliate and metazooplankton grazing on small algae (Ø ~3 μm) and abundance of small algae in L. Kaiavere and in the central and southern parts of L. Võrtsjärv in 2000.

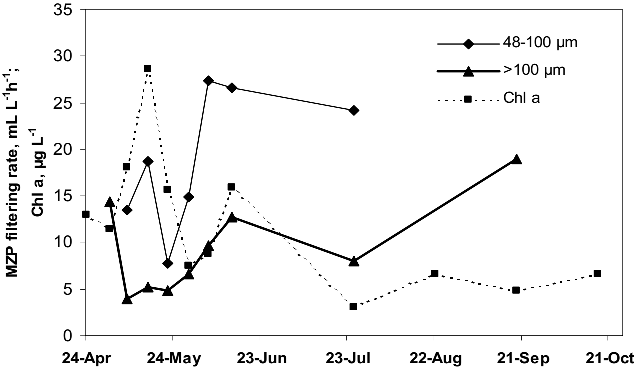

Fig. 7. Filtering rates of different metazooplankton size groups and chlorophyll *a* in L. Prossa in 2001.

Phytoplankton and molecular nitrogen fixation

In the central part of L. Võrtsjärv the Phy biomass reached its maximum in spring. In summer the biomass decreased but peaked again in autumn (Fig. 8). The Phy was dominated by blue-greens and diatoms. Most common blue-greens were *Limnothrix redekei*, *L. planktonica*, and *Aphanizomenon skujae* and the most common diatoms *Melosira* spp. and *Synedra acus*. The biomass of other Phy groups such as chlorophytes, chrysophytes, and dinophytes was low. In the southern part of L. Võrtsjärv the biomass values stayed lower than in the central part, and the maximum biomass was achieved in summer. The biomass peaked also in spring. In spring the Phy community was dominated by blue-greens but in summer by diatoms.

In L. Prossa the maximum Phy biomass was achieved in spring, but in summer and in autumn the biomass stayed at a very low level (Fig. 8). The Phy was dominated by chrysophytes (Chrysophyceae) and cryptophytes (Cryptophyta). In 2000 cryptophytes were the most important while in 2001 the crysophytes were predominant. The most abundant chrysophyte species in spring were *Dinobryon divergens* and *D. sociale* var., while in summer and in autumn the most abundant was *Uroglena* sp. In spring also diatoms (*Synedra ulna*, *S. acus*, *Melosira* sp.) were numerous.

In L. Kaiavere the Phy biomass was low in spring and reached its maximum during late summer or early autumn (Fig. 8). In spring the dominating Phy group was diatoms (*Melosira* sp., *Synedra ulna*, and *S. acus*). Blue-greens (*Aphanizomenon* sp., *Pseudanabaena calenata*, *Oscillatoria lauterbornii*, *Microcystis pulverea*, and *Aphanothece clathrata*) were the most important group in summer and autumn. In autumn, during the second peak of diatoms, the dominating species were *Acanthoceros* sp., *Fragilaria crotonensis*, and *Melosira* sp. Chlorophytes (*Scenedesmus* sp., *Pediastrum* sp., *Monoraphidium* sp.), chrysophytes

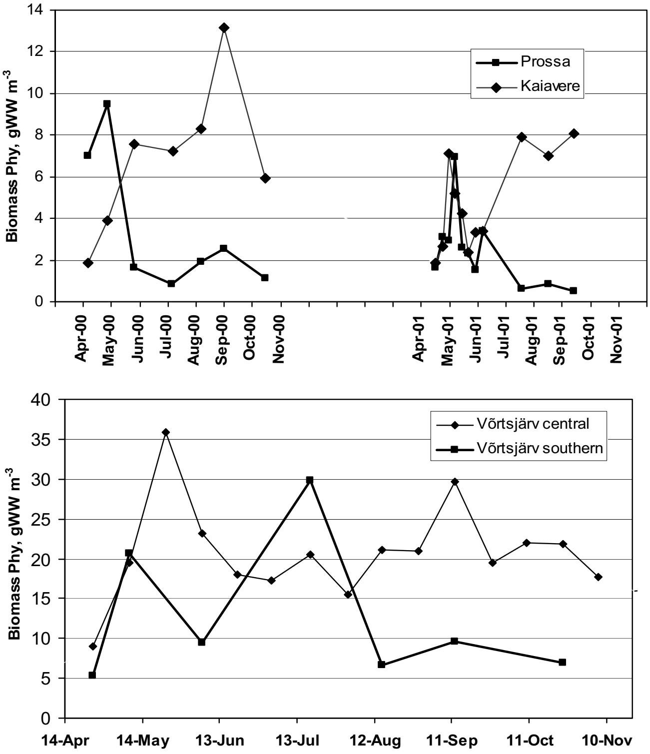

Fig. 8. Phytoplankton biomass in lakes Kaiavere and Prossa in 2000 and 2001 and in the central and southern parts of L. Võrtsjärv in 2000.

(*Dinobryon* sp., *Uroglena* sp.), cryptophytes, dinophytes, and euglenophytes were present but they were less important than blue-greens and diatoms. In the central part of L. Võrtsjärv N_2 fixation (N_2fix) was detected in August and September 2000. The highest N_2fix values were recorded in August (2.5 µgN L^{-1} day^{-1}). In the southern part no N_2fix was detected. In L. Kaiavere N_2fix was low (max 0.95 µgN L^{-1} day^{-1}) in September 2000. In L. Prossa no N_2fix was detected.

Macrophytes and epiphyton

The number of macrophyte species, percent volume infested (PVI), and the coverage of filamentous algae are given in Table 5. The area of water plant zones and dominant species in the zone of emergent plants are given in Table 6. In three lakes (Kaiavere, Prossa, and Võrtsjärv) the number of macrophyte species was

Table 5. Coverage of the studied lakes by aquatic plants, number of species, and percent volume infested (PVI)

Lake	Lake area occupied by plants, %	Shoreline plants from the plant occupied area, %	Dominating species of shoreline plants	Number of species	PVI, %	Coverage of filamentous and thalloid algae
Prossa	100	10	*Typha angustifolia*	19	41.21	Moderate
Kaiavere	33.6	10	*Schoenoplectus lacustris*	17	3.8	Moderate
Võrtsjärv	18.8	4.6	*Phragmites australis*	21	1.68	Moderate
Suurlaht	100	10	*Phragmites australis*	7	6.81	Very abundant
Uljaste	6.63	1.02	*Phragmites australis*	12	0.99	Moderate
Mustjärv	36.73	6.63	*Zizania aquatica*	9	13.16	Moderate

Table 6. Proportion of the area of water plant zones and dominant species in the emergent plant zone in the studied shallow lakes (EP = emergent plant area, FP = floating-leaved plant area, SP = submerged plant area, TP = total plant area) and epiphyton communities in the studied lakes in 2000. Significance of differences (*p*) between epiphytic communities on different plants (Plant) in each lake and similarity of communities in similar plant species, collected from different lakes (%)

Lake	EP, %	Dominant species	FP & SP, %	TP, %	*p*	Plant	%
Prossa	10	*Typha angustifolia*	90	100	0.004	*Typha latipholia*	20
Kaiavere	10	*Schoenoplectus lacustris*	23.6	33.6	0.8521	No data	
Võrtsjärv	4.6	*Phragmites australis*	14.2	18.8	0.001	*Chara* sp.	48
Suurlaht	10	*Phragmites australis*	90	100	0.0001	*Nuphar lutea*	10
Uljaste	1.02	*Phragmites australis*	5.61	6.63	0.0001	*Phragmites australis*	30
Mustjärv	6.63	*Zizania aquatica*	23.98	36.73	0.008	*Potamogeton lucens*	40

similar. According to the PVI and plant distribution area in L. Prossa submerged macrophytes (mostly *Chara*) grew in very dense mats on the bottom (PVI 41.2%). In L. Suurlaht submerged macrophytes were distributed in a comparable area (*Chara* being dominant again) but they were growing only in thin mats (PVI 6.8%). The epiphyton data gathered in 2000 are given in Table 6.

Fish

The fish community was most abundant in L. Võrtsjärv (Fig. 9), with eleven fish species captured. The abundance and variety of species differed greatly between the littoral and pelagic zones; however, the most abundant and even-spread species was roach followed by perch, bream flat, pike, and bleak. A mean littoral haul of 4 kg appeared to be multifold as compared to other lakes. The

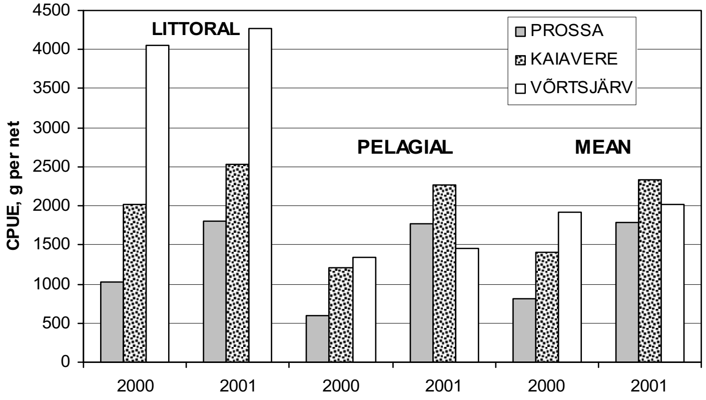

Fig. 9. Catch per unit effort (CPUE) per net in lakes Prossa, Kaiavere, and Võrtsjärv in 2000 and 2001.

pelagic zone with the mean haul of less than 1.5 kg was rich in smelt, bleak, ruff, and pikeperch. The littoral zone of L. Võrtsjärv was extremely rich in fishes of young age-groups.

In L. Kaiavere seven fish species were hauled with roach the most frequent and bleak, bream, and perch at heel. Of valuable fish species pike and pikeperch were abundant. The generic mean biomass of fish exceeded significantly that of the other small lakes. The mean CPUE of L. Kaiavere was 1407 g with 2018 g in the littoral and 1205 g in the pelagic zone. As compared to other lakes, juveniles make up a relatively greater fraction in L. Kaiavere.

Lake Prossa is poorer both in variety and abundance of fish as compared to the other studied lakes in the region. The dominant fish species were roach and perch, whereas pike and crucian carp were less frequent. The mean CPUE slightly exceeded 900 g.

DISCUSSION

The TN/TP mass ratio in L. Kaiavere (20–30) and especially in L. Prossa (34–45) indicates that in these lakes it is phosphorus rather than nitrogen that controls the development of Phy during the summer. Increased resuspension due to the scarcity of submerged macrophytes resulted in generally higher concentrations of total nutrients and suspended solids in L. Kaiavere. The high N/P ratio and the low phosphorus concentration in L. Kaiavere probably hindered N_2fix, as blue-greens with N_2fix ability were abundant already in August 2000, but N_2fix occurred only in September. It is known from the literature (Levine & Schindler, 1999; Smith & Bennett, 1999; Hambright et al., 2001) that nitrogen fixing cyanobacteria prefer a low N/P ratio.

The peak in soluble reactive phosphorus (SRP) in L. Prossa could probably be attributed to a release from redox-sensitive fractions in anoxic conditions often formed on the sediment surface beneath dense *Chara* beds. Still the peak was not very large and as there are limits to very precise determination of SRP, it can also be an artifact of determination.

The abundance of bacteria was higher in plankton-dominated L. Kaiavere than in L. Prossa. In L. Kaiavere the high fluctuation in bacterial abundance and production in spring 2001 was probably related to the development of Phy. Another possible explanation is competition for P. High bacterial production rates in late summer 2001 indicate availability of nutrients. However, the abundance of bacteria was low presumably because of high ciliate pressure. In L. Prossa the development of bacteria seemed to be associated to PP only in spring when macrophytes were not dominant. Differently from L. Kaiavere, the grazing of ciliates in macrophyte-dominated L. Prossa has no limiting effect on bacterial abundance.

In the southern part of L. Võrtsjärv, the influx of the nutrients via the Väike-Emajõgi River is the highest, e.g. in 1996 the TP and TN loading of this river made up 48% and 40% of the total load to the lake, respectively (Bilaletdin et al., 1998). Such a strong nutrient load supported the development of Phy, and the macrophytes could not act as really important competitors for nutrients in the water column. The increased PP and Chl a in the southern area (but also in the central part) seems to be a result of increased nutrient concentrations (PO_4-P in May and Nmin in July). It seems that nutrients do not limit the Phy development in the southern part as their concentrations were never very low there. The sharp decrease in Chl a concentrations in June could be due to zooplankton grazing.

The Phy biomass maximum in L. Võrtsjärv in spring is rather typical of macrophyte-dominated lakes. As the summer biomass values also stayed high and the clearwater period was not detected, we can say that the lake's central part acted like a plankton-dominated lake. High summer values were probably supported by the nutrient influx via the Väike-Emajõgi River. Also the powerful upward flux of nutrients in the lake, caused mainly by resuspension (Nõges et al., 1998), could enhance Phy growth. In the central part of L. Võrtsjärv N_2fix started when the TN/TP mass ratio was 20 (Tõnno & Nõges, 2003), this is much higher than the Redfield mass ratio 7 (Howarth et al., 1988). As the symptoms of N-limitation in L. Võrtsjärv's central part caused by the TN/TP ratio are greater than predicted by the Redfield ratio, we assumed the recycling rate of P to be higher than that of N and consequently the ratio of the recycled N to recycled P was lower than TN/TP.

Similarly to Phy, the high abundance and production of bacteria in the southern part of L. Võrtsjärv were to a large extent supported by the influx of nutrients via the Väike-Emajõgi River. Despite the high PP and Phy biomass, bacteria were not found to rely on Phy as a source of organic carbon as noted over various aquatic systems (e.g. Cole et al., 1988; Ducklow & Carlson, 1992). This decoupling may be a result of a time-lag in the response of bacteria to primary production, because the majority of organic matter fixed by Phy becomes available to bacteria after a crash in Phy biomass due to various biological processes (e.g. grazing). The ciliate grazing pressure on bacteria was low in the southern part compared to the central part of L. Võrtsjärv. Only in August, despite a high production, bacterial abundance remained low in the southern part of the lake, indicating an increased grazing pressure on bacteria.

The highest bacterial production and abundance in the central part of L. Võrtsjärv were achieved in June when the grazing pressure of ciliates was low because of the dominance of herbivorous species. The production of bacteria did not seem to be limited by the availability of nutrients and was related to Phy production. The substantial decrease in bacterial abundance and production in July coincided with a peak in ciliate abundance suggesting that top–down regulation of bacterioplankton development is significant. From previous observations it is known that ciliate grazing can exceed bacterial production in the central part of L. Võrtsjärv (Kisand & Zingel, 2000).

The increased grazing by pelagic zooplankton hiding in macrophytes during daytime (Timms & Moss, 1984; Søndergaard & Moss, 1998), as well as the grazing by macrophyte-associated zooplankton species (Lauridsen & Buenk, 1996), has been often considered among the most important factors controlling Phy biomass in macrophyte-dominated lakes. However, our case study showed that the MZP abundances were even slightly higher in plankton-dominated lakes. Due to that the observed differences in Phy biomass are hard to explain by differences in MZP grazing intensities.

The community of chydorids was most diverse in the littoral zones of macrophyte-dominated lakes. In the pelagial the chydorids were absent or represented only by one species. The mean abundance of chydorids was the highest in the littoral macrophyte habitat. There was no difference between the chydorids' mean abundances in the littoral biotopes without macrophytes and the pelagial. The higher abundance of chydorids in all biotopes in macrophyte-dominated lakes was due to the presence of several well-adapted chydorid species.

The highest abundances of planktonic ciliates were found in the central part of L. Võrtsjärv and in L. Kaiavere, i.e. in the plankton-dominated lakes, but the highest biomasses were found in the macrophyte-dominated ones. Ciliates' biomass was moderate compared with MZP in lakes Kaiavere and Prossa. It was only in L. Võrtsjärv that ciliates formed a significant part of the total zooplankton biomass.

In all studied lakes ciliates had a clear spring peak dominated by larger herbivorous ciliates, followed by a decrease and a second peak later in summer formed mostly by small bacterivores (in the plankton-dominated lakes) or by small bacterivores and larger herbivores (in the macrophyte-dominated lakes). Ciliate collapse at the beginning of summer coincided with the increase in MZP numbers. It is known that MZP prey intensively on ciliates (e.g. Heinbokel & Beers, 1979) and can so affect their numbers. According to Laybourn-Parry (1992), also the competition for food resources may be one of the main aspects controlling the temporal patterns of protozoan occurrence and abundance. It is unlikely that there exists sharp food competition between MZP and small bacterivorous ciliates. The macrophyte-dominated lakes showed generally lower MZP abundances than the plankton-dominated ones – and in the former the larger herbivorous ciliates were not suppressed during summer. So the small bacterivorous ciliates were more important in plankton-dominated lakes – causing higher summer peaks in abundance. This implies that the microbial loop must be considerably stronger in the plankton-dominated lakes. Our experiments showed a quite clear pattern: in the plankton-dominated lakes (L. Kaiavere and L. Võrtsjärv's central part) the ciliates' grazing rate on bacteria is higher than in the macrophyte-dominated ones (L. Prossa and L. Võrtsjärv's southern part). However, in grazing on small algae the highest rates were found in the macrophyte-dominated lakes (Fig. 4). This suggests that the microbial loop is weaker in macrophyte-dominated lakes and grows stronger when the lake enters the turbid state of plankton-dominated lakes. Yet we can see that the role of ciliates is important in both lake types as consumers of bacteria and small algae.

It is worth mentioning that in L. Kaiavere the maximum grazing rate of MZP coincided with the analogous minimum value in ciliates. Also in L. Võrtsjärv there was a negative trend between these two parameters. We can observe the same trend in grazing rates upon small algae. In L. Võrtsjärv both peaks in MZP grazing rates coincided with the sharp drop in the grazing rates of ciliates and in L. Kaiavere the grazing rate of ciliates dropped as the MZP grazing turned more important (Figs 5 and 6).

We found a negative trend between MZP filtering rate and Chl a concentrations in L. Prossa, which implies that zooplankters have an important role in achieving the clear-water phase. However, as the number of measurements was small, all the correlations were statistically not significant.

As the dynamics of nutrients was rather similar in both macrophyte- and plankton-dominated lakes, the different nutrient availability could hardly be the reason for the observed Phy decline in the macrophyte-dominated lakes in summer. In our study lakes the zooplankton had also a rather similar dynamics. The only observed difference was the summer dominance of herbivorous ciliates in the macrophyte lakes and hence also higher grazing rates on Phy. More intensive ciliate grazing can act as one factor causing a decrease in Phy numbers. Besides that the possible allelopathic influence of macrophytes on Phy, which was not checked, remains almost the only explanation for the observed clear-water phase.

ACKNOWLEDGEMENTS

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Ökoloogiliste protsesside võrdlus madalates makrofüüdi- ja planktonijärvedes

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On kirjeldatud ökoloogilisi protsesse kolmes eri tasakaaluseisundis olevas madalas järves: planktoni-, makrofüüdi- ja veel ühes järves, kus esinevad mõlemad seisundid. Uuringud on keskendunud nii abiootilistele faktoritele kui ka toitumisahela erinevatele lülidele. Makrofüüdi- ja planktonijärved erinevad selgelt vee läbipaistvuselt, mis on märgatavalt suurem makrofüüdijärvedes ja mille tingib fütoplanktoni suvine madalseis. Mõlemad järvetüübid on sarnased toitainete ja zooplanktoni dünaamikalt, mis tähendab, et fütoplanktoni madalseisu makrofüüdijärvedes tingib mingi alternatiivne kontrollmehhanism. Ripsloomadest domineerivad makrofüüdijärvedes herbivoorsed vormid. Ripsloomade intensiivsem toitumissurve fütoplanktonile võib olla üheks põhjuseks, miks fütoplanktoni hulk väheneb. Peale selle võib fütoplanktoni hulka vähendada ka suurtaimede allelopaatiline mõju, kuigi seda antud töös pole uuritud. Planktonijärvedes sõltub bakterite arvukus fütoplanktoni produktsioonist. Makrofüüdijärvedes pole sellist seost leitud. Planktonijärvedes on ripsloomade bakteritest toitumise kiirus suurem kui makrofüüdijärvedes. Juhul kui aga toitutakse vetikatest, on pilt vastupidine – suuremad toitumiskiirused on leitud makrofüüdijärvedest. Sellest võib järeldada, et makrofüüdijärvedes on mikroobne ling nõrgem ja tugevneb, kui järv muutub häguseveeliseks planktonijärveks.

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Factors controlling macrophyte distribution in large shallow Lake Võrtsjärv

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Abstract

We investigated the dependence of macrophyte parameters (distribution depth, width of the reed belt, density and length of shoots) on a number of abiotic factors (wind patterns, nutrient loading, slope of the littoral, granulometric sediment composition) in a large, shallow, and eutrophic Lake Võrtsjärv (270 km^2, average depth 2.8 m) in Estonia in 1997. The macrophytes colonized 19% of the lake area, whilst 95% was potentially suitable by depth. The most affected were the floating-leaved plants that colonized the smallest percentage (6%) of areas suitable for them with regard to depth. Factor analysis revealed a strong polarisation of the lake's vegetation both in west–east and north–south direction caused by (1) dominating westerly and south-westerly winds, (2) the shape of the lake narrowing down from north to south, and (3) concentration of bigger inflows at the west and south shores of the lake. The eutrophication process caused the disappearance of several species, on one hand, and the extension of the distribution areas of other species, on the other hand. *Myriophyllum spicatum* L. has become the dominating species among the submerged plants, replacing the earlier dominant, *Potamogeton perfoliatus* L.

Keywords: Macrophyte; Distribution factor; Shallow lake; Historical change in macrophytes composition

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1. Introduction

Larger lakes generally offer a wide range of habitats for submerged and emergent water plants, but in some cases also for floating-leaved plants, due to a broad variation in littoral geomorphology (Schmieder, 1995, 1996), exposure to wind and associated wave turbulence (Spence, 1982; Coops et al., 1996), water level fluctuations (Riis and Hawes, 2003), and gradients in nutrient availability (Chambers and Kalff, 1985). The latter is often due to anthropogenic point sources or river mouths (Best et al., 1984; Graneli, 1985; Rørslett, 1991; Kowalczewski and Ozimek, 1993; Scheffer, 1998). We studied the spatial variability in water plant abundance and potential causal factors in Lake Võrtsjärv, a large lake in Estonia, to assess the relative contribution of different factors within this co-varying complex. We were able to compare our results with studies from the 1910s (Mühlen and Schneider, 1920) and from the 1960s (Mäemets, 1973). In the present paper we address two questions:

1. what are the major factors determining water plant distribution across Lake Võrtsjärv;
2. what are the major changes observed in the macrophyte community of this large lake since the 1910s and can we explain them.

2. Site description

Lake Võrtsjärv is situated in Central-Estonia in a low preglacial basin. It has an elongated shape in the north–south direction narrowing down towards the south. The lake has an area of 270 km^2, length of 34.8 km and the largest width of 14.8 km. The approximate volume of water at mean water level is 750×10^6 m^3 (Jaani, 1973). Despite of the large area, the lake is shallow with a mean depth of 2.8 m and maximum depth of 6 m. The long-term average water level is 33.68 m a.s.l. On average, the water level in the lake fluctuates about 1.4 m per year, the maximum annual fluctuation has reached

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2.2 m and the difference between the highest and lowest water level is 3.2 m (Nõges and Nõges, 1998). The shoreline is 96 km long and rather simple characterised by a shoreline development index of 1.65. Some peninsulas and small till islets are found in the southern part of the lake. The shores are mainly low, swampy in the south and sandy in the north, only the eastern shore is relatively high (Kongo, 1973). The lake is rich in fine-grained sediments (sapropel, silt, sand), which are well sorted according to the wind action (Raukas, 1995). The lake is ice-covered on average for 153 days a year (Haberman et al., 1998). The predominant wind directions in this area are from south, southwest and west. The northern and eastern shore of the lake are influenced most by these winds.

Six larger and a dozen smaller streams drain the 3380-km^2 drainage area of the lake. The outflowing river Emajõgi flows into Lake Peipsi. The retention time of water is on average one year (Jaani, 1990). The catchment is mainly used for agriculture and cattle breeding, 36% of it is under forests. Lake Võrtsjärv has received annually 1300–4400 tonnes (4.81–16.3 $g\,N\,m^{-2}\,year^{-1}$) of total nitrogen and 35–100 tonnes (0.13–0.37 $g\,P\,m^{-2}\,year^{-1}$) of total phosphorus from the catchment (Järvet, 1997). As the catchment of the lake incorporates till areas rich in limestone, the water is rather hard. The sum of major ions is 227–370 $mg\,l^{-1}$ (Nõges, 1992). The water is well aerated and has an average pH of 8.1. The average total nitrogen concentration in Lake Võrtsjärv is 2 $mg\,N\,l^{-1}$ and total phosphorus concentration 0.05 $mg\,P\,l^{-1}$ that characterise the lake as eutrophic to hypertrophic (Haberman et al., 1998).

During the ice-free period, the transparency of water in Lake Võrtsjärv is around 1 m. Being mostly affected by the resuspension of sediments, the transparency in Lake Võrtsjärv is a function of wind and water level. At high water level in spring, light attenuation is mostly caused by humic substances (Nõges, 2000).

3. Material and methods

Data from the whole lake were collected in August 1997 using a combined transect and sampling quadrat method. The vegetation was described in 45 transects, which reached from the water line to the maximum colonisation depth of macrophytes. In the southernmost narrow part of the lake characterised by a higher diversity of macrophyte communities, the transects reached from one shore to the other. The number of transects was a little smaller than suggested by Jensen (1977) for a lake of this size (59), but given the large area of uniform vegetation in the eastern and northern part of the lake, it can be considered adequate. In transects we registered all species met, the dominants, and the depth boundaries of species and ecological groups (helophytes, floating-leaved, submerged plants). A more detailed analysis was made in 112 sampling quadrats of 1 m × 1 m (or 2 m × 2 m in case of sparse vegetation) where, besides analysing the species composition, we measured the shoot density and shoot length of dominant species.

We omitted the sparse stands of submerged plants found in places also in the deeper part of the lake, especially on heaps of stones which locally decrease the water depth. The importance of such stands in the whole lake is so small that leaving them out of the analysis should not have caused a significant error.

For plant-cover analysis, the area covered with macrophytes in Lake Võrtsjärv was divided into nine parts: seven shore reaches, the open water reach in the southern part of the lake and the reach around the islet Tondisaar (Fig. 1) more or less equally covered with sampling quadrats. This division followed the traditional approach of earlier investigators (Mühlen and Schneider, 1920; Mäemets, 1973) and was based on the apparent homogeneity of macrophyte communities within these reaches. In the community analysis the data collected in sampling quadrats in these reaches was summed up. For further comparison the reaches were grouped as follows: the northern part—reach 4; the southern part—reaches 1, 2 and 7; the eastern part—reaches 5 and 6; the western part—reach 3, the open water—reach 8, and the island—reach 9. The following indicators and indices were used.

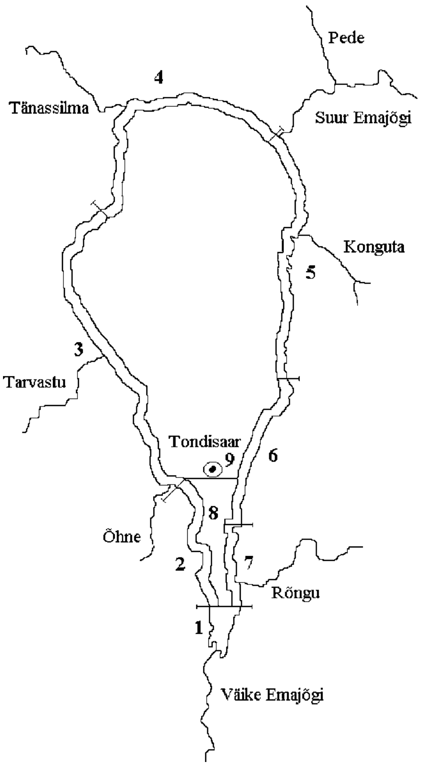

Fig. 1. The location of geobotanical reaches based on earlier studies (Mühlen and Schneider, 1920; Mäemets, 1973) in August 1997 in Lake Võrtsjärv.

Frequency of species occurrence (F)

$$F\,(\%) = \frac{N_a}{N} \times 100 \qquad (1)$$

where N_a is the number of reaches in which species a was found; N is the total number of reaches.

The relative abundance (A)

$$A\,(\%) = \frac{n_s}{n} \times 100 \qquad (2)$$

where n_s is the total shoot density of species s in all quadrats of one reach; n is the total shoot density of all species in all quadrats in the reach.

The average shoot length was measured for the three most common helophyte species in the lake: *Phragmites australis* (Cav.) Trin. ex Steud., *Schoenoplectus lacustris* (L.) Palla and *Typha angustifolia* L.

The width of the helophyte zone (E, m) was measured on aerial photographs of a scale of 1:10,000. Measurements were made at all transects (59) around the lake.

Areas covered by helophytes and floating-leaved plants were delimited by colour and measured. As submerged plants were not visible in aerial photographs, their distribution area was estimated according to the maximum colonisation depth measured on transects. Because of patchiness occurring at the lakeward edge of the submerged macrophyte zone, transects could randomly under- or overestimate the average extent of this zone. We had no reason to suspect a systematic bias in the estimate.

Areas potentially colonisable by macrophytes of different ecological groups were measured on the bathymetric map (scale 1:100,000) based on the measured absolute depth ranges (minimum, maximum) of species in the lake.

In order to find out changes in the vegetation, data on species distribution in 1997 were compared with the species distribution in 1965–1967 described by Mäemets (1973). We compared the lists of species by the above mentioned nine reaches using the original similarity index K:

$$K = \frac{\text{number of common species in two lists}}{\text{number of species in the shorter list}} \qquad (3)$$

This similarity index can obtain values from 0 to 1 similarly to the well-known indexes of Jaccard (1901) and Sørensen (1948).

To characterise the environment, four simple indices were used: the wind exposure index, the sediment index, the nutrient load index and the slope index.

An original wind exposure index W was worked out, which considers the frequency distribution of wind directions and the fetch of a shore. The calculations were made for the eight cardinal points of the compass using the following equation:

$$W = \sum_{i=1}^{8} \frac{S_i T_i}{8} \qquad (4)$$

where S_i is the frequency (%) of wind in time from direction i, T_i is the fetch of wind (km) from the direction i, as length along that direction across the lake surface.

The frequency distribution of wind directions was based on wind data for 1992–1997 from Tõravere Meteorological Station (20 km from the lake). The wind index was calculated for the two ending points and for the middle point of the each shore reach and the arithmetical mean was used in further analysis.

The sediment index was calculated on the basis of the map of granulometric sediment fractions (Raukas, 1995). Nine sediment fractions delimited on the map were given ascending numbers (f_i) from 1 to 9 (the bigger the number the finer the sediment) and

$$G = \sum_{i=1}^{9} \frac{f_i c_i}{100} \qquad (5)$$

the sediment index G for each shore reach was calculated as the average sediment fraction number weighed by the percent cover of each fraction in that shore reach (c_i). A sediment type, which constituted more than 40% of all types in a particular lake reach, as considered to be dominant.

In order to get an estimate of the eutrophication stress, the nutrient loads from rivers (kg ha^{-1} year^{-1}) discharging to each shore reach, were summed up. If a river entered the lake on the border between two delimited shore reaches, its loading was divided between the reaches. As we supposed a major effect of the R. Väike Emajõgi, the main inflow from the south, to the whole southern part of the lake, its load was equally shared between the southern reaches 1, 2, 7, and 8. The riverine nutrient loads were taken from the balance calculated for the years 1988–1991 (Nõges and Järvet, 1998).

The slope index was measured from the 1:100,000 map at the locations of the transects (59) as the distance (L, m) between the 0-m and the 1-m isobaths. So the slope index is the reciprocal of the percental slope.

Factor analysis with Principal Component Extraction method was performed using STATISTICA for Windows 6.0 (2001). As input variables we used macrophyte characteristics, abiotic indices, and also the geographical co-ordinates of the centre points of each analysed reach. For correlation analysis we used nonparametric Spearman rank correlations, which not obligatorily require a normal distribution of data. The significance of differences between mean values of zones was assessed with the help of Tukey tests.

4. Results

4.1. Macrophyte indices

We recorded 32 macrophyte phanerogam species in the lake. The most frequent species in helophyte zone was *P. australis*, occurring in eight reaches out of nine (Table 1). Among floating-leaved and submerged plants *Nuphar lutea* L. and *Myriophyllum spicatum* L. were the most frequent species, the latter occurring in all reaches.

The most numerous species in the helophyte zone was *Butomus umbellatus* L. (Table 1) growing in thick monodominant stands mostly in the northern part of the lake. The average shoot densities of floating-leaved and submerged plants

Table 1
Frequency of occurrence (*F*) and average abundance (*A*), depth range (median), average shoot density, and shoot length (±standard deviation) of the most common macrophyte species in nine reaches (Fig. 1) in Lake Võrtsjärv in August 1997

Species or ecological group	*F* (%)	*A* (%)	Colonisation depth (m)	Shoot density (m^{-2})	Length of shoots (m)
Helophytes					
Rorippa amphibia	33	0.9 ± 0.004	0–0.8(0.4)	3.7 ± 3.2	
Butomus umbellatus	22	34.5 ± 0.4	0–0.8(0)	104.5 ± 54.4	
Schoenoplectus lacustris	56	28.7 ± 0.1	0–1.7(0.6)	74.8 ± 41.9	2.4 ± 0.3
Phragmites australis	89	43.5 ± 0.3	0–1.9(0.8)	33 ± 14.1	2.9 ± 0.4
Typha angustifolia	33	6.0 ± 0.03	0–1.3(0.5)	12.4 ± 3.5	2.9 ± 0.4
Floating-leaved plants					
Nymphaea alba	22	3.6 ± 0.04	0.6–1.7(0.8)	13.4 ± 10.2	
Nuphar lutea	44	21.1 ± 0.1	0.5–1.8(1.2)	25.8 ± 16.4	
Submerged plants					
Myriophyllum spicatum	100	16.3 ± 0.3	1.5–3(1.5)	4.8 ± 3.6	
Potamogeton lucens	22	1.4 ± 0.01	0.6–2.8(1.4)	1.4 ± 0.7	
Potamogeton perfoliatus	44	4.9 ± 0.4	0.4–2.2(0.9)	7.5 ± 4.6	

were generally low except for *Ceratophyllum demersum* L., which reached the greatest density among all macrophyte species (168 shoots m^{-2}) and carpeted large bottom areas in southern part of the lake. Among the three helophyte species of which shoots were measured, *P. australis* and *T. angustifolia* had an equal mean length of 2.9 m while the shoots of *S. lacustris* were about half a meter shorter (Table 1).

During August 1997, the water level in Lake Võrtsjärv was about 40 cm below the long-term summer (VI–VIII) average. Hence, the helophyte zone was partly exposed, which is marked as 0 m in Table 1. In this zone *P. australis* reached the widest range of colonisation depth (1.9 m). In the zone of floating-leaved plants, the colonisation range of the two common species, *Nymphaea alba* and *N. lutea*, was, accordingly, 1.1 and 1.3 m. Submerged plants colonised the deepest areas: *Potamogeton perfoliatus* down to 2.2 m, *Potamogeton lucens* to 2.8 m, and *M. spicatum* to 3 m. The relative abundance of the two most common species, *P. australis* and *M. spicatum*, tended to increase with increasing depth (Fig. 2).

The average width of the helophyte zone in the lake was 95 m, varying from 0 to 480 m. It was the narrowest along the southern and eastern shores, and the widest but most variable along the northern shore of the lake. In this part both the mean width of the reed belt and its variability were significantly higher (Tukey test, $p < 0.05$) than in other areas.

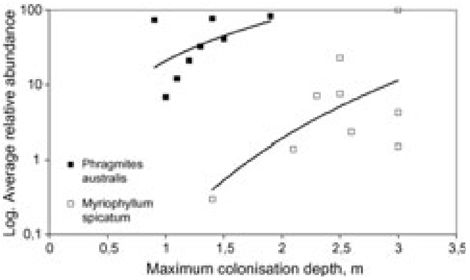

Fig. 2. Maximum colonisation depth and average relative abundance (*A*) of two most common macrophyte species in shore reaches (Fig. 1) in Lake Võrtsjärv in August 1997.

According to the bathymetry of the lake and the ranges of colonisation depth, macrophytes could potentially colonize 95% of lake area, but in reality they colonized only 19% of it. The most suppressed were the floating-leaved plants, which colonized only 6% of areas within their suitable depth range. Helophytes were able to colonize 19% and submerged plants 26% covered of the suitable depth range.

4.2. Ecological factors

According to the wind index, the northern and eastern shores were most wind exposed while the most sheltered reaches were located in the south (Table 2). The northern shore was characterised by the coarsest sediments ($G = 1.9$) while the shores as well as the open water reach in the southernmost end of the lake were dominated by fine sapropel sediments. The biggest nutrient loading index was found for reaches 1, 2, 7 and 8 (Table 2; Fig. 1) located in the southern part of the lake. In reaches 6 and 9 the loading index was zero because of the absence of significant inflows in these shore reaches. The littoral area mostly had a very gentle slope: the average width of the belt until 1-m depth was 250 m, varying from 50 to 700 m. The littoral of the northern shore was significantly broader than in other parts of the lake (Tukey test, $p < 0.05$). Generally, the width of the helophytes zone tended to increase in reaches with a gentler slope (Fig. 3) and only on five transects the emergent vegetation extended further from the 1-m isobath line. The helophytes were most suppressed in reaches 1, 5 and 9 where gaps in the belt made up more than 40% of the length of the shoreline (Table 2).

4.3. Results of factor analyses

In the first factor analysis carried out among abiotic variables, the first two factors described 84% of the total variability (Table 3). In factor F1A higher factor loadings were

Table 2
The sediment index (*G*), the widespread sediment types (A—sapropel, B—sand, C—gravelly sand, D—sandy silt, F—silt), the loading indices of nitrogen and phosphorus (K_N and K_P) and wind index (*W*) for the delimited reaches in Lake Võrtsjärv

Reach No.	% of gaps in the helophyte belt	*G*	Dominating sediment type	*W*	K_N (kg ha^{-1} year^{-1})	K_P (kg ha^{-1} year^{-1})
1	42	7	A	18.8	61.3	1.3
2	38	3	A, B	16.5	61.3	1.3
3	3	4.3	F, D	45.9	20.9	0.2
4	23	1.9	B, D	94.3	19.9	0.6
5	46	3.1	F, D	99	6.5	0.2
6	27	4.4	F, D	55.5	0	0
7	20	2.5	A, B	25.1	61.3	1.3
8	–	7	A	34.7	61.3	1.3
9	79	2.5	B, D	53.6	0	0

Numbering of shore reaches according to Fig. 1.

accounted for the geographic latitude, the wind and the loading indices. With F2A associated the geographic longitude and the sediment index.

Correlation analysis between abiotic and plant variables (Table 4) showed a decrease of the species richness from north to south while the relative abundance of the two dominants *M. spicatum* and *P. australis* increased. The latter showed strong negative correlations with nutrients. The shoot density of *M. spicatum* increased with the wind exposure.

In the second factor analyses carried out among macrophyte variables and geographic co-ordinates, the two separated factors described 63% of the total variability (Table 5). With F1B associated both geographic latitude and longitude, the number of species, relative abundances of both dominant species, *M. spicatum* and *P. australis*, and the maximum colonization depth of the latter. In F2B higher factor loadings were accounted for by the shoot densities of both dominants.

4.4. Historical changes in the vegetation

Comparing the list of aquatic macrophytes given by Mühlen and Schneider (1920) with our data from 1997, we could conclude upon the definite disappearance of six species of submerged macrophytes, which colonized mainly the sheltered narrow southern end of the lake (2 unidentified species of *Chara*, *Ranunculus trichophyllus* Chaix, *Elodea canadensis* Michx., *Potamogeton pectinatus* L., *P. pusillus* L.). One species, *C. demersum* L., not mentioned by the first investigators, occurred in 1997 often in masses carpeting the bottom. If this species would have occurred with a similar abundance in the 1910s, it would probably not have been overlooked by the investigators. The calculated similarity index for the two lists equalled 0.77.

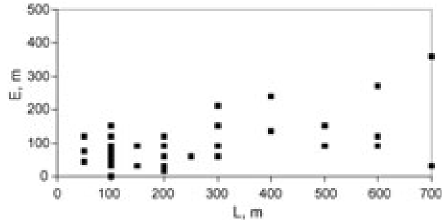

Fig. 3. The width of the helophyte zone (*E*) and the slope index of the littoral zone (*L*) (Spearman $R = 0.39$, $p = 0.003$) in transects in Lake Võrtsjärv in August 1997.

The comparison of our species list with that from 1967 yielded an average similarity of 0.77 (±0.13) for the whole lake. We found the biggest changes for the open water reach of the lake ($K = 0.50$) while the leeward western shore had the highest similarity ($K = 0.92$). In the rest of the lake the extent of changes was rather uniform. *E. canadensis* and *P. pectinatus* mentioned by Mühlen and Schneider (1920) were still found in 1967 but not any more by us. Other changes included the disappearance of *Stratiotes aloides* L. and *Potamogeton crispus* L. Two species, not mentioned by earlier investigators were identified in 1997: *Myriophyllum verticillatum* L. and *Rumex maritimus* L. We observed also a remarkable extension of the distribution areas of *C. demersum*, *Rorippa amphibia* (L.) Bess., *Nuphar luteum* and *M. spicatum*. The latter has become the dominant species among the submerged plants, replacing the earlier dominant, *P. perfoliatus* L. and is now considered a nuisance in large areas south of the islet Tondisaar, tending to overgrow the whole open water area.

5. Discussion

The results of the factor analysis of abiotic variables (Table 3) revealed a strong polarisation of the environmental conditions in the lake. Since geographic co-ordinates have high loadings on the principal components, we can consider F1A to

Table 3
Factor loadings (marked loadings are >0.70) of abiotic variables in Lake Võrtsjärv and the percent of total variance explained

Characteristic	F1A	F2A
Latitude	**−0.82**	+0.02
Longitude	−0.34	**−0.85**
Sediment index	+0.12	**+0.93**
Wind index	**−0.91**	−0.06
N loading index	**+0.87**	+0.42
P loading index	**+0.86**	+0.38
Percent of total variance explained	52	32

Table 4
Spearman rank order correlations for environmental (G—sediment index, W—wind index, K_N—nitrogen loading index, K_P—phosphorus loading index) and macrophyte variables in Lake Võrtsjärv, bold marked correlations are significant at $p < 0.05$

Characteristic	Latitude	Longitude	G	W	K_N	K_P
Number of species	**−0.85**	−0.15	+0.16	−0.33	+0.37	+0.32
Shoot density of *P. australis*	+0.45	+0.07	−0.09	+0.43	−0.36	−0.44
Maximum distribution depth of *P. asutralis*	+0.54	+0.31	−0.33	+0.33	−0.54	−0.49
Abundance of *P. australis*	**+0.97**	+0.59	−0.26	+0.69	**−0.97**	**−0.94**
Shoot density of *M. spicatum*	+0.57	−0.06	−0.07	**+0.82**	−0.44	−0.40
Maximum distribution depth of *M. spicatum*	+0.17	+0.11	−0.13	−0.40	+0.28	+0.30
Abundance of *M. spicatum*	**+0.85**	+0.20	−0.22	+0.35	−0.37	−0.31

Table 5
Factor loadings (marked loadings are >0.70) of the geographic longitude and latitude and macrophyte variables in Lake Võrtsjärv and percent of total variance explained

Characteristic	F1B	F2B
Latitude	**0.89**	0.32
Longitude	**0.81**	0.08
Number of species	**−0.78**	−0.49
Shoot density of *P. australis*	0.26	**0.94**
Maximum distribution depth of *P. asutralis*	**0.72**	−0.19
Abundance of *P. australis*	**0.76**	0.48
Shoot density of *M. spicatum*	0.08	**0.92**
Maximum distribution depth of *M. spicatum*	0.41	0.31
Abundance of *M. spicatum*	**0.86**	−0.04
Percent of total variance explained	46	27

describe a gradient of variables in north–south direction and F2A in east–west direction. Wind exposure decreased from north to south and the loading indexes increased. Our sediment index had the highest loading with longitude showing an increasing sediment grain size from west to east.

The second factor analysis of the macrophyte indices together with the geographic co-ordinates (Table 5) yielded one factor (F1B), which included the influence of both geographic co-ordinates and could be considered as a compound spatial gradient while shoot densities of the two dominant species were the main determinants of the other axis (F2B). The spatial gradient was important for the number of species, which decreased in south–north and west–east directions. Also the maximum colonisation depth of *P. australis* and the relative abundances of *P. australis* and *M. spicatum* increased in same direction.

Rank correlation among environmental and macrophyte variables supported the suggested spatial gradients (Table 4). The number of species decreased from south to north and only a few species were able to tolerate the exposed conditions at the northern shore. This decrease in the number of species caused the increase in the relative abundance of the most tolerant species, *M. spicatum* and *P. australis* in the northern part of the lake. The negative correlation between loading indexes and relative abundance of *P. australis* was a reflection of the same phenomenon: the shallow sheltered southern end of the lake, which receives the major part of the nutrient loading, still appears a suitable environment for a larger number of species from all three ecological groups.

There are three main reasons that cause the observed polarised conditions in Lake Võrtsjärv.

5.1. Main wind directions

Westerly and south-westerly winds predominating in the area affect mostly the northern and eastern shores. The main winds determine the sediment composition and areas of mechanical stress for macrophytes, especially among submerged plants (Agami and Waisel, 1986; Barko and Smart, 1986; Barko et al., 1991; Schmieder, 1995; Sand-Jensen, 1998). The wind fetch has a similar influence on macrophyte distribution like the water depth. The length of the wind fetch, from which waves start to affect macrophytes, is approximately 500–800 m. (Rea et al., 1998). In case of Lake Võrtsjärv the fetch for dominating southerly and westerly winds exceeds this value by an order of magnitude. The strong wind stress at northern and eastern shores is clearly expressed in the macrophyte parameters, which differ significantly from those in the sheltered parts (south and west part) of the lake.

5.2. The irregular distribution of inflows

The larger inflows, Väike Emajõgi, Rõngu and Õhne, enter the lake from the south and from the west causing an uneven availability of nutrients in different parts of the lake.

5.3. The shape of lake basin

Lake Võrtsjärv has an elongated shape in the north–south direction with the width narrowing down towards south. The morphology of the lake coupled with it's considerable size and prevailing wind directions generated a distinct contrast in sheltered south western and exposed north eastern shores. The narrower and more heavily affected southern section formed a sheltered basin. Together this explained species richness, abundance and depth penetration of the predominant emergent and subemerged species.

Besides the factors with a clearly polarised character, water transparency and water level fluctuation have a more general effect on the distribution of aquatic macrophytes. Large fluctuations of the water level in Lake Võrtsjärv together with eutrophication have decreased the species diversity in places to monodominant communities. This concerns especially the submerged plants, because of their higher sensitivity to physical and chemical conditions of water compared to other ecological groups (van den Brink et al., 1991). The low transparency of water in Lake Võrtsjärv is also an important parameter limiting the depth distribution of macrophytes. According to Nõges (2000) the dysphotic bottom area unsuitable for macrophyte growth due to bad light conditions, ranges from 30 to 90% of the total lake area depending on seasonal and inter-annual changes in water level and water transparency. The attenuation of light causes the disappearance of macrophytes from deeper parts of the lake and assembling in shallow parts, which in turn causes a more intense interspecific competition (Schmieder, 1996). The comparison of the species composition in 1997 with that in the 1910s and 1960s demonstrates that most of the observed changes have taken place during the last period—*Myriophyllum* sp. replaced *Potamogeton* sp. and *Ceratophyllum* sp. became abundant in the sothern section, when the eutrophication pressure to the lake had its peak (Nõges and Järvalt, 2004).

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VI

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SEASONAL AND VERTICAL CHANGES IN THE SURFACE AREA/BIOMASS RATIO OF POTAMOGETON LUCENC L. IN A CLEAR AND TURBID SHALLOW LAKE

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Seasonal and Vertical Changes in the Surface Area/Biomass Ratio of *Potamogeton lucens* L. in a Clear and a Turbid Shallow Lake

TÕNU FELDMANN[1] AND P. NÕGES[1,2]

ABSTRACT

To determine the influence of different growth conditions on the architecture of *Potamogeton lucens* L., we measured several morphological parameters of the plants from May to September 2001 in a clear macrophyte-dominated lake and a turbid phytoplankton-dominated lake in Central Estonia. The main difference between the lakes was the higher summer water transparency in the macrophyte-dominated lake. All size related parameters of *P. lucens* tended to be larger in the macrophyte-dominated lake, but only the total above-ground plant surface area and the surface area of leaves differed significantly ($p < 0.05$) between lakes. The relationship between surface area (A, in cm^2) and dry weight (DW, in g) for the measured 25-cm sections of above-ground parts of the plants could be described as:

$$A = 312.9 \pm 9.4\ DW + 26.5 \pm 6.8\ (\pm \text{ standard error})$$
$$(R^2 = 0.649;\ n = 607;\ p < 0.001)$$

Better light conditions in summer and shorter wind fetch in the macrophyte-dominated lake were likely factors stimulating further ramification on the plants in August and a more uniform vertical distribution of plant surfaces in this lake compared to the plankton-dominated lake.

Key words: macrophytes, macrophyte-dominated lake, plankton-dominated lake, shallow lake, surface area/dry weight ratio.

INTRODUCTION

Rich stands of submerged aquatic macrophytes carpeting the bottom of shallow lakes contribute to water clarity by suppressing sediment resuspension (Barko and James 1998), competing with phytoplankton for light and nutrients, and providing a refuge for zooplankton against planktivorous fish (Jeppesen et al. 1999). However, dense stands of aquatic vegetation can create a nuisance for boating and swimming and obstruct water flow (Nes et al. 2002). Not only the abundance but also the growth form of macrophytes is important in this respect. Studies on the architecture of terrestrial plants show that plant species have different growth strategies (Halle et al. 1978, Barthelemy et al. 1989). Further, plants of the same species living under different light and trophic conditions in terrestrial (Kull 1995, Möller and Cronka 2001) and aquatic systems (Gerber et al. 1994) can exhibit important morphological differences. Knowledge about the distribution of surface area and biomass of macrophytes is important for understanding the ecophysiological role of aquatic plants in lake processes (Gerber et al. 1994). The vertical distribution of leaf surfaces in the water column and the surface area to biomass ratio characterize light adaptation and can be used to assess the growth conditions of plants. The surface area of plants is also often used to describe the quantitative relations between submerged macrophytes and epiphytic organisms (Cattaneo and Carigan 1983, Galanti and Romo 1997, Kelly and Hawes 2005). In shallow lakes rich in submerged macrophytes, epiphyton becomes an important component of the primary productivity and a major regulator of nutrient fluxes (Jorgensen and Loffler 1990, Wetzel 1990). Detailed surface area/DW relationships have been published only for a small number of aquatic plants (Sher-Kaul et al. 1995, Armstrong et al. 2003).

Seasonal variation of biomass and growth rates of submerged plants in shallow waters are often related to light conditions (Sand-Jensen and Madsen 1991, Hawes et al. 1999, Gevaert et al. 2002). Depending on the nutrient status, eutrophic shallow lakes can reach two alternative stable states: a vegetated state with clear water and a turbid state dominated by phytoplankton (Scheffer et al. 1993, Scheffer 1998). Although caused by differences in nutrient availability, the switching of aquatic systems between macrophyte- and phytoplankton-dominated states is triggered by light availability (Sheffer et al. 1993, Schwartz and Hawes 1997).

We hypothesized that the differences in light conditions experienced by plants in clear and turbid lakes create substantial differences in their growth form. For the present study we selected the shining pondweed (*Potamogeton lucens* L.), one of the few species we found in two lakes of different types. Our study had two aims:

(1) to describe the differences in plant architecture in lakes of different light conditions (clear macrophyte-dominated vs. turbid plankton-dominated); and (2) to monitor the changes occurring during seasonal growth.

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Table 1. Morphological, hydrological, and chemical characteristics of studied lakes from April to October 2001 (according Nõges et al. 2003).

Characteristic	L. Prossa	L. Kaiavere
Area, km^2	0.33	2.51
Mean (max.) depth, m	2.2 (4.2)	2.8 (5.0)
Water retention time, y	0.56	0.33
PVI of submerged plants, %	40	6
Secchi depth, m	2.5	1.2
pH	8.4	8.6
HCO_3, mmol/l	3.6	3.6
Total P, mg L^{-1}	0.02	0.05
Total N, mg L^{-1}	1.0	1.6

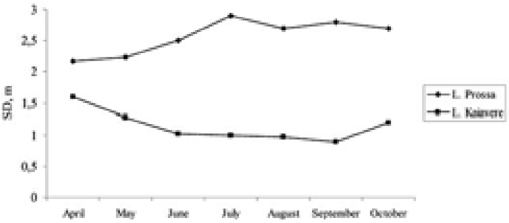

Figure 1. Seasonal dynamics of the Secchi depth in studied a clear (L. Prossa) and a turbid (L. Kaiavere) lake (according Nõges et al. 2003).

SITE DESCRIPTION

The two eutrophic lakes, Prossa and Kaiavere, situated in Central Estonia (Table 1), were selected for our study because of the contrasting light conditions (Figure 1). Smaller Lake Prossa is dominated by submerged macrophytes; the percent volume infested with plants (PVI; Canfield et al. 1984) is 40%. Throughout the year the bottom of the lake is covered with a thick mat of charophytes: *Chara tomentosa* in shallow parts and *Nitellopsis obtusa* in deeper parts. In 2001, after the vernal phytoplankton peak, the water remained clear in L. Prossa during the summer. Much larger Lake Kaiavere, located about 10 km from L. Prossa, is a plankton-dominated lake with a PVI of only 6%, composed mainly of *Potamogeton* spp. In L. Kaiavere the water remained turbid during the whole ice-free period (Nõges et al. 2003). Shining pondweed (*Potamogeton lucens* L.), one of the most frequent plants in L. Kaiavere was present also in L. Prossa.

The relief in this area was formed by the continental ice sheet in the last glaciation and is dominated by elongated moraine drumlins and calcareous eutrophic shallow lakes located between them. The lakes are ice-covered usually from mid-November until the end of April. Most of the catchment area of the lakes is cultivated.

MATERIAL AND METHODS

Samples of *P. lucens* were collected from May to September 2001. At each sampling occasion we collected five sample plants from areas of visually similar plant density (individual shoots cut at the sediment surface), mostly within a depth range of 1.5 to 2.5 m. The plant stands were rather sparse to exclude the effect of density-dependent growth. In the period of fast plant growth in May, samples were collected once a week (only in L. Prossa; no plants were in L. Kaiavere), in June fortnightly, and once a month in July through September. To describe seasonal changes in plant architecture, the shoots were split into 25-cm sections starting from the top. Each plant section was laid out wet on a glass sheet to avoid leaf folding and overlap of plant parts and scanned (O'Neal et al. 2002) in color mode with a resolution of 300 dpi (Epson Perfection 2480 Flatbed Scanner). For area measurements the images were converted to monochrome black-and-white bitmaps and analysed using the program Pindala v.1.0, Indrek Kalamees© 1994. The total area of leaves and stipules was calculated by doubling the measured projection area. The area of stems was calculated as area of cylinder from its projection (Sher-Kaul et al. 1995). After scanning, all plant sections were dried (105 C for 24 h) and weighed for DW using a mechanical torsion prescription balance. To character-

Table 2. Measured characteristics in *Potamogeton lucens* L. in studied lakes from June to August 2001. A = above-ground surface area; DW = dry weight; CV = coefficient of variation (standard deviation/average).

	Macrophyte-lake (L. Prossa)			Plankton-lake (L. Kaiavere)		
Characteristic	Median (Average)	Quartiles (Abs. range)	CV	Median (Average)	Quartiles (Abs. range)	CV
Number of plants	30			30		
Height, cm	190 (206)	143-268 (71-343)	0.38	171 (166)	130-194 (76-270)	0.28
DW, g	3.9 (4.4)	1.9-4.6 (1.4-11.3)	0.57	2.5 (3.6)	2-4.8 (0.8-11.9)	0.76
A, cm^2	1464 (1582)	927-1995 (639-3450)	0.47	974 (1227)	628-1902 (311-3375)	0.69
Leaves/stems Area ratio	4.35 (3.57)	2.85-5.26 (1.41-8.33)	0.52	3.13 (2.78)	2.5-5.0 (0.93 6.67)	0.62
Stems % of A	18 (20)	15-25 (11-40)	0.36	23 (24)	16-27 (12 49)	0.40
Leaves % of A	78 (75)	72-81 (43-87)	0.12	72 (72)	67-80 (46 84)	0.14
Stipules % of A	4 (5)	2-5 (1-33)	1.15	4 (5)	3-6 (1 9)	0.47
A/DW of whole plants, cm^2 g^1	371 (385)	333-428 (258-602)	0.22	337 (352)	286-416 (204-540)	0.25

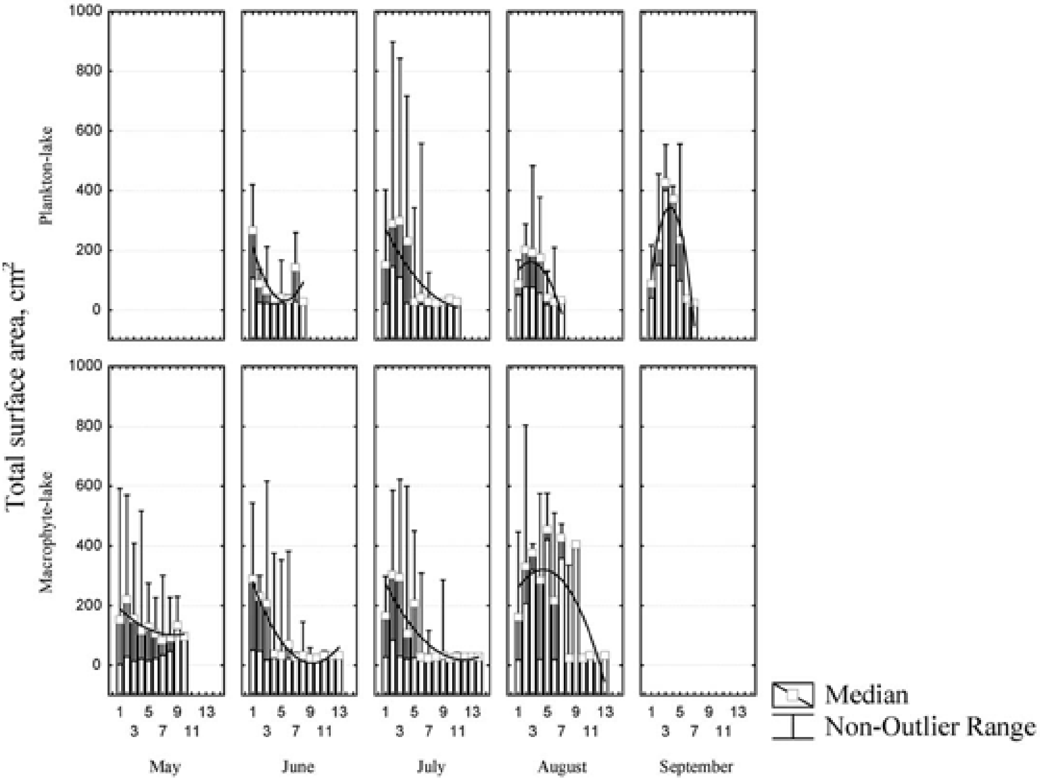

Figure 2. The seasonal dynamics of the vertical distribution of plant surface area in the studied lakes. In each subfigure, column 1 corresponds to the top-most 25-cm section of plants, and the sections are numbered in ascending order downward on the plants. The polynomial fit was added to median values to better visualize the distribution type.

ize plant growth conditions, water temperature, transparency, pH, conductivity, alkalinity, concentration of total phosphorus, total nitrogen, and oxygen were measured in both lakes. Mann-Whitney U-test (Statistica for Windows 7.0) was used to study the differences between sample groups. For comparability purposes we used the variation coefficient (standard deviation/average) to describe the variability of different plant parameters.

RESULTS

At the beginning of sampling in May the average height of *P. lucens* in L. Prossa was already about 1 m. The plants reached their full height (about 2 m) by July. The average total area partitioning among leaves, stems, and stipules was close to 75:20:5%, respectively. Only two plant parameters, the total surface area of shoots and the surface area of leaves, differed significantly ($p < 0.05$) between lakes, with the area of shoots and surface area of leaves being larger in the clear macrophyte-dominated lake (Table 2). In addition, all other size-related parameters of the plants (total height, DW, area/DW ratio, stem and stipule area, leaf percentage of the total area, and leaf/stem area ratio) tended to be larger in the macrophyte-dominated lake; however, these differences remained insignificant because of large variability of the individual plants. The variation coefficient for most absolute size parameters ranged from 0.3 to 0.8 in both lakes but was smaller for relative parameters like the ash content (0.09), the percentage of leaf area (0.12-0.14), and the surface area/DW ratio (0.22-0.25). The latter did not differ between the lakes, and thus the average relationship calculated on the basis of all measured 25-cm sections of plants could be described as:

$$A = 312.9 \pm 9.4\ \mathrm{DW} + 26.5 \pm 6.8\ (\pm \text{ standard error})$$
$$(R^2 = 0.649;\ n = 607;\ p < 0.001)$$

In the beginning of the growing season, in May and June, the maximum surface area of plants was located in the topmost

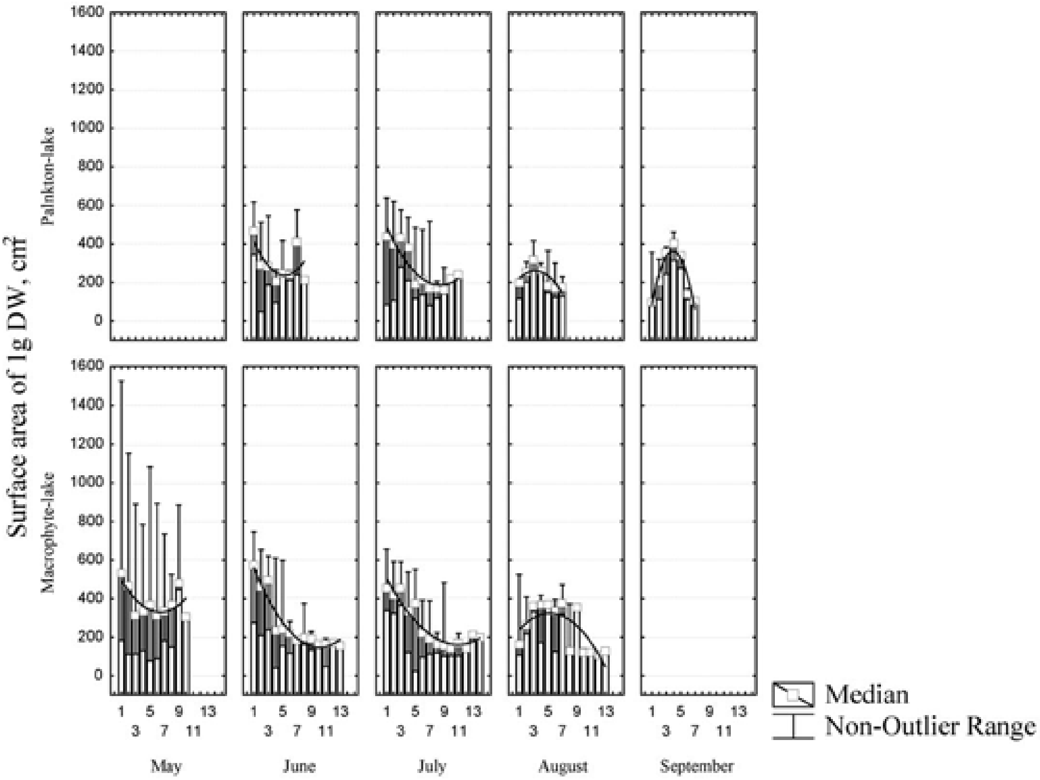

Figure 3. The seasonal dynamics of the vertical distribution of plant surface area/dry weight ratio in the studied lakes. Other explanations as in Figure 1.

sections but shifted in the course of plant growth to lower sections located 0.25 to 0.75 m from the top (Figure 2). In August, a new branching of the plants in the macrophyte-dominated lake created an even more uniform profile of the plant surfaces within the depth range of 0.25 to 2 m. The same pattern also characterized the seasonal changes of the area/DW ratio in both lakes (Figure 3).

DISCUSSION

The published values describing the surface area/DW relationships in aquatic macrophytes (Table 3) vary within one order of magnitude, from around 100 $cm^2 g DW^{-1}$ for simple and thick stems of the emergent *Schoenoplectus lacustris* (L.) Palla (Tessier et al. 2004), *Potamogeton zosteriformis* Fern., and *P. pusillus* L. (Armstrong et al. 2003) to more than 1200 $cm^2 g DW^{-1}$ for *Elodea canadensis* Michx., *Myriophyllum spicatum* L., *Nitellopsis obtusa* (Desv.) J.Gr. (Sher-Kaul et al. 1995), and *Utricularia vulgaris* L. (Armstrong et al. 2003). This variability has been attributed mainly to differences in morphology and thickness of plant stems (Sher-Kaul et al. 1995, Armstrong et al. 2003, Tessier et al. 2004). Armstrong et al. (2003), who made multiple comparisons of the relationship between surface area and biomass of six aquatic plants, found species-specific differences in 14 of 15 cases. Plants with dissected morphology do not necessarily offer the largest surface area per unit biomass (Sher-Kaul et al. 1995), although it has been argued in some studies (Cheruvelil et al. 2001, Gosselain et al. 2005). Armstrong et al. (2003) did not find general groupings of the surface-to-weight relationships based on leaf morphology.

Contrary to our expectations, we did not find substantial differences in the area to biomass ratio of *P. lucens* between the clear and the turbid lake. One possible reason is that light conditions in spring during the fast growth phase of the plants did not differ much (Figure 1), and the plants had already reached nearly their full length by the time one of the lakes cleared. Based on research that measured sur-

TABLE 3. PUBLISHED VALUES DESCRIBING THE ABOVE-GROUND SURFACE AREA TO DRY WEIGHT RELATIONSHIPS IN SOME AQUATIC MACROPHYTES. SD = SECCHI DEPTH; E_{PAR} = EXTINCTION OF THE PHOTOSYNTHETICALLY ACTIVE RADIATION.

Species	A/DW ratio, cm^2 g^{-1} or slope of linear regression (*)	Light conditions	Remarks	Reference
Ceratophyllum demersum L.	230*-427*	E_{PAR} 0.7-1.6 m^{-1}	Averages for different lakes	Armstrong et al. 2003
Elodea canadensis Michx.	1255	Not given	L. Geneva	Sher-Kaul et al. 1995
Myriophyllum exalbescens Fern.	522*	E_{PAR} 0.7-1.6 m^{-1}	Boreal Plain lakes, Canada	Armstrong et al. 2003
M. spicatum L.	1205	Not given	L. Geneva	Sher-Kaul et al. 1995
Nitellopsis obtusa (Desv.) J.Gr.	1205	Not given	L. Geneva	Sher-Kaul et al. 1995
Potamogeton lucens L.	348 (204-602) 313*	SD 1.2-2.5 m	Eutrophic lakes, Estonia	Present study
P. lucens L.	371 (258-602) 313*	SD 2.5 m	L. Prossa	Present study
P. lucens L.	337 (204-540) 313*	SD 1.2 m	L. Kaiavere	Present study
P. lucens L.	653	Not given	L. Geneva	Sher-Kaul et al. 1995
P. pectinatus L.	500	Not given	L. Geneva	Sher-Kaul et al. 1995
P. perfoliatus L.	762	Not given	L. Geneva	Sher-Kaul et al. 1995
P. pusillus L.	124*	E_{PAR} 0.7-1.6 m^{-1}	Boreal Plain lakes, Canada	Armstrong et al. 2003
P. richardsonii (Benn.) Rydb.	766*	E_{PAR} 0.7-1.6 m^{-1}	Boreal Plain lakes, Canada	Armstrong et al. 2003
P. zosteriformis Fern.	108*	E_{PAR} 0.7-1.6 m^{-1}	Boreal Plain lakes, Canada	Armstrong et al. 2003
Schoenoplectus lacustris (L.) Palla	~70	E_{PAR} 0.050-0.064 m^{-1**}	Lago di Candia, Italy.	Tessier et al. 2004
Trapa natans L.	145 (83-238)	Not given	Leaf rosettes (fruits excluded)	Galanti and Romo, 1997
Utricularia vulgaris L.	1779*	E_{PAR} 0.7-1.6 m^{-1}	Boreal Plain lakes, Canada	Armstrong et al. 2003

**—light extinction measured within *S. lacustris* stand.

face area/DW ratio of one species in several lakes, however, the lake specific differences have been small. A study carried out in Boreal Plain lakes in Canada found the relationship between surface area and biomass for three of the four species found in more than one lake was not detectably different among lakes, despite the wide range in nutrient concentration and light extinction coefficient (Armstrong et al. 2003). We also did not find any significant differences in weight specific surface areas between our lakes, despite rather different light conditions in the water column in summer. Considerable variability occurred in both lakes between individual plants, however, as well as in the seasonal scale. In addition to methodical differences in plant surface area measurement, the nearly two times smaller area/DW ratio we found for *P. lucens* in Estonian lakes compared to that measured in L. Geneva (Sher-Kaul et al. 1995) can possibly be attributed to major latitudinal differences in light climate and differences in trophic state and size-related hydrodynamics of the lakes.

The localization of the plant surface area maximum in the top segment of plants during their length growth is related to photomorphogenesis and enables the best light harvesting given the strong attenuation by phytoplankton in spring. After the top of a plant reaches saturating light levels near the water surface, the surface area is maximized in optimum light conditions for photosynthesis. A similar depth distribution of plant biomass as observed by us was also described for *Potamogeton pectinatus* in canals in the Amsterdam Waterworks where the maximum biomass of plants of all length classes was concentrated in the upper 0.2 to 0.5 m of the water column (Best and Boyd 2003). In macrophyte-dominated L. Prossa, the improvement of light conditions in summer possibly stimulated further ramification on plants and the formation of a more uniform vertical distribution of plant surfaces. Another possible explanation for the lower ramification on plants in the plankton-dominated L. Kaiavere, where all size parameters of *P. lucens* tended to be smaller, is the stronger hydrodynamic pressure in this lake because of a longer wind fetch. Numerous studies have shown the importance of fetch on the distribution of aquatic macrophytes (Rea et al. 1998). Idestam-Almquist and Kautsky (1995) show in their study that plants growing in strong wave action area have a different morphology compared to plants growing in a sheltered area.

In our study, the above-ground surface area/biomass ratio of *Potamogeton lucens* L. did not differ significantly between the plankton-dominated and macrophyte-dominated lakes. In contrast, the total surface area and leaf surface area were significantly higher in the macrophyte-dominated compared to the plankton-dominated lake. In the beginning of the growing season the maximum above-ground surface area of plants was located in the topmost sections but shifted in the course of plant growth to lower sections located at 0.25 to 0.75 m from the top.

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VII

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PRIMARY PRODUCTION OF AQUATIC MACROPHYTES AND THEIR EPIPHYTES IN TWO SHALLOW LAKES (PEIPSI AND VÕRTSJÄRV)IN ESTONIA
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Primary production of aquatic macrophytes and their epiphytes in two shallow lakes (Peipsi and Võrtsjärv) in Estonia

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Abstract In shallow lakes with large littoral zones, epiphytes and submerged macrophytes can make an important contribution to the total annual primary production. We investigated the primary production (PP) of phytoplankton, submerged macrophytes, and their epiphytes, from June to August 2005, in two large shallow lakes. The production of pelagic and littoral phytoplankton and of the dominant submerged macrophytes in the littoral zone (*Potamogeton perfoliatus* in Lake Peipsi and *P. perfoliatus* and *Myriopyllum spicatum* in Lake Võrtsjärv) and of their epiphytes was measured using a modified ^{14}C method. The total PP of the submerged macrophyte area was similar in both lakes: 12.4 g C m^{-2} day^{-1} in Peipsi and 12.0 g C m^{-2} day^{-1} in Võrtsjärv. In Peipsi, 84.2% of this production was accounted for by macrophytes, while the shares of phytoplankton and epiphytes were low (15.6 and 0.16%, respectively). In Võrtsjärv, macrophytes contributed 58%, phytoplankton 41.9% and epiphytes 0.1% of the PP in the submerged macrophyte area. Epiphyte production in both lakes was very low in comparison with that of phytoplankton and macrophytes: 0.01, 5.04, and 6.97 g C m^{-2} day^{-1}, respectively, in Võrtsjärv, and 0.02, 1.93, and 10.5 g C m^{-2} day^{-1}, respectively, in Peipsi. The PP of the littoral area contributed 10% of the total summer PP of Lake Peipsi sensu stricto and 35.5% of the total summer PP of Lake Võrtsjärv.

Keywords Primary production · Epiphytes · Submerged macrophytes · Large shallow lake

Introduction

Littoral zones of aquatic ecosystems are among the most productive communities on earth (Goldsborough et al. 2005). In a shallow lake with a large biomass of submerged macrophytes and epiphytes, the littoral zone may be an important contributor to total lake primary production (PP) and an important regulator of nutrient fluxes (Galanti and Romo 1997). Attached microalgae can make important contributions to the total annual PP, especially in shallow lakes with large littoral zones. In the large, shallow, and alkaline Borax Lake (California), benthic periphyton contributed 69% of the total annual PP (Wetzel 1964). Epiphytic algae have been reported to contribute 6–71% toward the total littoral PP (Müller 2000).

Several papers report the relative contributions of macrophytes, periphyton, and phytoplankton to total lake PP. Sand-Jensen and Borum (1991) determined that phytoplankton, periphyton, macroalgae, and rooted macrophytes contributed about 35–55, 10–15, 25–35 and 15–20%, respectively, toward the total PP in

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Roskilde Fjord, Denmark. In comparison, models for lacustrine wetlands in the semi-arid Laramie Basin (western United States) estimated that the relative contributions of phytoplankton, epiphytes, epipelon, submerged macrophytes and emergent macrophytes to the total littoral PP were 3–15, 20–32, 1–10, 15–67 and 0–50%, respectively (Hart and Lovvorn 2000). In a large widening of the St. Lawrence River known as Lac St. Pierre, the modeled contributions of phytoplankton, submerged macrophytes, and emergent macrophytes to the total PP were 29–38, 14–19, 25–29 and 23%, respectively (Vis et al. 2007).

Productivity studies in shallow water environments demonstrate that epiphytic algae can provide an abundant, rapidly renewed, and easily assimilated food resource that can be more important than that of macrophytes (Wetzel 2001). Epiphytes represent a food resource complementary to that of phytoplankton for consumers and increase the biological diversity of all trophic levels (Galanti and Romo 1997). The macrophyte–epiphyte complex has been described as a unique ecological unit within shallow aquatic ecosystems, possessing complex inter-relationships not found in open water zones (Goldsborough et al. 2005).

Although epiphyte productivity contributes significantly to the total annual PP in the littoral zones, its relative importance varies seasonally owing to species phenology. In spring, diatoms are commonly the dominant group in epiphyton, but in summer blue–green or green algae may be dominant epiphytes (Cattaneo 1983; Meulemans 1988; Müller 1994). Epiphyte biomass also increases during the growing season (Borum and Wium-Andersen 1980; Devyatkin 1979; Jenkerson and Hickman 1986; Müller 1995).

Epiphyte biomass and growth are strongly influenced by abiotic factors such as nutrient and light availability (Sand-Jensen and Borum 1991). Light availability can control the rate and vertical distribution of PP, while extremely high light intensities can inhibit photosynthesis (Hansson 1992). For periphyton it is important to consider the self-shading effect if their biofilms grow too dense (Boston and Hill 1991). High phytoplankton densities can also severely reduce the availability of light for periphyton and macrophytes (Sand-Jensen and Borum 1991; Hansson 1992).

The aim of the present study was to estimate the contribution of submerged macrophytes and their epiphytes to the total PP in the littoral zones of two large, shallow lakes in the northern temperate region. The contribution of the littoral PP to total lake PP was also estimated.

Study area

Lake Võrtsjärv (58°16′N 26°02′E) is situated in central Estonia. With a surface area (A_o) of 270 km^2 and catchment area of 3,374 km^2, it is the country's second largest lake. Lake Võrtsjärv is shallow (maximum depth $Z_m = 6$ m, mean depth $\overline{Z}$= 2.8 m), highly eutrophic (Tuvikene et al. 2004; mean chlorophyll $a = 24$ µg l^{-1}) and polymictic (Nõges et al. 2007). Macrophytes cover 50.7 km^2 (18.8% A_o): 35.2 km^2 submerged, 12.3 km^2 emergent, and 3.2 km^2 floating (Feldmann and Mäemets 2004). In the 1960s, the dominant submerged macrophyte was *Potamogeton perfoliatus*; however, *Myriopyllum spicatum* is currently dominant.

Lake Peipsi (58°40′N 27°26′E) has an A_o of 3,555 km^2 and is located on the border between Estonia and Russia (Jaani 2001). The lake consists of three basins: (1) the northern basin Peipsi s.s. ($A_o = 2{,}611$ km^2, $Z_m = 12.9$ m, $\overline{Z} = 8.3$ m), which is meso-eutrophic (Pihu and Haberman 2001), (2) the strait-like middle basin named Lake Lämmijärv ($A_o = 236$ km^2, $Z_m = 15.3$ m, $\overline{Z} = 2.5$ m), and (3) the southern basin named Lake Pihkva ($A_o = 708$ km^2, $Z_m = 5.3$ m, $\overline{Z} = 3.8$ m). Lake Peipsi has extensive areas with a depth <3m, which is potentially suitable for macrophyte growth. However, because of intensive wind-induced erosion, macrophyte bottom cover is only about 1.7% (or 44.4 km^2: 4.8 km^2 emergents, 38.9 km^2 submergents, 0.6 km^2 floating) in Peipsi s.s. and up to 8% in Lakes Lämmijärv and Pihkva (Mäemets and Mäemets 2001). The dominant submerged species is *P. perfoliatus* (Mäemets et al. 2006).

A location map of Lakes Peipsi and Võrtsjärv is provided by Nõges et al. (2007).

Materials and methods

Estimates of PP in Lake Võrtsjärv were undertaken within submerged macrophyte stands along the western shoreline. In Peipsi s.s. (referred to hereafter as Peipsi), experiments were undertaken on the western shoreline near Varnja (population 250). Macrophytes for the experiments were sampled during the summer months (June, July and August) of 2005. For measuring the PP of epiphytes and macrophytes, the dominant submerged macrophyte species were selected from both lakes: *P. perfoliatus* in Peipsi and *M. spicatum* and *P. perfoliatus* in Võrtsjärv. PP was estimated in situ using the ^{14}C assimilation technique first introduced by Steeman-Nielsen (1952), following modifications by Kairesalo (1976) and Cattaneo and Kalff (1980).

Macrophytes were carefully removed from the lake and pieces of leaves from upper, middle, and lower sections were placed separately in 30 ml glass bottles filled with lake water with 2 μCi $NaH^{14}CO_3$ (VKI, Denmark). The average (±1 S.D.) dry weight (DW) of macrophyte material per bottle was 0.13 ± 0.09 g. The bottles were incubated for 4 h within macrophyte stands at depths representing natural conditions: 0.2 m for upper macrophyte sections, 0.5 m for middle sections, and 0.7 m for lower sections. Three light replicates were used for each depth. Nonphotosynthetic carbon fixation was measured in darkened bottles and subtracted from the carbon fixed in the light bottles. After incubation, three sub-samples were taken from each bottle and placed in scintillation counter vials. First, 5 ml of water was taken before shaking off the epiphytes. Production in this sub-sample represented production by phytoplankton. Second, epiphytes were removed from macrophytes by vigorous shaking for 2 min (Kassim and Al-Saadi 1995; Galanti and Romo 1997; Cattaneo et al. 1998) and a second 5 ml water sample was taken. Production in this sub-sample represented the sum of phytoplankton and epiphyte production. Lastly, each macrophyte section was removed from the bottle and placed in a vial containing 5 ml of distilled water; 150 μl of 0.5 N HCl was added to each sub-sample to remove $^{14}C_{inorg}$. All vials were held in the laboratory for 24 h to allow the $^{14}C_{inorg}$ fraction to evaporate (Lignell 1992), then 10 ml of OptiPhase HiSafe 3 (Perkin Elmer) scintillation fluid was added to each vial and radioactivity was measured using an LSC RackBeta 1211 (Wallac, Finland).

Macrophyte sections were then removed from the vials and dried for 24 h at 105°C. Epiphyte and macrophyte production were calculated according to Ærtbjerg-Nielsen and Bresta (1984) and were expressed as mg C assimilated per g macrophyte DW per hour (mg C g^{-1} h^{-1}). Daily values of PP were calculated using an equation relating daily PP (PP_{day}) to hourly PP at midday (PP_{hour}), obtained for Lake Võrtsjärv by Nõges and Nõges (1998): $PP_{day} = PP/[0.230-(8.9 \times 10^{-3}\ DL)]$, where DL denotes the number of hours of daylight.

Relative epiphyte biomass was determined as mg chlorophyll *a* (Chl *a*) in the epiphyte sample per g macrophyte tissue DW (mg Chl *a* g^{-1}). For relative biomass determinations, macrophytes were collected from the sites at which the production experiments were undertaken (above). Upper (top 20 cm) and lower (lowest 10 cm) macrophyte sections were sampled for epiphyte biomass. Epiphytes were removed from the macrophyte sections by shaking vigorously for 2 min in 500 ml glass bottles with 100 ml distilled water (Kassim and Al-Saadi 1995; Galanti and Romo 1997; Cattaneo et al. 1998). Ten millilitre of each resulting suspension was then filtered through GF/C filters (1.2 μm). Chl *a* was extracted from the filters with 96% ethanol (Moss et al. 2003), measured spectrophotometrically and calculated as per Arvola (1981). Macrophyte sections were dried for 24 h at 105°C and weighed. To compare the PP of phytoplankton with the littoral production of epiphytes and macrophytes we used the results of depth-integrated pelagic phytoplankton PP estimates. Concurrent phytoplankton PP measurements were carried out by the ^{14}C assimilation technique (see Arst et al. 2008). Areal epiphyte and macrophyte PP (mg C m^{-2} day^{-1}) were calculated using available information on macrophyte biomass (g m^{-2}, DW) for both lakes. Data in Mäemets et al. (2006) were used for the littoral biomass of *P. perfoliatus* on the Estonian side of Lake Peipsi s.s. (37.6 g m^{-2}). Littoral biomasses of *P. perfoliatus* (8.37 g m^{-2}) and *M. spicatum* (15.96 g m^{-2}) in Lake Võrtsjärv were from databases compiled from routine monitoring programs (Feldmann, unpubl. data).

To calculate the total PP in the littoral and pelagic zones, we applied the estimated littoral zone areas for both lakes. The littoral, defined here as the area covered with macrophytes, made up 44.39 km^2 (1.7% of the total area) in Peipsi s.s. (Mäemets and Mäemets 2001) and 50.7 km^2 (18.8% of the total area) in Võrtsjärv (Feldmann and Mäemets 2004). We used the measured areal production of submerged macrophytes and their epiphytes to calculate the PP of the entire littoral zones.

We used ANOVA of Statistica for Windows version 7.0 to assess differences in PP among the lakes, taxa, and macrophyte sections, the General Linear Model application of SAS to test the impact of different factors (macrophyte part and month) on PP.

We used Secchi depths provided by the State Monitoring Program of the Estonian Ministry of Environment. Incident photosynthetically active radiation (PAR) was measured by irradiance quantum sensor Li-Cor 190SA (Li-Cor Biosciences) at the Estonian Institute of Hydrology and Meteorology (EMHI).

Results

Macrophyte and epiphyte production

Average *P. perfoliatus* production in Lake Peipsi was high in June (8.0 mg C g^{-1} h^{-1}) and August (7.7 mg C g^{-1} h^{-1}). In July, *P. perfoliatus* production was lower (4.6 mg C g^{-1} h^{-1}). In June, production in the middle and lower macrophyte sections was greater ($P < 0.05$) than in the upper sections (Fig. 1a). Conversely, production was highest in the upper sections in July and August (Fig. 1a). Epiphyte production was highest in August (0.039 mg C g^{-1} h^{-1}) and lowest in July (0.002 mg C g^{-1} h^{-1}; Fig. 1d). In June, epiphyte production was high in the lower and middle macrophyte sections, but in July production was greatest in the lower sections and lowest in the middle sections (Fig. 1d). In August, production was highest in the upper sections of *P. perfoliatus* (Fig. 1d).

In Lake Võrtsjärv, *P. perfoliatus* production was highest in July (9.6 mg C g^{-1} h^{-1}), with production in June and August being slightly lower (9.4 and 7.75 mg C g^{-1} h^{-1}, respectively) (Fig. 1b). Epiphyte production on *P. perfoliatus* remained relatively constant throughout the sampling period, remaining within the range of 0.005–0.01 mg C g^{-1} h^{-1}. In June, *P. perfoliatus* production was highest in the middle sections, whereas production was highest in the upper sections in July and August (Fig. 1b). Epiphyte production on *P. perfoliatus* was highest in the middle sections in June and July, but highest in the lower sections in August (Fig. 1e). The lowest epiphyte production occurred in the lower part of the macrophyte in June and July and in the upper part of the macrophyte in August. Production of *M. spicatum* (Fig. 1c) was highest in June (11.4 mg C g^{-1} h^{-1})

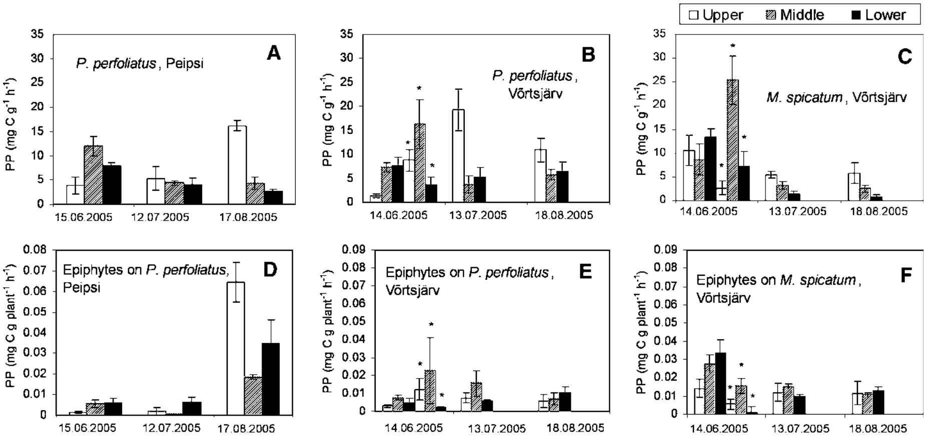

Fig. 1 Primary production (PP) of different parts (upper, middle, lower) of *P. perfoliatus* and *M. spicatum* (**a**, **b**, **c**) and epiphytes on these macrophyte parts (**d**, **e**, **f**) in Lakes Peipsi and Võrtsjärv in 2005. PP was measured from 11.00 to 15.00 h on June 14 in Võrtsjärv; the second measurement series (*) was performed in the afternoon (from 16.00 to 20.00 h). Standard *error bars* of parallel measurements are denoted

and much lower in July (3.4 mg C g^{-1} h^{-1}) and August (3.06 mg C g^{-1} h^{-1}). Epiphyte production was also highest in June (0.014 mg C g^{-1} h^{-1}), but only slightly lower in July and August [0.012 and 0.01 mg C g^{-1} h^{-1}, respectively (Fig. 1f)]. The production of *M. spicatum*, like that of *P. perfoliatus*, was highest in the middle part of the macrophyte in June and in the upper part of the macrophyte in July and August (Fig. 1c). In June, epiphyte production on these macrophytes was high in the middle and lower parts of the macrophyte, in July in the middle and upper parts, while in August the PP was almost the same in all parts of the macrophyte (Fig. 1f).

During our measurements incident PAR was 1,600 µmol s^{-1} m^{-2} in June and July, and 1,200 µmol s^{-1} m^{-2} in August (Fig. 2), Secchi depth in Võrtsjärv (0.5–1 m) was considerably lower than in Peipsi (1.2–2.6 m).

Average daily production of *P. perfoliatus* in June–August, 2005 was 305 mg C g^{-1} day^{-1} in Võrtsjärv and 278 mg C g^{-1} day^{-1} in Peipsi. The average daily epiphyte production on *P. perfoliatus* was 0.303 mg C g^{-1} day^{-1} in Võrtsjärv and 0.53 mg C g^{-1} day^{-1} in Peipsi. The average daily production of *M. spicatum* and its epiphytes in Võrtsjärv were 253 and 0.70 mg C g^{-1} day^{-1}, respectively. Our results of epiphyte production relative to macrophyte biomass are consistent with values reported by other investigators, but our macrophyte production values per unit biomass exceed the literature values quite substantially (Table 1).

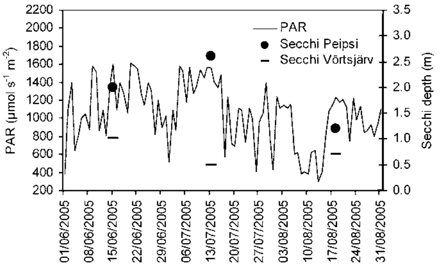

Fig. 2 Photosynthetically active radiation (PAR) from 11.00 to 15.00 h in June–August, 2005 at Tõravere meteorological station (58°16′N 26°26′E) and Secchi depth in Lakes Peipsi and Võrtsjärv on the days of primary production measurements

The factors that significantly affected the productivity of macrophyes and epiphytes in Lake Peipsi were sampling month and macrophyte section (upper, middle, lower). For epiphyte production the effect of the month was highly significant ($P < 0.0001$) and the effect of the macrophyte part was moderately significant ($P = 0.04$). For macrophyte production both month ($P = 0.02$) and macrophyte part ($P = 0.02$) were equally significant. The combined effect of month and macrophyte part was highly

Table 1 Primary production of macrophytes and epiphytes in different water bodies (all studies employed C^{14}-uptake method)

Species	Primary productivity (mg C g macrophyte DW^{-1} day^{-1})		Total P (µg l^{-1})[a]	A_o (km^2)	Lake
	Epiphytes	Macrophytes			
Ruppia maritima	n.a.	46	n.a.	0.4	Borax Lake, California[b]
Myriophyllum spicatum	1.26	15	12	102	Lake Memphremagog, Québec[c]
Potamogeton richardsonii	0.66	18	12	102	Lake Memphremagog, Québec[c]
Vallisneria americana	0.39	28	12	102	Lake Memphremagog, Québec[c]
Chara tomentosa	1.19–1.55	34–61	23	0.33	Lake Prossa, Estonia[d]
Potamogeton perfoliatus	0.53	278	34	2,611	Lake Peipsi s.s., Estonia[e]
Potamogeton perfoliatus	0.303	305	37	270	Lake Võrtsjärv, Estonia[e]
Myriophyllum spicatum	0.699	253	37	270	Lake Võrtsjärv, Estonia[e]

[a] In lake water

[b] Wetzel (1964)

[c] Cattaneo and Kalff (1980)

[d] Luup (2003)

[e] Present study

significant for both epiphyte ($P = 0.001$) and macrophyte ($P < 0.0001$) production. In Võrtsjärv, the significant factors for the production of *P. perfoliatus* were the macrophyte part ($P = 0.02$) and the combined effect of macrophyte part with month ($P = 0.004$). For epiphyte production on *P. perfoliatus* none of these effects proved significant ($P = 0.45$). For production of *M. spicatum* and its epiphytes the only statistically significant factor was the month ($P < 0.01$).

Epiphyte biomass

In Lake Peipsi, mean epiphyte biomass was highest in June (56 μg Chl *a* g^{-1}) and somewhat lower in July and August (36 and 34 μg Chl *a* g^{-1}). In Lake Võrtsjärv, mean epiphyte biomass on *M. spicatum* was highest in June (44 μg Chl *a* g^{-1}), quite similar in August (37 μg Chl *a* g^{-1}), and lowest in July (13 μg Chl *a* g^{-1}). Epiphyte biomass on *P. perfoliatus* did not change much during the study period; in June it was 32 μg Chl *a* g^{-1}, in July 31 μg Chl *a* g^{-1}, and in August 34 μg Chl *a* g^{-1} (Fig. 3a).

Statistical analyses showed that the lakes did not differ significantly in the production of *P. perfoliatus* ($P = 0.28$) and that the difference between *P. perfoliatus* and *M. spicatum* in the same lake was not significant ($P = 0.70$). Despite the higher ($P = 0.01$) biomass of epiphytes on *P. perfoliatus* in Lake Peipsi (42.0 μg Chl *a* g^{-1}) than in Lake Võrtsjärv (32.3 μg Chl *a* g^{-1}), epiphyte production did not differ significantly between lakes ($P = 0.09$). Epiphyte biomass did not differ statistically on the different macrophyte species in Võrtsjärv ($P = 0.4$), but its production was significantly higher ($P = 0.006$) on *M. spicatum* (0.0138 mg C g^{-1} h^{-1}) than on *P. perfoliatus* (0.00845 mg C g^{-1} h^{-1}).

Share of different producers in the total PP of the lakes studied

From June to August in both lakes and both macrophyte stands, epiphyte production was very low in comparison with phytoplankton and macrophyte production (Fig. 3b, c, d); daily averages were, respectively, 0.01, 5.04, and 6.97 g C m^{-2} day^{-1} in Võrtsjärv and 0.02, 1.93, and 10.5 g C m^{-2} day^{-1} in Peipsi. Average daily total PP of submerged macrophyte area was similar ($P = 0.67$ for the difference) in the two lakes: 12.4 g C m^{-2} day^{-1} in Lake Peipsi and 12.0 g C m^{-2} day^{-1} in Lake Võrtsjärv. In Peipsi, 84.2% of this production was accounted for by macrophytes, while the shares of phytoplankton and epiphytes were low (15.6 and 0.16%, respectively). In Võrtsjärv, macrophytes contributed 58%, phytoplankton 41.9%, and epiphytes 0.1% to littoral

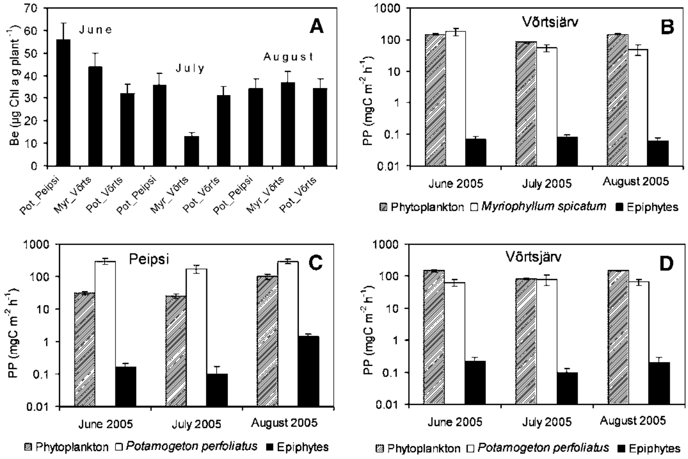

Fig. 3 Epiphyte biomass (Be) on *M. spicatum* and *P. perfoliatus* in Lakes Peipsi s.s. and Võrtsjärv (**a**), and primary production (PP) of phytoplankton, macrophytes, and epiphytes in *M. spicatum* stands in Võrtsjärv (**b**), and in *P. perfoliatus* stands in Peipsi (**c**) and Võrtsjärv (**d**) in June–August 2005. Standard *error bars* of parallel measurements are denoted

Table 2 Average primary production (PP) of different producers in June–August, 2005

	Total	Phytoplankton	Epiphytes	Macrophytes
Peipsi s.s.				
PP (g C m^{-2} day^{-1})	12.4	1.93	0.02	10.5
% in PP of submerged macrophyte area		15.6	0.16	84.2
PP (tons C per day)				
of submerged macrophyte area 38.93 km^2	483	75	0.77	407
of total macrophyte area 44.39 km^2 [a]	551	86	0.88	464
of open water area 2566.6 km^2	4965	4965		
Total PP in lake	5516			
% of littoral PP in lake	10.0			
% in total PP of lake		91.6	0.02	8.4
Võrtsjärv				
PP (g C m^{-2} day^{-1})	12.0	5.04	0.01	6.97
% in PP of submerged macrophyte area		41.9	0.10	58.0
PP (tons C per day)				
of submerged macrophyte area 35.2 km^2	423	177	0.42	245
of total macrophyte area 50.7 km^2 [a]	609	255	0.61	353
of open water area 219.3 km^2	1105	1105		
Total PP in lake	1714			
% of littoral PP in lake	35.5			
% in total PP of lake		79.4	0.04	20.6

[a] Measured production of submerged macrophytes and their epiphytes is applied in this calculation

production. The PP of the littoral area contributed 10% to the total summer PP of Peipsi s.s. and 35.5% to the total summer PP of Võrtsjärv (Table 2).

Discussion

Our results showed that macrophyte and epiphyte production was variable throughout the growing season in both lakes, for the same macrophyte species (*P. perfoliatus*) in different lakes, and for different macrophyte species (*M. spicatum* and *P. perfoliatus*) in the same lake (Fig. 1). In large lakes, strong wave action may adversely affect epiphyte establishment and growth (Devyatkin 1979; Strand and Weisner 1996). However, according to our data, the biomass of epiphytes was greater in the larger Peipsi than in Võrtsjärv. In the shallower Lake Võrtsjärv, stands of submerged macrophytes occupy much larger areas and are more exposed to wind action and mechanical disturbance by waves than in the deeper Lake Peipsi, where submerged macrophytes can develop only in sheltered areas close to the shoreline.

Owing to differences in leaf architecture, *M. spicatum* offers a larger leaf area suitable for epiphyte attachment than *P. perfoliatus.* Differences in epiphyte production between macrophyte species may occur because of these different macrophyte structures (Romo and Galanti 1998). Our analysis in Võrtsjärv showed that the average epiphyte production was significantly higher on *M. spicatum* than on *P. perfoliatus*, although the epiphyte biomass did not differ statistically between the macrophyte species.

Different macrophyte species may exhibit seasonally variable growth patterns (Wetzel 2001). In our study, *M. spicatum* production was highest in June and decreased toward August, while the production of *P. perfoliatus* was relatively constant during the study period. The distribution of production between the different macrophyte parts was quite similar in both macrophyte species. The differences in production among macrophyte parts could be explained by differences in the light conditions to which those parts were exposed. Generally, greater light availability should increase photosynthesis for the upper macrophyte part (Wetzel 2001), while light that is too intense may also inhibit photosynthesis (Rae et al. 2001). In our study, the light intensities in June and July were quite similar, while the water was more transparent in June (Fig. 2). Therefore, the upper macrophyte parts were exposed to more intense light in June and production was likely to be photoinhibited. In August, the light intensity was lower, Secchi depth was quite small and, consequently, photoinhibition did not occur.

In spite of the generally positive correlation between macrophyte and epiphyte production in our study, the seasonal production pattern of epiphytes differed from that of the macrophytes. Besides the influence of light and nutrient availability, fish and invertebrates can graze epiphyton, reducing its biomass (Cattaneo 1983). At the same time this grazing may increase the specific production of epiphytes by diminishing self-shading and competition for nutrients (Cattaneo and Kalff 1980; Hatcher 1983; Hay 1991). Changes in epiphyte production can also be induced by changes in the epiphyte algal community (Cattaneo and Kalff 1979).

Our comparison of the PP of different producers (epiphytes, macrophytes and phytoplankton) showed that macrophytes are important primary producers in the littoral zone in both studied lakes, but epiphytes had a very low share of production, only 0.1–0.2%. Although the calculated daily summer PP of the submerged macrophyte area was similar (about 12 g C m^{-2}) in both lakes, different producers had different shares in this PP. In highly eutrophic Võrtsjärv the share of macrophytes (58%) was lower and the share of phytoplankton (41.9%) was higher than in meso-eutrophic Peipsi s.s. where macrophytes and phytoplankton, respectively, contributed 84.2 and 15.6% of the daily summer PP in the submerged macrophyte area. In more eutrophic lakes, high phytoplankton biomass may shade macrophytes and epiphytes (Romo et al. 2007), causing a reduction in their share in the total PP. However, the share of littoral PP in the total PP of the lake was 3.6 times greater in Võrtsjärv than in Peipsi. In the larger and deeper Peipsi the littoral area is smaller than in Võrtsjärv (Table 2), and on a relative scale the difference between the two lakes is more than tenfold: the littoral zone occupies about 1.7% of the total area of Peipsi s.s. and 19% in Võrtsjärv. Therefore, the share of littoral PP in the total PP of the lake was also much greater in Võrtsjärv.

Our results on macrophyte production exceed the literature values quite substantially (Table 1). Moreover, the share of epiphytic algal PP in the total littoral primary production estimated in our study (0.1–0.2%) is substantially lower than the values reported in the literature (5.5–71% as reviewed by Müller 2000). In Lake Lawrence (Michigan), epiphytic algae were responsible for 31.3% of the total littoral production and for 21.4% of the total annual production of the whole lake (Allen 1971). However, the A_o of Lake Lawrence is only 0.05 km^2, and most of the other studies reviewed have also been conducted in small lakes. Lake Memphremagog (Québec) is a large but very long and narrow lake, and McPherson Bay, where the study of Cattaneo and Kalff (1980) was conducted, has a rather small area. Lakes Peipsi and Võrtsjärv are large lakes with quite simple shorelines, and our measurements were made in the littoral adjoined to the large open water area. We assume that in such large lakes as Peipsi and Võrtsjärv, the macrophyte stands are much more actively disturbed by wave action, which interferes with the colonization of macrophytes by epiphytic algae and at the same time supplies nutrients to macrophytes. Therefore, the productivity of macrophytes in such systems is much higher and the contribution of epiphytes to the total primary productivity is much less important than in small lakes.

As the main aim of our study was to estimate the contribution of submerged macrophytes and their epiphytes to the total PP of large and shallow lakes, our most important result was that for the first time the total primary productivity and the share of different producers (epiphytes, macrophytes, and phytoplankton) was estimated in large shallow eutrophic temperate lakes. These results would give a basis for the further intra- and supra-regional comparisons and will also serve as the basis of the calculation of the carbon budget of these large lakes. In our further studies, we plan to use more sophisticated equipment for the measurements of seasonal and vertical distribution of light in the macrophyte beds and to discuss more thoroughly the causes of the seasonal and vertical variations of the productivity.

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TWO DECADES OF MACROPHYTES EXPANSION IN THE
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Two decades of macrophyte expansion on the shores of a large shallow northern temperate lake—A retrospective series of satellite images

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ABSTRACT

We made use of a 22-year (1985–2007) retrospective archive of moderate resolution Landsat TM and ETM+ satellite images to estimate the changes in cover of emergent macrophytes in the large shallow eutrophic Lake Võrtsjärv (270 km^2) in Estonia. An original non-parametric image interpretation methodology was applied on late summer images. The combined GIS and statistical analysis of 217 coastal sections showed that the helophytic macrophyte belt, dominated by common reed (*Phragmites australis*), has rapidly widened during the last two decades, with an average expansion rate of 2.2 m per year. Statistical model revealed that the vicinity of large inflows had the strongest positive effect on the expansion of macrophytes, on average 1.6 times. In some sub-regions of the lake shore, we found the suppressing effect of the presence of small inflows on the change of helophytic belt width. This effect, however, was probably interconnected with the presence of human activity at the shoreline, which itself had statistically near-marginal suppressing effect on the widening of the reed belt.

We showed that medium resolution satellite images can successfully be used for the retrospective monitoring of macrophyte vegetation in the littoral zone of large water bodies by applying very simple image classification methodology. As the lake coastal areas showed a tendency to become overgrown with reed and other macrophytes even in conditions of generally reduced agricultural intensity in the catchment area, we hypothesize that the clonal expansion of reed is probably triggered by the complex of drivers: large seasonal fluctuations in the water level create specific low water conditions in estuaries in combination with nutrients supply resolved from lake bottom or brought by rivers. Estuary areas are characterised by mineral sediments suitable for anchoring and protection-provision against destructive wave- and ice-action.

Probably the most efficient biodiversity conservation policy to revealed macrophytic expansion is the reactivation of disrupted management activities along the coastline.

1. Introduction

Recent studies have demonstrated continuously increasing overgrowth of coastal zones by aquatic macrophytes, mostly by common reed (*Phragmites australis* (Cav.) Trin. ex Steud.), in several European large boreal and northern temperate lakes (Andersson, 2001; Feldmann and Mäemets, 2004; Partanen and Luoto, 2006). Emergent vegetation at shorelines is often a desired aspect, because it prevents erosion of the lakeshore, absorbs nutrients and provides shelter for fish and waterfowl (Kühl and Zemlin, 2000; Engloner, 2009). Extreme expansion of tall macrophytes, however, causes biodiversity loss and the reduction of ecosystem services provided by coastal habitats, such as recreational areas used for swimming, boating and fishing, and therefore excessive growth of macrophytes affects lakes' economic potential (Rørslett, 1991; Güsewell and Klötzli, 1998; Lenssen et al., 2000; Andersson, 2001; Rannap et al., 2007; Daniel and Rydin, 2008).

During recent decades, a remarkable change in land use intensity and management has occurred in Central and Eastern European countries (Liira et al., 2008). This has caused changes in the state of natural habitats and environment, including shallow lake ecosystems. Like many other large lakes in the northern temperate and boreal region of Europe, Lake Võrtsjärv has benefited from an improvement in conditions after the decrease of agricultural activities. Despite improvements in water quality, however, a significant increase in emergent macrophytes has been observed (Feldmann and Mäemets, 2004; Feldmann and Nõges, 2007). Common reed (*P. australis* L.) is the main species, forming large clumps of vege-

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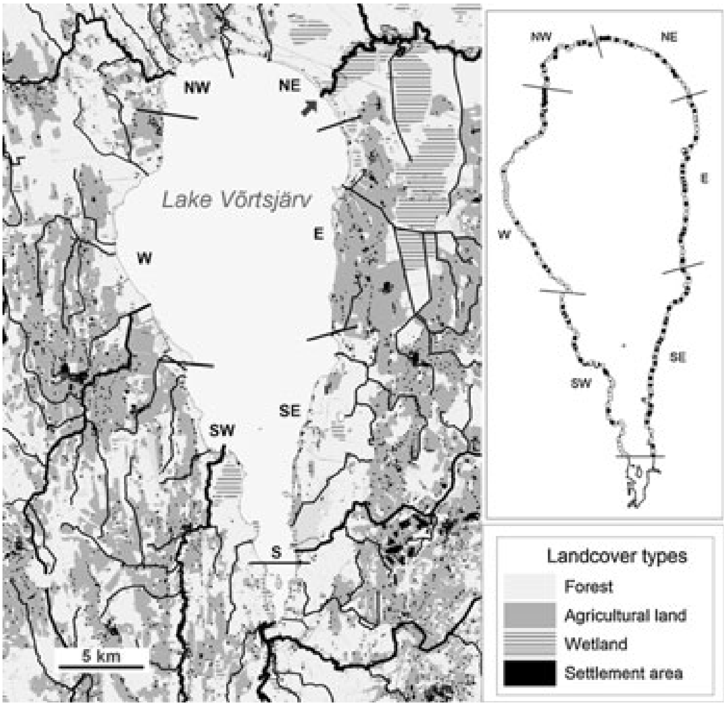

Fig. 1. Land cover map of the closest vicinity of Lake Võrtsjärv, where land use intensity is illustrated with a color gradient from light gray to black (a). The shoreline regions of the lake that were used in the study are shown with abbreviations and separated with short perpendicular lines. The inflows are shown as black lines, with the line width corresponding to inflow size. The outflow from the lake in the NE region is indicated with an arrow. Shoreline sections used in the study with active anthropogenic influence are shown with filled circles on separate scheme in the right (b).

tation along the shoreline. Long stretches of shore areas that a few decades earlier attracted numerous holidaymakers are now overgrown, mostly by *P. australis*, and canals have to be cut or dug to reach open water (Tavast, 2004).

Effective and large scale environmental monitoring systems of lake ecological status are still in the evolutionary phase (Feldmann and Nõges, 2007), and therefore retrospective analyses of historical vegetation data are a valuable option to analyze these changes. Without adequate retrospective field data, it is difficult to assess the long-term changes of emergent macrophyte communities in lakes (Partanen and Hellsten, 2005). High-resolution aerial photographs have been used to map aquatic macrophyte phenotype groups and changes in their cover (Güsewell et al., 2000; Valta-Hulkkonen et al., 2005; Rannap et al., 2007; Daniel and Rydin, 2008). However, the seasonal timing of obtained aerial images is not optimal, since aerial photographs for national mapping projects are preferably taken in spring or early summer season, and the acquisition frequency over years is also lower than required for monitoring of changes. The monitoring of environmental and vegetation change can be based, instead, on a retrospective multi-temporal series of satellite images. That is the case of medium resolution Landsat and SPOT satellite images, which date back to the mid-1980s. These images might make possible a retrospective view of the area dynamics of littoral helophyte vegetation that form relatively wide strips along coastlines and can therefore be monitored with images with 20–30 m spatial resolution. Several studies have reported medium resolution Landsat TM images as being promising for the assessment of aquatic macrophytes (Brivio et al., 2001; Nelson et al., 2006).

We addressed the following questions: (1) Are there measurable changes in the cover of emergent macrophytes that could be consistently estimated with medium spatial resolution satellite images? (2) What are the main determining factors of the expansion of emergent macrophyte vegetation in a large shallow lake environment?

2. Materials and methods

2.1. Study area

Lake Võrtsjärv, the second largest lake in the Baltic countries, is located in a shallow pre-glacial basin in the southern part of Estonia, centred at 58°17′N and 26°3′E. The lake has an elongated shape in the meridional direction, with a length of 34.8 km, a maximum width of 13.3 km and an area of 270 km^2 (Fig. 1). The maximum depth is only about 6 m in a very limited area, but most parts are rather shallow (mean depth 2.8 m), thus facilitating the growth of emergent macrophytes. Significant seasonal and annual water level fluctuations (mean annual amplitude 1.4 m) cause remark-

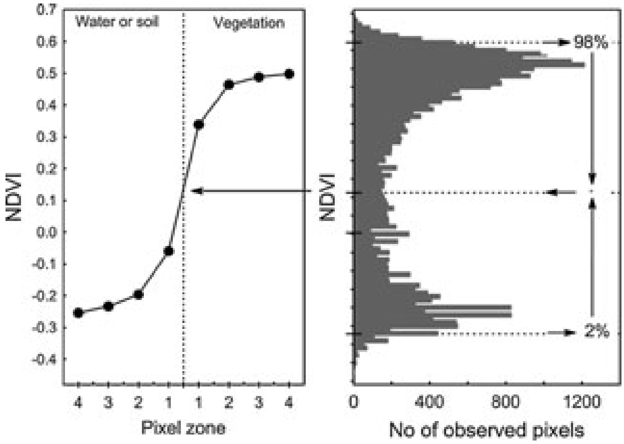

Fig. 2. An example of the bimodal distribution of NDVI values of a 200 m wide coastal zone, observed along the shoreline of the whole lake, calculated from the Landsat ETM+ image from 09 August 2007. Pixels with low NDVI values represent water or lake bottom, whereas pixels with high NDVI values represent patches of coastal macrophytes. 2nd and 98th percentile values of frequency distribution are used to define the threshold for shoreline vegetation delineation. The defined threshold points to the sharpest gradient of NDVI values in the zone between vegetation and non-vegetated cover (water or soil). Mean pixel values of the first four pixel zones in both directions from the vegetation boundary in the whole lake are shown.

able changes in both lake surface area and volume (Järvet, 2004). Due to such extreme water level fluctuations and extensive areas of shallow water (water depth < 2 m) in the lake, large areas become seasonally exposed after the disappearance of the high water in spring on the NE and E lakeshores. After the spring inundations, during the summer drawdown in the low water years, the belt of exposed lake bottom can be more than a hundred meters wide.

The littoral area has mostly a very gentle slope: the average width of the belt up to 1-m depth is 250 m, varying from 50 to 700 m. The littoral slope is covered by a wide zone of macrophytic vegetation, dominated by the *P. australis* (common reed) and some other helophytes *Schoenoplectus lacustris* L. Palla (common club rush) and *Typha angustifolia* L. (narrow leaf cattail), and frequently bordered with nymphaeid *Nuphar lutea* L. Sm. (yellow water lily) (Feldmann and Nõges, 2007). The stands of helophytic vegetation are quite dense. In the years 2006–2008, the average densities of reed reached 14–23 stems per m^2, the densities of club rush and cattail 30–37 and 13–14 stems per m^2, accordingly (unpublished monitoring data).

Six larger streams and rivers serve as the major inflows into the lake, supplemented with several large-sized drainage ditches and multiple small-sized ditches. The outflow by the River Emajõgi is from the north-eastern part of the lake.

Agriculture and forestry are the main land cover types, both in the coastal areas and in the drainage area as a whole (Fig. 1). The proportion of arable land is highest in the eastern and western coastal areas, and lowest in the northern and southern coastal areas. The proportion of wetlands is highest in the southern and north-eastern coastal areas.

According to a general agreement among researches, the primary production is not nutrient-limited in Lake Võrtsjärv (Tuvikene et al., 2004). The increase in nutrient concentrations has occurred since 1982 due to extensive livestock farming and the use of fertilizers on agricultural lands. The largest external loading of phosphorus to the lake also occurred in the 1980s and the highest phosphate and total phosphorus concentrations in Lake Võrtsjärv were measured in 1986 and 1987 (Nõges and Nõges, 1999; Tuvikene et al., 2004). After a rapid decrease in agricultural land use intensity in Estonia (Mander et al., 1995; Liira et al., 2008) since 1992, the annual average concentrations of phosphates and total nitrogen have stabilized since 1998, but nutrients carried into the lake during the 1980s have been accumulated in the sediments and remain in circulation as resuspension from sediments (Nõges et al., 1999; Tuvikene et al., 2004).

2.2. Satellite images and image processing

The reflectance characteristics and density of aquatic macrophytes are known to change seasonally, as is the case with terrestrial vegetation (Jensen et al., 1993). For that reason, we targeted the period of maximum abundance of aquatic macrophyte vegetation, i.e. we exploited the substantially cloud-free images of late summer, from mid-July till early September. The time period covered by medium resolution satellite images from Landsat Thematic Mapper (TM) and Landsat 7 Enhanced Thematic Mapper Plus (ETM+) was 22 years, from 1985 to 2007 (Appendix 1). The maximum solar zenith angle at the time of satellite overpass was 59°. The wind speed during data acquisition was no greater than $5\ \mathrm{m\ s^{-1}}$.

The satellite images were geo-referenced using the Estonian basic map and digital orthophoto quads at the scale 1:10,000, with approximately 25 ground control points per image (maps provided by Estonian Land Board). The nearest neighbour resampling method was used in geocorrection.

The measured spectral reflectance or radiance data are often represented by vegetation indexes based on radiance or reflectance measured in the red (RED) and near infrared (NIR) spectral regions. Studies of such indexes have proved to correlate well with green leaf area, biomass and absorbed photosynthetically active radiation (Tucker, 1979; Asrar et al., 1984). We transformed Landsat TM and ETM+ images in the visible and near infrared spectral regions into Normalized Difference Vegetation Index (NDVI) values. The NDVI is derived as the ratio between red and near infrared reflectance ($\mathrm{NDVI} = (\mathrm{NIR} - \mathrm{RED})/(\mathrm{NIR} + \mathrm{RED})$) (Rouse et al., 1974). NDVI values range from -1 to $+1$, whereas negative values correspond to an absence of vegetation. We used the NDVI to increase the contrast among pixel values in the transition zone from vegetated to non-vegetated areas (open water or lake bottom in low water conditions).

The spectral signatures of emergent aquatic vegetation largely overlap with the signatures of terrestrial vegetation. Such a similarity can lead to poor results in the classification of aquatic and terrestrial vegetation patches in their transitional areas. For that reason, terrestrial areas around the lake were blocked out using a mask of the lake derived from the national digital base map (Estonian Land Board). The same mask was applied on every dataset in order to obtain comparable results regarding changes in the area of aquatic vegetation, and the expansion of the reed belt was followed at the water-ward edge.

We used thresholds to assign pixels of the 200 m belt from the shoreline of lake to one of two classes – "emergent macrophytes" or "other", the latter being either water or exposed lake bottom (Fig. 2). The NDVI value of coastal zone's pixels has bimodal distribution (Fig. 2b), which is not a very common result obtained from satellite images (see also Peterson et al., 2004). But where such saddle-like distribution occurs, this can be efficiently utilized for very simple and flexible non-parametric interpretation of images, elaborated and tested by Peterson et al. (2004) and Liira et al. (2006) for forest mapping form winter images. The saddle-like bimodality of NDVI values in the coastal zone of water bodies in the images is created by the combined distribution of patches of two different land cover types – non-vegetated water or lake bottom and green vegetation. The classification threshold value separating vegetated patches from non-vegetated ones was estimated for each image separately as the average of the 2nd and 98th percentile values of that bimodal frequency distribution of the NDVI. This thresholding methodology has shown to efficiently detect the critical value, at which there is the most likely change between these land cover types, i.e. from vegetation to open water or lake bottom (see connection between Fig. 2b and a).

The width of the reed belt in each coastal section was derived by dividing the belt area in a section by the length of the generalized coastline in that section. This method eliminated most of the boundary noise error caused by a single pixel location unpredictability in the images.

2.3. Data to evaluate the interpretation of satellite images

Satellite image interpretation quality was evaluated with four independent methods.

First, the mapping stability of helophytic vegetation area was evaluated by estimating the relative error of area comparing the interpretation results derived from the images of the same year, acquired with very short time interval. The years we had more than one late summer image were 1999, 2002, 2003 and 2006 (Appendix 1).

Secondly, we evaluated the detection precision of reed patch boundaries with on-ground GPS-recording results obtained in July and August of 2006 and 2007.

Thirdly, color aerial photographs of the whole lake area were used to assess the accuracy of vegetation mapping with medium resolution satellite images. The aerial photographs were acquired specifically for the purpose of assessing aquatic vegetation on 5 August 1997 by FM Kartta OY. The photographs were taken with a Leica RC30 camera equipped with a UAG-S 13260 153 mm lens on Kodak color film. The flight altitude was 4596 m, and the image scale was 1:30,000. The photographs were scanned to a spatial resolution of 1 m and were geo-referenced to the Estonian base map. The photographs were visually interpreted and emergent aquatic vegetation patch boundaries were digitized manually in the MapInfo GIS environment.

Finally, permanent 1-m wide belt transects were established perpendicular to the shoreline (Feldmann and Nõges, 2007). The beginning and end-points of these transects were recorded in the field using GPS. Data were collected along transects using 1-m^2 sample quadrates. Data on the species composition, stem density and stem height of the aquatic macrophyte vegetation were obtained in the summers from 2005 to 2008.

2.4. Statistical analysis

The shoreline regions (see Fig. 1) were generated by numerical generalization of the lake polygon on the National Basic Map of Estonia. Minor shifts in the generalized shoreline nodes (resp. lake region boundaries) were performed to match the soil polygon transitions in the national soil map at the scale of 1:10,000 in case such transitions occurred in the vicinity. Seven shoreline regions were derived from the simplification of the shoreline, representing differently exposed stretches of shoreline. Six of the seven regions were used in the analyses. The southernmost tip of the lake, the muddy estuary of the Väike-Emajõgi river with islands, covering altogether 4 km^2 of the lake area was omitted from the analysis, because it represents a very different ecologic region concerning geology and vegetation (Mäemets, 1973; Raukas and Tavast, 2002; Tavast, 2004; Feldmann and Mäemets, 2004). For instance, in addition to coastal reed, this part of the lake is widely covered by floating leaf plants, mostly *N. lutea*.

The study sites, as coastal sections, were initially delineated relative to the presence of housing, boat landing sites and holiday beaches (Fig. 1). A perpendicular line to the shoreline was drawn at such sites and a ±50 m buffer zone was created to the line to form a coastal section. It was expected that these are the sites where direct human influence is most strongly expressed at the shoreline. The presence of a settlement was estimated from the National Basic Map created from orthophotos imaged in 1995 and checked from orthophotos acquired in 2002. The same method was utilized to define the coastal sections around small inflows. The impact regions around large inflows were defined on the basis of the shoreline configuration around these inflows. We created a total of 217 coastal sections from which reliable data were acquired.

The extension of the macrophyte belt from the shoreline toward the lake was estimated as the average change in reed belt width in studied sections of the shore. We also tested the change in reed belt area relative to the less than 2 m deep zone in these sections, but as the results of the analysis were very similar, we will treat only absolute estimates of reed belt width in Section 3 of the paper.

We applied a multi-factorial general linear mixed model (GLMM) to examine the effect of drivers on the horizontal extension of coastal reeds in 217 coastal sections. For that purpose we built a statistical model with proc MIXED in SAS ver 9.1 (Littell et al., 1996). In the model we included the following categorical factors: the coastal region of the lake, the potential occurrence of anthropogenic disturbances (no/yes), the presence of small inflows (drainage ditch up to 6 m wide: no/yes), the impact region of large inflows (large streams, rivers and ditches more than 6 m wide: no/yes) and year of observation. Interaction terms were included among these effects that were plausible according to prior knowledge or prescribed by hypotheses. The complex structure of the covariance matrix was defined with the repeated statement considering temporal autocorrelation among observations and sections.

We excluded from the analysis that those data readings that had only one pixel classified as reed (respective area 0.0625 ha), resulting in the exclusion of 22 observations.

3. Results

3.1. Method evaluation

The quality of emergent aquatic vegetation mapping from medium resolution Landsat TM images was estimated with multiple methods. First, the relative estimation error of the area of macrophytic vegetation belt for the late summer period in years 1999, 2002, 2003 and 2006 fluctuated between 1.9% and 2.5% of total area. That is rather accurate considering the elongated shape of polygons. The comparison of vegetation boundary lines derived from late summer images of year 2002 gave an average absolute error of boundary line location 6.9 m.

Two evaluations of boundary detection on satellite images gave relatively similar results, showing the precision of boundary line definition from medium resolution satellite images to be within the size of half a pixel, without directional bias. In detail, the vectorized macrophyte patch boundaries obtained from satellite image of year 2007 were compared to on-ground GPS-recorded patch boundaries collected in 2006 and 2007 giving an average boundary estimation error of ±12.5 m, i.e. resolution of half a pixel. The comparison of the macrophyte boundary location defined from a satellite image of year 1997 to that digitized from FM Kartta OY aerial photographs from the year 1997 gave an average estimation error of boundary location of ±17.6 m.

The reed belt width estimated on monitoring transects and interpreted from satellite images had a correlation rate of $r = 0.63$ (in 2006) and $r = 0.67$ (in 2007), with $P < 0.05$ for both. Additionally, during these years, the average increase of reed belt width along transects was in average ca. 1.5 m per year, whereas the maximum expansion speed reached 4 m per year (unpublished monitoring data).

3.2. Analysis of reed expansion

The earliest medium resolution satellite image data (Landsat TM) covering the lake area date back to the late summer of 1985. *Phragmites* patches covered almost the whole perimeter of the lake shoreline and were absent only on short stretches several hundred meters long on the eastern shoreline. On average, over the last 23 years the belt of coastal macrophytes has been widest on the lake's north-western shore (on average 191 m) and south-western shore (166 m). The reed belt is narrowest on the western and eastern shores (70 and 77 m respectively).

From 1985 onwards, during the last more than two decades, the total area of coastal macrophytes has increased 1.5 times. Excluding the southernmost tip of the lake, where an extensive area is covered by floating-leaved vegetation, the total area covered by reeds has increased from 797 ha (average of years 1985–1987) to 1166 ha (the average for 2006 and 2007). During this period, the average width (extension) of the coastal macrophyte belt has increased from 95 to 141 m respectively (Fig. 3).

The results of the general linear mixed model analysis show that the extension of the reed belt has large between-shore-region variation that is affected by the presence of large and small inflows and by anthropogenic activities (disturbances) (Table 1). In detail, the mixed model estimated that the expansion of the reed belt at the water-ward edge has proceeded at an average annual speed of 2.2 m per year from 1985 to 2007 (Fig. 3). Nevertheless, there is a significant variation between regions – the most significant expansion of the belt has occurred on the lake's north-western coast (ca. 5.6 m per year). The smallest changes took place in the north-eastern and south-western parts of the lake (ca. 0.8–0.9 m per year).

Large inflows support the expansion of the reed belt in general, as the belt is 29 m wider in the impact zone of large inflows (Fig. 3). Large inflows support reed expansion by speeding up its growth by on average 1.6 times (2.8 m per year with large inflows vs. 1.7 m per year without large inflows). The positive effect of large inflows is, however, very region-specific (Fig. 4), being strongest in the north-western region around the estuary of the Tänassilma River (Fig. 4). Around that estuary, the enhancement of the reed belt is 5.6 times (NW coast of Fig. 5). On eastern coasts, the closeness to the inflows has also increased the speed of expansion twofold ('E coast' in Fig. 4). A somewhat unusual suppressing effect of the large inflow was observed on the north-eastern coast, while no special effect of large inflows was observed in other coastal regions of the lake.

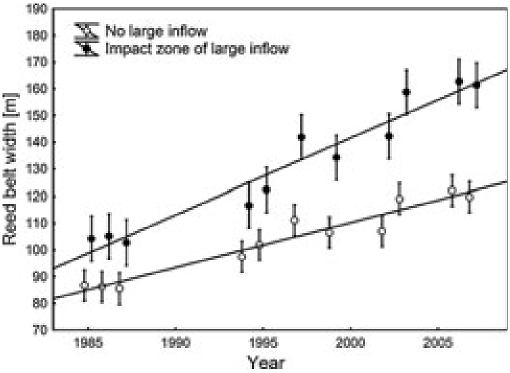

Fig. 3. Change in the average reed belt width within and beyond the impact zone of large inflows within the 22-year period (1985–2007) in Lake Võrtsjärv.

Of local factors at the scale of coastal sections, the main effect of small inflows was not significant, but the model revealed that the presence of a small inflow in a section predicted the suppression of reed belt expansion on the south-western, western and south-eastern coasts (model term Year × Region × Small inflow $P = 0.023$; Fig. 6). Such suppression may, however, partly be related to anthropogenic activities in these sections, as many small inflows are used by fishermen as entries onto the lake.

We observed that management activities have suppressed the width of the reed belt by an average of 18 m across the lake ($P = 0.024$). For example, we observed large variation in reed belt width over the years in the north-eastern region and that can be explained by the detrimental effect of coastal meadow management on reed belt width. However, note that in the model the significance of the interaction factor Year × Region × Anthropogenic disturbance is borderline insignificant ($P = 0.068$).

4. Discussion

P. australis is known to be a generalist species found on various substrates, whose dominance in boreal lakes is widely reported (Brix, 1999; Andersson, 2001; Mäkelä et al., 2004; Partanen and Luoto, 2006). Common reed is the most abundant species in the emergent vegetation belt around Lake Võrtsjärv. The expansion of the macrophytic belt is described to occur since the early sixties of the previous century (Mäemets, 1973), this event is also emphasized in several later surveys (Feldmann and Mäemets, 2004; Feldmann and Nõges, 2007). It has, however, not been possible to exactly quantify the expansion rate of macrophytic belt in a very long term. In recent years the monitoring of coastal vegetation has been started within the framework of the national environmental monitoring programme, but it cannot provide information about long-term changes over decades retrospectively. Instead, we showed in the present study that using satellite images one can obtain a sufficiently long-term recursive review of vegetation dynamics in the coastal zone of large lake. According to trends revealed we can suggest that reed has not yet reached its maxi-

Table 1
The test results of fixed effect in the GLMM analysis of reed belt width (log-transformed). In table, DF denotes the estimates for the degree of freedom used in the *F*-test of factors in the model; *P*-values <0.05 are shown in bold.

Factor in model	Num DF	Den DF	*F*-value	*P*-value
Region	5	241	23.09	**<0.0001**
Vicinity of large inflow	1	241	14.88	**<0.0001**
Presence of small inflow	1	241	2.35	0.1267
Presence of anthropogenic disturbance	1	241	5.13	**0.0244**
Region × Large inflow	5	241	2.51	**0.0310**
Region × Small inflow	5	241	0.47	0.7977
Region × Anthropogenic disturbance	5	241	0.59	0.7078
Anthropogenic disturbance × Small inflow	1	241	0.25	0.6163
Year	10	2369	18.70	**<0.0001**
Year × Region	50	2369	7.69	**<0.0001**
Year × Large inflow	10	2369	2.08	**0.0230**
Year × Small inflow	10	2369	0.87	0.5584
Year × Anthropogenic disturbance	10	2369	1.18	0.2995
Year × Region × Large inflow	50	2369	2.67	**<0.0001**
Year × Region × Small inflow	50	2369	1.45	**0.0228**
Year × Region × Anthropogenic disturbance	50	2369	1.32	0.0677
Year × Anthropogenic disturbance × Small inflow	10	2369	0.82	0.6132

mum potential extent in the lake, as many shallow coastal areas are still unvegetated.

The primary assumption about causes of reed expansion, according to literature, could be related to water eutrophication (Andersson, 2001; Partanen and Hellsten, 2005; Zeng et al., 2009; Mäemets et al., 2010). It is reported that the six major inflows of the lake account for 80% of the catchments area and also for 80% of the total phosphorus and nitrogen loading (Järvet and Nõges, 1994; Nõges et al., 1999). Nutrient loadings are related to leaching from agricultural fields and cattle or pig farms, widely available in the catchment areas of the north-western and eastern coasts of Lake Võrtsjärv. The positive effect of large inflows is supported by the recording of the highest density of shoots of common reed and its shoot lengths near these inflows (Feldmann and Mäemets, 2004; Feldmann and Nõges, 2007). However, as the reduction of agricultural land use intensity since the 1990s has been reported for at least a decade (Mander et al., 1995; Tuvikene et al., 2004; Liira et al., 2008), then it is assumed that present day source of nutrients in Lake Võrtsjärv can be the lake's sediments, releasing accumulated nutrients by wave turbulence during low water seasons (Nõges et al., 1999; Nõges & Nõges, 1999). If this assumption holds and nutrients are the critical factor, the expansion of reed should look like more similar in all coastal regions than it actually is observed from our mapping efforts.

Several studies have, however, shown that factors other than eutrophication can be responsible for reed growth (Engloner, 2009). For instance, the positive effect of large inflows' estuary areas can also be related to the protection from exposition to the destructive activity of waves or ice, as has been suggested according to observations in Lake Võrtsjärv (Nõges et al., 1999) and shown by earlier studies elsewhere (Jupp and Spence, 1977; Coops et al., 1991).

Water level fluctuations have also been considered to be an important environmental driver determining the spread of emer-

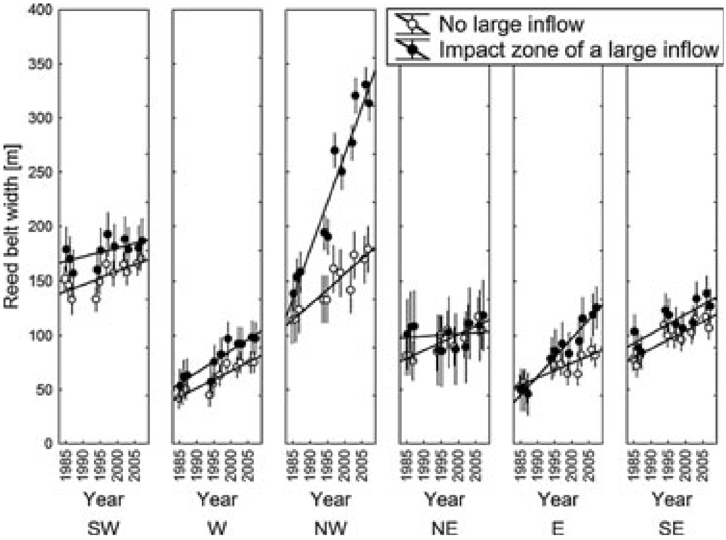

Fig. 4. Change in the average reed belt width within and beyond the impact zone of large inflows within the 22-year period (1985-2007) in six shoreline regions of Lake Võrtsjärv.

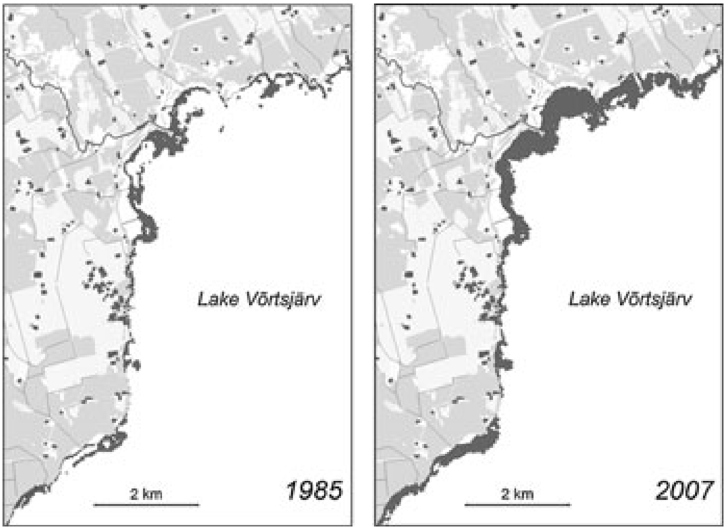

Fig. 5. Change in the coastal reed belt in the north-western part of Lake Võrtsjärv, within the estuary of the large inflow of the River Tänassilma, where the expansion of the reed belt has been the most significant over the 22 years. See also the reed dynamics at the NW coastal reach in Fig. 4.

gent vegetation on lakeshores, particularly in such shallow lake as Lake Võrtsjärv is. Low water levels in summer may provide suitable conditions for the down-slope germination and clonal expansion of helophyte species, including common reed (Coops et al., 2004). The rapid increase of water level in winter causes uprooting of plants from soft bottom by ice and that also can suppress the reed's growth and expansion (Feldmann and Nõges, 2007). In some years, ice-push during late winter and early spring can cause the local destruction of vegetation. We had an intention to test the average rate of yearly change of reed belt width against the growth period's low water level records (unpublished data obtained from Estonian Meteorological and Hydrological Institute), but only some non-conclusive correlations revealed. We also could not visually detect the reduction of reed after winters with

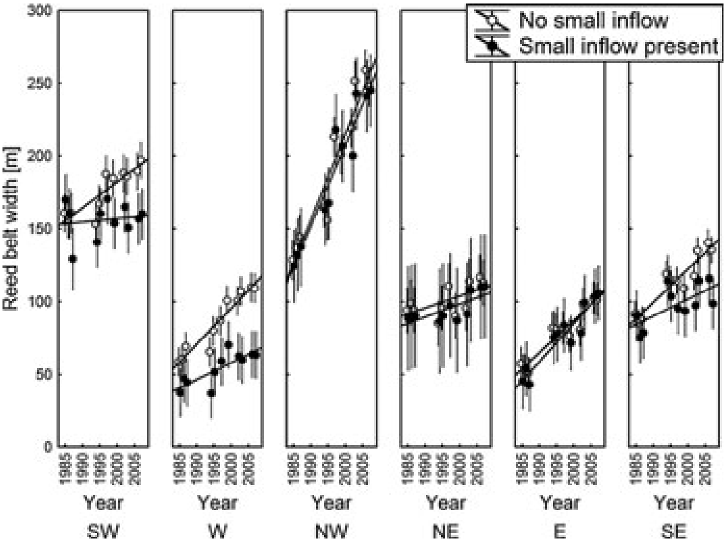

Fig. 6. Change in the average reed belt width within and beyond the impact zone of small inflows within the period of 22 years (1985–2007) in six shoreline regions of Lake Võrtsjärv.

heavy storms. We found that for trustful analysis of these relationships in helophytic vegetation dynamics, even higher frequency of observations over years is required. Therefore, these aspects need more elaborated studies in the case of Lake Võrtsjärv and, to obtain the full statistical power of analysis, an additional set of satellite images should be included as an important source of raw data.

The potentially suppressing effect of housing and coastal vegetation management on vegetation expansion has been suggested by earlier studies (Mäemets and Freiberg, 2004). Historically in the region, hay production for cattle forage has been the most common. It has reduced the encroachment of trees and shrubs (mostly willow), but also reed. We found that in coastal sections of housing or recreational areas, the macrophytic belt width was generally thinner throughout the observational period, suggesting on certain controlling effect. The intensity of coastal use for fishing, hay making, holiday activities and the activity of building new houses have been the lowest in the last two decades. We observed a significant potential indirect indication of management on changes of reed belt width in several regions near small inflows of southern regions and only a nearly significant direct indication of the anthropogenic management effect in the north-eastern region. The suppressing effect of small inflows on expansion is probably related to some indirect anthropogenic disturbance effect – the active use of small inflows by fishermen to access the lake. North-eastern region has been the main holiday region on the shores of Võrtsjärv, but during the period covered by images of the present study, the recreational activity has been in depression, and only in latest years, the holiday and tourist activities have intensified again. Lately, financial support for coastal meadow mowing has begun to be provided by national government and by the European Union. The cost-efficiency analysis of various management methods has shown that various methods can help to restore wet meadows (Liira et al., 2009). This seems to be a positive case also around Lake Võrtsjärv – even if these effects are still very sporadically local, and wide-scale improvements cannot be detected yet. However, if our assumptions are correct then in future, stronger effects in coastal meadow management will be evident and reanalysis with updated data should reveal more definite trends.

Large number of small inflows in some regions, however, is also related to paludification on coast and mud rich lake bottom in the southern region of the lake (Tavast, 2004). Because of small within-lake turbulence and currents, the lighter bottom sediments and small-grained fractions are being eroded from the shallow northern areas and transported to deeper areas in the southern part of the lake (Raukas and Tavast, 2002). In other studies, reed occurrence has been found to be positively affected by the finer sediments, but mostly by higher content of mineral soil, more than organic sediments (Jupp and Spence, 1977; Lenssen et al., 2000; Partanen and Luoto, 2006). The high organic matter content in sediments has been shown to suppress macrophyte growth as not providing sufficient solid ground for anchoring. This makes reed more vulnerable to wave action.

We showed that late summer medium resolution satellite images can be used for the estimation of emergent macrophyte dynamics in a large lake in the shortage or absence of ground data. The analysis of satellite images revealed that the generally expanding changes in the coastal reed areas over the last 22 years are mostly related to the neighbourhood of large inlets and their estuary areas, suggesting very complex set of potential factors, including wide and shallow coastal littoral zone dominated by mineral sediments, shelter from wave action, and the combination of these factors with lake's seasonally very low water levels may likely be the main trigger of reed expansion. However, we have to admit that for definite conclusions, appliance of the same methodology on longer time period of observations and addition of some other recursive remote data sources are required.

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Appendix A. Appendix 1

Satellite images used in the study, with water level data at image date. Water level is presented relative to 33.01 m above sea level, and the measure is provided by the Estonian Meteorological and Hydrological Institute (EMHI) according to the image acquisition date on the River Emajõgi, 300 m from the outflow at the NE part of the lake.

Satellite and sensor	Path/row	Acquisition date	Water level (cm)	Used for
Landsat 4 TM	186/19	1985 August 12	76	Mapping
Landsat 5 TM	186/19	1986 July 30	57	Mapping
Landsat 5 TM	186/19	1987 August 18	73	Mapping
Landsat 4 TM	186/19	1988 August 12	44	Mapping
Landsat 5 TM	187/19	1994 July 27	71	Mapping
Landsat 5 TM	186/19	1995 August 24	49	Mapping
Landsat 5 TM	186/19	1997 August 29	11	Mapping
Landsat 7 ETM+	187/19	1999 August 02	68	Mapping
Landsat 7 ETM+	187/19	1999 August 18	45	Evaluation
Landsat 7 ETM+	187/19	2002 July 09	61	Evaluation
Landsat 7 ETM+	186/19	2002 July 18	47	Evaluation
Landsat 7 ETM+	187/19	2002 August 10	21	Evaluation
Landsat 7 ETM+	186/19	2002 August 19	10	Mapping
Landsat 5 TM	186/19	2002 September 04	−6	Evaluation
Landsat 5 TM	186/19	2003 July 29	1	Mapping
Landsat 5 TM	187/19	2003 September 06	4	Evaluation
Landsat 5 TM	186/19	2006 July 05	−9	Evaluation
Landsat 5 TM	186/19	2006 August 06	−40	Mapping
Landsat 5 TM	186/19	2007 August 09	−11	Mapping

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KUI PEIPSI JÄRVE SEISUNDI INDIKAATORI
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AEROLASERSKANEERIMISE INTENSIIVSUSE PARANDAMINE JA
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KARIN KAUER

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