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Sari Partanen

RECENT SPATIOTEMPORAL CHANGES AND MAIN DETERMINANTS OF AQUATIC MACROPHYTE VEGETATION IN LARGE LAKES IN FINLAND

FACULTY OF SCIENCE,
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UNIVERSITY OF OULU

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SARI PARTANEN

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Abstract

During the past half century several large lakes in Finland have experienced notable changes in their ecological condition, induced mainly by water level regulation, eutrophication and land use transformation. The objective of this thesis was the quantification of the spatiotemporal changes of aquatic macrophyte vegetation in Finland during the second half of the 1900s. Mapped aquatic macrophyte cover from historic (1947–1963) and present day (1996–2000) aerial photographs, additional macrophyte data and several environmental variables were used to identify the main determinants of aquatic macrophyte distribution, abundance and change. Furthermore, factors influencing the littoral paludification process were identified.

The study was conducted in 24 boreal lakes (41–1116 km^2) with multisource vegetation data. Selected environmental variables of water level regulation, eutrophication and geomorphology were collected and analyzed. More than 402 km of littoral shoreline in historic and present day aerial photographs was analyzed with stereoscopic visual interpretation. A total of 474 habitat level study sites were used to examine the determining environmental factors of occurrence, abundance and change of emergent vegetation. Finally, 289 vegetation transects were performed in order to study the occurrence, types and main determinants of littoral paludification.

Water level regulation was found to be the primary factor behind aquatic macrophyte vegetation development at the whole lake level. The major vegetation changes were determined by the mean water level rise or reduction, decreased fluctuation range and reduced spring flood. The vegetation response was less pronounced in a lake with water level regulation similar to natural fluctuation. Eutrophication influenced aquatic macrophytes at the site level. Land use variables of tributary and agriculture, indicating nutrient increment, corresponded positively with vegetation occurrence and abundance. Geomorphology explained vegetation development at the habitat level. Clay and related deposits and the shore slope specified the vegetation occurrence and affected the abundance of vegetation. Water level regulation, eutrophication, clay and shallowness were found to influence paludification. Helophyte species, common reed (*Phragmites australis*) and water horsetail (*Equisetum fluviatile*), dominated the emergent vegetation in the studied lakes.

Keywords: aerial photography, environmental factors, eutrophication, geomorphology, overgrowth, paludification, water level regulation

Partanen, Sari, Ranta- ja vesikasvillisuuden ajalliset ja alueelliset muutokset suomalaisissa suurjärvissä viime vuosikymmeninä
Luonnontieteellinen tiedekunta, Maantieteen laitos, Oulun yliopisto, PL 3000, 90014 Oulun yliopisto, NorNet/Thule-instituutti, Oulun yliopisto, PL 7300, 90014 Oulun yliopisto
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Tiivistelmä

Viimeisen puolen vuosisadan aikana suomalaisiin suurjärviin on kohdistunut lukuisia muutoksia, jotka ovat vaikuttaneet järvien ekologiseen tilaan. Muutoksia ovat aiheuttaneet pääasiallisesti vesistöjen säännöstely, rehevöityminen sekä maankäytön muuttuminen. Tämän väitöskirjan tarkoituksena on analysoida noin viimeisten 50 vuoden aikana suomalaisissa suurjärvissä tapahtunutta ranta- ja vesikasvillisuuden pitkäaikaismuutosta. Historiallisilla (1947–1963) ja nykyisillä (1996–2000) ilmakuvilla, muilla kasvillisuusaineistoilla sekä useilla ympäristömuuttujilla tunnistettiin keskeisiä tekijöitä, jotka vaikuttivat kasvillisuuden esiintymiseen, runsauteen ja muutokseen. Tämän lisäksi tutkittiin rantojen pysyvän umpeenkasvun kehitysprosessia.

Tutkimusta varten kasvillisuudesta kerättiin monilähdeaineistoa kaikilta Suomen päävalumaalueilta yhteensä 24 eri järveltä, joiden koko vaihteli 41–1116 km^2:n välillä. Tämän lisäksi useita vesistöjen säännöstelyn, rehevöitymisen ja geomorfologian ympäristömuuttujia kerättiin ja analysoitiin. Stereoskooppisella visuaalisella ilmakuvatulkinnalla tutkittiin yli 402 kilometriä rantaviivaa historiallisista ja nykyisistä ilmakuvista. Ilmaversoisen ranta- ja vesikasvillisuuden esiintymistä, runsautta ja historiallista muutosta analysoitiin 474 habitaattitason tutkimuspisteellä. Rantojen pysyvän umpeenkasvun esiintymistä, umpeenkasvun eri tyyppejä ja sitä määrittäviä tekijöitä tutkittiin 289 kasvilinjalla.

Tutkimuksen tuloksena havaittiin, että järvitasolla vesistöjen säännöstely oli tärkein kasvillisuuden historialliseen kehitykseen vaikuttava tekijä. Huomattavimmat kasvillisuusmuutokset määräytyivät keskiveden noston, pienentyneen säännöstelyvälin, vähentyneen kevättulvan ja lasketun keskiveden tason seurauksena. Kasvillisuusmuutokset eivät olleet niin selviä, jos säännöstely muistutti luonnontilaista säännöstelyä. Rehevöityminen vaikutti ranta- ja vesikasvillisuuteen paikallisesti. Ravinteisuutta ilmentävät maankäytön muuttujat, ojat sekä maanviljelys, lisäsivät kasvillisuuden esiintymistä ja runsautta. Geomorfologiset tekijät selittivät kasvillisuuden kehitystä habitaattitasolla. Savinen maaperä sekä rannan mataluus lisäsivät vesi- ja rantakasvillisuuden esiintymistä sekä kasvillisuuden runsautta. Vesistöjen säännöstely, rehevöityminen, savinen maaperä sekä rannan mataluus lisäsivät rantojen pysyvää umpeenkasvua. Ilmaversoiset kasvilajit, järviruoko (*Phragmites australis*) ja järvikorte (*Equisetum fluviatile*), hallitsivat kasvillisuutta tutkituissa järvissä.

Asiasanat: geomorfologia, ilmakuvat, rehevöityminen, umpeenkasvu, vesistöjen säännöstely, ympäristötekijät

Field work, Kainuu, July 2003

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List of original papers

This thesis is based on the following original papers, referred to in the text by their Roman numerals I–V

I Partanen S & Hellsten S (2005) Changes of emergent aquatic macrophyte cover in seven large boreal lakes in Finland with special reference to water level regulation. Fennia 183: 57–79.

II Valta-Hulkkonen K, Partanen S & Kanninen A (2003) Remote sensing as a tool in the aquatic macrophyte mapping of a eutrophic lake: a comparison between visual and digital classification. Proceedings of the 9th Scandinavian Research Conference on Geographic Information Science, 4.–6.6.2003, Espoo, Finland, 79–90.

III Partanen S, Keto A, Visuri M, Tarvainen A, Riihimäki J & Hellsten S (2006) The relationship between water level fluctuation and distribution of emergent aquatic macrophytes in large, mildly regulated lakes in the Finnish Lake District. Verhandlung Internationale Vereinigung Limnologie 29: 1160–1166.

IV Partanen S, Luoto M & Hellsten S Habitat level determinants of emergent macrophyte occurrence, abundance and change in two boreal lakes in Finland (submitted).

V Partanen S & Luoto M (2006) Environmental determinants of littoral paludification in boreal lakes. Limnologica 36: 98–109.

Contributions

I Sari Partanen (SP) and Seppo Hellsten (SH) planned the study. SP conducted the study and wrote the paper. SH commented the manuscript.

II Sari Partanen (SP), Kirsi Valta-Hulkkonen (KV-H) and Antti Kanninen (AK) planned the study, conducted the field survey and data analysis; SP the visual classification, KV-H the digital classification and AK the classification accuracy assessment. KV-H wrote most of the paper and SP and AK contributed their results.

III Sari Partanen (SP), Antton Keto (AK) and Seppo Hellsten (SH) planned the study. SP, AK, Mika Visuri (MV), Anne Tarvainen (AT) and Juha Riihimäki (JR) performed the field survey. SP and AK analysed the data; SP was responsible for the aerial photograph analysis and AK for the vertical water level analysis. MV, AT and JR assisted in the analysis. AK contributed his results and SP wrote most of the paper. SH commented the manuscript.

IV Sari Partanen (SP), Miska Luoto (ML) and Seppo Hellsten (SH) planned the study. SP conducted the field survey and data analysis and ML was responsible for the modelling. ML contributed his results and SP wrote the paper.

V Sari Partanen (SP) and Miska Luoto (ML) planned the study. SP conducted the field survey and data analysis and ML was responsible for the modelling. ML contributed his results and SP wrote most of the paper.

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1 Introduction

Lakes belong to the most distinctive features of the earth's landscape. In physical geography, lakes are one of the most comprehensive study objects. Due to a lake's relative location in the geographical basic unit, the river basin area, all physical and human action in the surroundings ultimately affects the lake. Over time, physical factors such as climate and the geological cycle have been altering the conditions and the physical environment of each lake, while setting up the framework for other environmental factors (Clements 1936, Hutchinson 1957, Kuusisto 2005). As a result of their extreme importance for all natural organisms including humans, lakes have been a subject of interest to governments, industry, researchers and civilians. Water and nutrition supply, rich soils, favorable landscapes and several other factors have traditionally attracted human settlement to lakeshores (see Willén 2001). As a result of wide-ranging human activity, many lakes can no longer be regarded as being in their natural state.

Regardless of the fact that human activities have been impacting lakes for centuries, large scale environmental changes have started to occur only relatively recently, approximately during the past half century. Drastic decades of heavy industrialization, intensified agricultural production, wastewater increase and water level regulation have been followed by ecological changes in lake environments (Uotila 1971, Willén 1972, Makarewicz & Dilcher 1988, Meriläinen & Hamina 1993, Hellsten *et al.* 1996, Itkonen *et al.* 1999, Wade 1999, Andersson 2001, Meriläinen *et al.* 2001). More recently, large lakes have started to recover from the most impacted decades of the 1960s and 1970s as a result of changes in agriculture, environmental development in industry and water purification actions (Cullen & Forsberg 1988, Makarewicz & Dilcher 1988, Meriläinen *et al.* 2001, Wilander & Persson 2001, Willén 2001, Riihimäki *et al.* 2003). Despite the apparent improvements, which are often measured from the open lake, the littoral zone on the shore has not recovered from the environmental changes in several lakes (Hellsten 2000, Andersson 2001).

The demand for information regarding lakes will increase in the future together with management attempts, decreased amounts of pristine shoreline and public awareness resulting from lake research. The task of monitoring long-term anthropogenic impacts in lake environments has been proceeding for decades. Due to the variety of lake environments in different geographical regions, altitudes and latitudes, the monitoring needs and methods vary. Recently, the study approach has evolved from the previous emphasis on physical properties towards an ecosystem approach (European Union 2000). The most important research question today is still: how to examine the change? In the judgement of long-term ecological change, historical data provides a necessary window to the past (Egertson *et al.* 2004). Different aquatic organisms, plants and animals, have been used in the monitoring processes as they act as indicators of the nutrient content or other changes in the lakes.

This thesis was originally initiated from several water level regulation development projects. It was reinforced by the EU Water Framework Directive studies. The research was motivated by the lack of information concerning the effects of long-term water level regulation on the aquatic macrophyte vegetation in large regulated lakes and reasonable means for studying it. Along with the regulation impact the contributing factors affecting macrophytes were added. The scientific approach in this work is based on the methods of physical geography. Physical geography as a discipline devotes itself to the study of structures of the earth's physical environment (Haggett 1983). The field of phytogeography under physical geography studies the present and past distribution and occurrence of vegetation and environmental factors affecting it (Kalliola 1973, Tivy 1999). A holistic ecological approach is attempted by combining data from several levels starting from the individual species and habitats and moving to the population and community levels, with multiple data sources. This thesis contributes to our knowledge of aquatic macrophyte development in large boreal lakes after the large-scale water level regulation and eutrophication in the second half of the 1900s.

1.1 Outline and the aims of the study

In this work (I–V) aquatic macrophyte vegetation was studied on species, habitat, population and community levels in 24 large boreal lakes in Finland. Multiple historical and present data sets were combined to study the long-term vegetation changes in large boreal lakes during the time period from 1947–1963 to 1996–2000.

In Paper I the historic and present day hectare cover of mainly emergent aquatic macrophyte vegetation was mapped in seven study lakes. Comparable data sets from 35 different study sites were formed from historic (1947–1963) and present day (1996–2000) aerial photographs. The results of this study feature temporal and spatial vegetation cover changes of helophytes and nymphaeids and they are discussed in the framework of the major environmental factors, mainly water level regulation.

Paper II describes the aerial photograph interpretation methodology used in this study. Two aerial photograph interpretation methods, visual and digital classification, were compared in one study lake. The obtained results cover overall classification accuracies, categories of taxonomical classification, consumed time and hectare cover of macrophyte vegetation.

In Paper III the relationship between the horizontal and vertical macrophyte distribution was examined to test the modelled historical vertical occurrence of selected helophyte species. The modelled relationships between annual water level regulation and the vertical zonation of helophyte species was verified with observed emergent macrophyte coverage data from historic (1947–1953) and present day (1996–2000) aerial photographs and 280 present day vegetation transects in four study lakes. As a result of this study, the observed coverage change and the modelled vertical change are presented with species-specific cover of macrophyte species.

In Paper IV the emergent macrophyte occurrence, abundance and historic change were investigated at the habitat level with selected environmental factors. GIS-based factors, groups of soil type, land use and habitat morphology were analyzed in 474 habitat sites in two study lakes to define the determining factors of the vegetation variables. Results of this study identify the various habitat level factors in emergent macrophyte occurrence and abundance.

Paper V investigated the occurrence, types and main determinants of the littoral paludification in 20 study lakes. At the lake level, catchment characteristics, water quality and water level regulation were analyzed. At the habitat level, habitat morphology, soil quality and aquatic vegetation were analyzed from 289 vegetation transects. As a result of this study, the paludification occurrence, the type and the main determinants at the lake and habitat level were obtained.

The main aims and objectives of the study are:

1. To quantify the spatiotemporal changes of aquatic macrophytes in large regulated boreal lakes in Finland during the second half of the 1900s
2. To investigate the potential of novel aerial interpretation methodology in aquatic macrophyte mapping and monitoring
3. To explore the relative importance of different environmental factors in aquatic macrophyte development on multiple spatial scales

1.2 Boreal lakes, aquatic macrophytes and water level regulation

Boreal lakes are unique in their ecological characteristics in comparison to the other lakes of the world. The duration of the growing season is short. Regardless of the fact that the number of the lakes is high, the total volume of the water is small. Lakes have mainly originated from glaciations producing a long and sinuous shoreline broken into various bays, peninsulas and islands (Vaarama 1961, Kuusisto 2005). Together with a small average depth and continuing land uplift (Vaarama 1961, Willén 2001), this results in a wide productive littoral zone providing a large proportion of the annual production of the lake (Howard-Williams *et al.* 1995). Finally, a majority of the larger boreal lakes in several countries are under artificial water level regulation (Rørslett 1988, Alasaarela *et al.* 1989, Andersson 2001, Marttunen *et al.* 2001). Increased public awareness of environmental issues has enforced actions towards the research of large boreal lakes. Major developments of water regulation practices have been made during the past decade (see Willén 2001, Kuusisto 2005). The EU Water Framework Directive emphasizes ecological elements, such as aquatic macrophytes, in the monitoring and final judgments on the ecological state of lakes (Janauer 2001).

Aquatic macrophytes are vascular plants, aquatic bryophytes and taller algae totally or partially adapted to the aquatic environment (Sculthorpe 1967). They can be divided into different growth forms of helophytes, nymphaeids, isoetids, elodeids, ceratophyllids, lemnids, bryids and charids based on their structures and environmental adaptation (Mäkirinta 1978). The most important environmental factors controlling macrophyte development are water level fluctuation (Rørslett 1989), water quality, exposure (Segal 1971, Weisner 1991), bottom quality (Barko & Smart 1983) and the amount of light (Spence 1982).

Aquatic macrophytes are important for boreal lakes. In addition to phytoplankton and algae, macrophytes are responsible for the ecological base production in photosynthesis and they consume oxygen when decaying. Macrophytes provide shelter and nutrition for the bottom fauna and zooplankton, and a substrate for the epiphytic algae (Lindström 1973, Nurminen *et al.* 2001). They contribute to the provision of prey and reproduction areas for fish (Lindström 1973, Tikkanen *et al.* 1988, Palomäki & Hellsten 1996). Waterfowl nutrition and habitat is dependent on macrophytes (Makarewicz & Dilcher 1988, Knapton & Petrie 1999). Well-developed aquatic vegetation protects the shore from erosion and affects the quality and quantity of the sedimentation. It also secures the nutrients flowing from the shore to the open water (Sculthorpe 1967). On the other hand, aquatic macrophytes are reponsible for the paludification, i.e. the permanent overgrowth of the littoral shoreline (Papchenkov 1999, Hellsten *et al.* 2006).

Characteristic to aquatic macrophyte research in large boreal lakes is the small number of studies which have been performed. The majority of the classical macrophyte distribution studies were conducted in very small lakes and ponds (Seddon 1972, Keddy 1982, Sjöberg & Danell 1983, Weisner 1991, Toivonen & Huttunen 1995). Studies concerning eutrophication have mainly been performed in smaller lakes (Churski 1983, Ozimek & Kowalczewski 1984) and the emphasis in boreal lake research has recently also been towards smaller lakes (Jeppesen *et al.* 2000, Heegaard *et al.* 2001, Mäkelä *et al.* 2004, Valta-Hulkkonen *et al.* 2004). In ecological water level regulation assessments, fish and invertebrate studies outnumber vegetation studies (Bodaly *et al.* 1984, Hill *et al.* 1998). Larger boreal lakes were subjects for more intensive aquatic macrophyte research in recent decades (Kurimo 1970, Uotila 1971, Andersson 1972). Issues of pollution and eutrophication (Suominen 1968, Kurimo 1970, Uotila 1971) and water level regulation (Hudon 1997, Hellsten 2000) have been covered previously. Reference studies in the boreal zone in North America and Russia are few (Wilcox & Meeker 1991, Hudon 1997, Gottgens *et al.* 1998, Naumenko *et al.* 2000).

Ecologically the study of aquatic macrophytes is based on their indication of environmental conditions. Macrophyte species can be divided into categories varying from eutrophic to oligotrophic according to their nutrient preferences. Different species and growth form groups respond differently to water level changes and other physical factors such as freezing, flooding and ice movement. Aquatic macrophytes are best suited to describing long-term changes in the lakes (Sculthorpe 1967, Seddon 1972, Ilmavirta & Toivonen 1986). According to the vegetation strategy analysis by Grime (1977), external factors that limit plant biomass may be classified as either stress or disturbance. Stress-factors that restrict aquatic macrophyte production are associated with shortage of light, water, or mineral nutrients and non-optimal hydrostatic pressure. With disturbance, plant biomass is totally or partially destructed and it arises from substrate erosion, freezing, wave action or vegetation removal. Plants respond to these limiting factors with three types of strategies: stress tolerant, disturbance tolerant and competitive (Grime 1977). Based on the intermediate disturbance hypothesis (Connell 1978), biodiversity is greatest with intermediate amounts of disturbance.

Regarding **water level regulation**, in unregulated lakes water level fluctuation follows a certain natural annual rhythm depending on seasonal weather variations, resulting in a vertical macrophyte zonation to the littoral zone (Andersson 1973, Spence 1982). In regulated lakes the yearly water levels differ from the natural variation. Lakes are regulated mainly for hydropower production purposes, together with setting favorable conditions for flood protection, water supply, recreational use and lake restoration (Rørslett 1988, Hudon 1997, Marttunen *et al.* 2001). Water level regulation effects are complex, and they vary from shorter-term transient effects to longer-term persistent effects (Rørslett 1988). The harmful effects of water level regulation have been observed to be primarily comparable to the regulation amplitude, i.e. the difference between the maximum and minimum water levels (Wilcox & Meeker 1991). Secondly, water levels can be either raised or lowered at the beginning of the regulation (see Toivonen & Nybom 1989). Thirdly, the yearly rhythm can diverge from the natural variation even if the regulation amplitude still resembles the overall natural variation (Hejny 1971).

The most significant differences usually occur during the early spring when regulated lakes are emptied due to the high demand for electricity (Lindström 1973, Rørslett 1988, Hellsten 1997). Spring floods are delayed and lowered as a result of the diminished discharges (Hellsten *et al.* 2006). The annual maximum is reached during the summer, as compared to May-June in a natural lake. The harmfulness of water level regulation is based on the species-specific reactions of individual species to the hydrological changes (Sjöberg & Danell 1983). Regulation patterns in the lakes are always case-specific, depending primarily on the environmental conditions and secondly on the regulation plan. Among the regulated lakes there are several types of regulations ranging from large fluctuation storage reservoirs to milder regulation (Rørslett 1988). The effects of water level regulation can also be indirectly due to changes in flow conditions and further in water quality as shown in the recent study of Åman (2000).

2 Study areas

The study lakes in this thesis include some of the most important lakes covering major geographical regions in Finland, ranging from oligotrophic to eutrophic and regulated to non-regulated with varying human impact. In Finland, approximately one fourth of the lakes larger than 40 square kilometers have been studied. The selection of the study lakes was based on individual project needs in VTT and SYKE during the study period of 1998–2006. All major study lakes and their selected geographical and water quality properties are illustrated in Figure 1.

1) Lake Päijänne is a mainly oligotrophic (P-tot 13.0 µg/l, N-tot 490 µg/l), deep (mean depth 18.1 m) and clear water (color 35 mg Pt/l, chlorophyll-a 4.4 µg/l) lake in the Kymijoki River Basin in south-central Finland. It is the third largest (1116 km^2) lake in Finland and has been regulated since 1964 with the main emphasis on preventing harmful flooding. The number of different study sites in L. Päijänne was 11 for aerial photograph interpretation (I, III) covering 52.3 km of the shoreline. L. Päijänne is discussed in Papers I and III in this study.

2) Lake Näsijärvi (256 km^2) is an oligo-mesotrophic (P-tot 14.0 µg/l, N-tot 510 µg/l) relatively deep (mean depth 13.0 m) and relatively clear water (color 40 mg Pt/l, chlorophyll-a 4.4 µg/l) lake in the Kokemäenjoki River Basin in western Finland. Water level regulation started officially in 1980, with a longer unofficial history dating back to the late 1800s. Water level regulation was planned to benefit hydropower production by raising the water level. In L. Näsijärvi four study sites were included in the aerial photograph interpretation, totaling 73.5 km of shoreline (I, III, IV). In addition, 50 paludification study transects (V) and 313 habitat level study sites (IV) were included. L. Näsijärvi is discussed in this study in Papers I, III, IV and V.

3) Lake Pyhäjärvi (122 km^2) is a meso-eutrophic (P-tot 25.0 µg/l, N-tot 630 µg/l), relatively shallow (mean depth 6.2 m) and medium turbid (color 35 mg Pt/l, chlorophyll-a 10.0 µg/l) lake in the Kokemäenjoki River Basin in western Finland. Water level regulation was implemented in 1962 and the water levels have been decreased. Altogether three study sites were selected for the aerial photograph interpretation, which covered 49.2 km of the shoreline (I, III, IV). 50 paludification study transects (V) and 161 habitat level study sites (IV) were also included. L. Pyhäjärvi was studied in Papers I, III, IV and V.

4) Lake Vanajavesi (160 km^2) is a eutrophic (P-tot 36.0 µg/l, N-tot 980 µg/l), shallow (mean depth 5.5 m) and medium turbid (color 48 mg Pt/l, chlorophyll-a 9.2 µg/l) lake in the Kokemäenjoki River Basin in southwestern Finland. Water

level regulation in the lake was started in 1962, with the result that spring floods have decreased in severity. In L. Vanajavesi three study sites were included in the aerial photograph interpretation, totaling 68.2 km of studied shoreline (I). An additional 50 study transects were included in the paludification study (V). L. Vanajavesi was studied in Papers I and V in this study.

5) Lake Unnukka (80 km^2) is a mesotrophic (P-tot 15.0 µg/l, N-tot 510 µg/l), relatively shallow (mean depth 7.5 m) and average turbid (color 40 mg Pt/l, chlorophyll-a 7.8 µg/l) lake in the Vuoksi River Basin in eastern Finland. Water level regulation of the lake was started in 1972 and the yearly water level interval is only 0.2 m, the smallest in Finland. From L. Unnukka, two different study areas were studied in the aerial photograph interpretation, totaling 58.8 km of studied shore (I). L. Unnukka is discussed in this study in Paper I.

6) Lake Kallavesi (473 km^2) has a mesotrophic (P-tot 17.0 µg/l, N-tot 600 µg/l) water quality, and it is a relatively deep (mean depth 12.1 m) and medium turbid (color 50 mg Pt/l, chlorophyll-a 6.4 µg/l) lake in the Vuoksi River Basin in eastern Finland. Water level regulation started in 1972 and the water level fluctuation closely resembles the natural variation. In L. Kallavesi, six different study areas were formed for the aerial photograph study (I, III) covering 77.4 km of the shoreline. Altogether 28 study transects were included in the paludification study (V). L. Kallavesi was studied in Papers I, III and V in this study.

7) Lake Kemijärvi (231 km^2) has a mesotrophic (P-tot 16.0 µg/l, N-tot 318 µg/l, chlorophyll-a 6.7 µg/l) and slightly dystrophic (color 80 mg Pt/l) water quality. It is a relatively shallow (mean depth 5.2 m) lake in northern Finland in the Kemijoki River Basin. Waters in L. Kemijärvi have been regulated since 1965 with a regulation interval of almost 7 m, the highest in Finland. Two larger areas and five former islets were used in the aerial photograph study (I) covering over 23 km of the shoreline. L. Kemijärvi is discussed in Paper I.

8) Lake Onkivesi (123 km^2) is a shallow (mean depth 3.5 m) and eutrophic (P-tot 56 µg/l) regulated lake situated in the Vuoksi River Basin. A more detailed description of L. Onkivesi can be found in Paper II.

9) Lakes Haukivesi, Kermajärvi, Kiantajärvi, Kiimasjärvi, Koitere, Kostonjärvi, Lammasjärvi, Lentua, Nuasjärvi, Ontojärvi, Puulavesi, Simpeleenjärvi, Suontee, Pyhäjärvi (Säkylä), Vuokkijärvi and Yli-Suolijärvi are regulated and non-regulated lakes with varying size (41–560 km^2), depth (mean depth 3.7–11.8 m) and water quality (P-tot 4.5–21.5 µg/l, color 20–85 mg Pt/l) and situated in all the major river basins in Finland. In the habitat level paludification study, 4–10 study

transects from each lake were included (V). These lakes are described in more detail in Paper V.

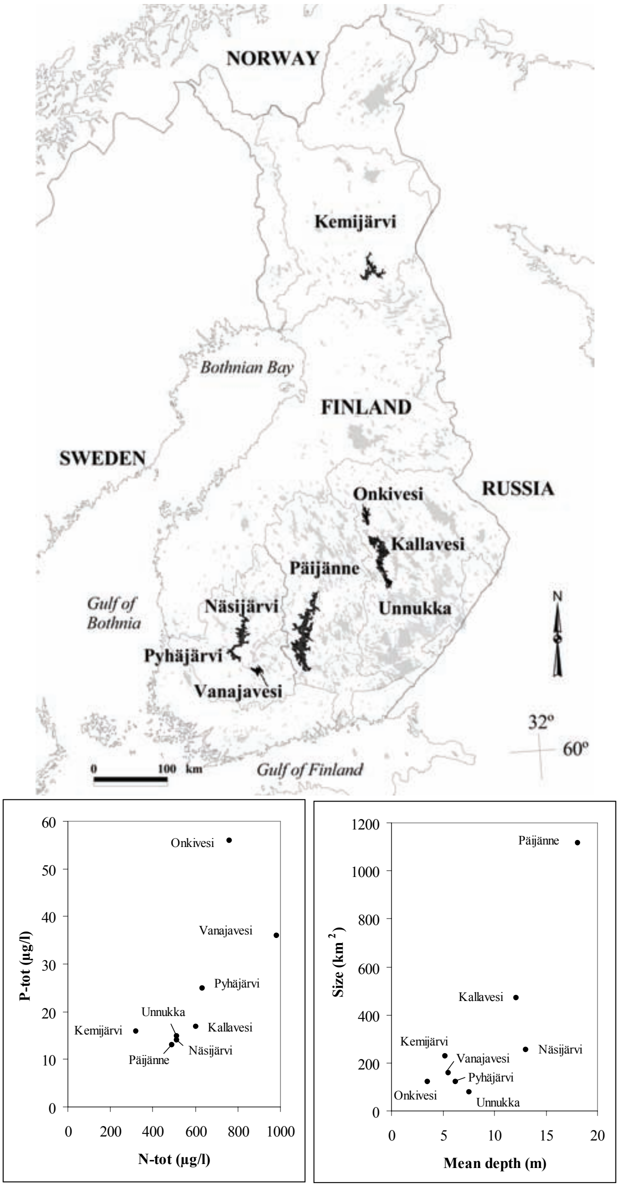

Fig. 1. The location of the main study lakes Päijänne, Näsijärvi, Pyhäjärvi, Vanajavesi, Unnukka, Kallavesi, Kemijärvi and Onkivesi along with the mean depth, size and water quality properties of total phosphorus and total nitrogen.

3 Material and methods

A combination of complementary methodology and data was used to study aquatic vegetation and environmental factors from single species to habitats, populations and vegetation communities. The different materials and methods used in this study are covered briefly in this section. Detailed descriptions of the material and methods are given in Papers I–V.

3.1 Vegetation data

3.1.1 Stereoscopic visual aerial photograph data (I, II, III, IV)

The field observations were based on the species-specific occurrences of helophytes and nymphaeids, i.e. emergent and floating leaved vegetation. The field observations for the visual classification consisted of the interpretation, comparison and classification of vegetation, mainly emergent. The aquatic vegetation was investigated either from a boat or from the shore. The location and species composition of the macrophyte communities were marked on the printout of the aerial photograph and verified with GPS when necessary. Growth depth, density and biomass were not measured. In visual classification the aerial photographs were scanned. This digital image was geo-referenced on the Finnish digital base map of scale 1:20 000. The vegetation was digitized using the coastline of the Finnish digital base map as a reference layer. In the current day situation (1996–2000), the classification was performed with a species and growth form accuracy. In the historic situation (1947–1963), mainly emergent vegetation was classified into one category. Stereoscopic glasses were used to obtain a three-dimensional view specifically with the historic data. The visual classification was carried out using ArcView and MapInfo.

In the habitat level study (IV), based on the remotely sensed data, data set of 474 habitat sites was formed by locating study sites at 100 m intervals along the main shoreline. The historic vegetation and the present day vegetation were measured as present or absent. In addition, vegetation was measured in length (m) at sites perpendicular to the shoreline.

3.1.2 Vegetation transects (III, V)

The current day data sets from the study lakes were collected using a belt transect method, which is a transect divided into zones. This method differs slightly from a recently developed main belt transect method (see Leka *et al.* 2003). A zone transect is defined as a 10 m wide area that runs from the highest water level to a depth of approximately 2.5–3.0 m, up to the last occurrence of aquatic macrophytes. Vegetation is divided into zones according to the species or the growth form in such a way that if a certain species clearly forms a zonal population it is recorded as an individual zone. Populations can be overlapping.

All zone transects are measured with a levelling instrument and a level rod. The instrument is placed on the shoreline and the beginning and the ending level of each zone is recorded with a rod reading which is later bound to the actual water level of the current day. In the water the actual depths were recorded. The beginning and ending distance of each zone was also measured. Each transect was photographed from both ends and the GPS-coordinates and the bottom quality were recorded.

All the encountered species from the whole zone transect were recorded in one form. Aquatic mosses and algae were not recorded. The abundance of each species was recorded on a scale from 1 to 7, which was converted to percentages as follows: 1) very rare, one observation, 2) rare, < 1%, 3) rather rare, 1–5%, 4) moderately common, 6–25%, 5) rather common, 25–50%, 6) common, 51–75% and 7) very common 76–100%. The macrophyte species analyzed here are based on the studies by Linkola (1932, 1933) and true aquatics, aquatics in a broad sense and species commonly living in the water were included.

3.1.3 Paludification data (V)

In littoral paludification (V), three different processes causing paludification were identified from the shores: a) bottom ward overgrowth by accumulating dead organic matter, peat and very dense vegetation, b) surface ward overgrowth by plant species and c) overgrowth within the water column by plant species (see Segal 1971, Papchenkov 2003, Hellsten *et al.* 2006). One or more characteristics were noted at the same site. At the habitat level the paludification was measured as present or absent. At the lake level, paludification was measured as the percentage of the paludified transects of the total number of transects for each lake.

3.2 Environmental data

Environmental data of water level regulation, geomorphology, land use and water quality have been used along with the aquatic macrophyte data (see Figure 2). A combination of general lake level characteristics of surface area, length of the shoreline, maximum depth, mean depth, water volume, river basin area above the lake, duration of the ice-free period, and mean water level were presented at the general level of each lake (I, II, III, IV). Several lake level characteristics were used in the statistical analysis of the environmental factors of paludification (V).

3.2.1 Water level regulation (I, III, V)

The hydrological water level analysis was based on a long-term water level measurement action by the environmental authorities (SYKE database). Daily water levels over a known period of time have been plotted for general water level analysis in the lakes (I, III). Detailed water level analysis in all the studied lakes (I, III, V) was based on the REGCEL-application developed by the SYKE Water Resources Management Division (Hellsten *et al.* 2002). REGCEL calculates more than thirty parameters from the daily water level values. The differences in the hydrological conditions between different periods were deduced by re-calculation of the natural water levels from the regulated water levels to adjust to the same hydrological conditions.

3.2.2 Geomorphology: soil, exposure and slope (I, IV, V)

A general soil type description was based on previous literature (see I) for lake level soil type analysis and on 1:20 000 soil maps of the Geological Survey of Finland at the general study site level (I). A detailed habitat level soil type analysis (IV) was based on Maps of Quaternary Deposits 1:20 000 of the Geological Survey of Finland. The dominant soil at the habitat was noted based on GEO classification and further grouped into rock, moraine, sand, clay and peat. The bottom soil was included in the study when two soils occurred in layers (IV).

In the study on littoral paludification (V), the habitat level bottom soil quality was marked as present or absent with a scale of peat, rock, gravel, sand, sandy mud and clay based on the belt transect method. In the lake level analysis, the soil type was analyzed from the 85 m pixel digital Finnish soil map (SYKE database) using a classification of sand, clay, rock peat and moraine. The proportion of different classes in the lake was determined by the percentage of the study transects in different soil types.

The impact of shore exposure, an opening angle from the habitat to the open lake (Håkanson & Jansson 1983, Palomäki 1992), was measured at the habitat level (IV, V) by a maximum angle of two 500 m segments. The opening angle was measured using the radiating lines and points tool (see Ekebom *et al.* 2003) with a 5 degrees threshold. If openness was not achieved, the measurement was repeated with a 1 degree threshold. The sloping angle (%) of the shore at the habitat level (IV) was calculated from the closest mapped depth contour line, 2–3 m in basic maps, perpendicular to the shore line. In belt transect data it was measured using the maximum measured distance and the depth of the furthest growing vegetation zone (V).

3.2.3 Land use (I, IV)

The main land use type at the site level was recorded from the 1:20 000 base maps (I). In the habitat level analysis (IV) the following variables were measured. Permanent and recreational settlement, i.e. housing, was measured as present or absent within a 30 m zone from the habitat. Houses from the historic material (1947–1950) were measured from the aerial photographs and verified with base maps (mapped 1949–1952) (Agricultural Quaternary deposits 1:20 000 National Land Survey of Finland 1958, 1962). From the current day material (1998–2000) houses were measured from the digital base maps. The effect of agriculture was measured as the presence or absence of fields within a 50 m zone from the habitat. In the historic situation black and white aerial photographs were used and in the current situation the digital base map field layer was used. The effect of incoming nutrients from the sub-catchments via small tributaries was measured as present or absent within a 100 m distance of the shoreline from the habitat. In delta or river mouth openings all sites were taken into account within 100 m of the opening.

3.2.4 Water quality (I, II, III, IV, V)

A combination of several water quality parameters of total nitrogen, total phosphorus, water color, clorophyll-a, pH, and secchi depth were presented at the general level for each lake (I, II, III, IV). Color and total phosphorus (V) were used for statistical analysis as environmental factors in the paludification study.

4 Results and discussion

4.1 Environmental factors in emergent macrophyte development

Several environmental variables, physical and anthropogenic, were studied to determine the emergent aquatic macrophyte vegetation development in large boreal lakes in Finland. These contributing environmental variables can be categorized into three main groups of factors, namely water level regulation, eutrophication and geomorphology. In previous studies, these major determinants were found to control macrophyte development in lakes (Segal 1971, Barko & Smart 1983, Rørslett 1989, Weisner 1991). In this study, the main groups of environmental factors were found to influence the emergent vegetation at different levels (see also Hellsten 2000). Firstly, water level regulation forms the most important environmental factor at the lake level, i.e. the aspect of the whole lake. Secondly, eutrophication affects mostly at the site level, which is defined here as a smaller regional section of the lake. Thirdly, geomorphology defines the vegetation development at the habitat level, covering the immediate local environment of aquatic vegetation on the shore. In the following sections these environmental factors are discussed in more detail. There is also a group of other physical and chemical factors working in the littoral zone, which fall outside the scope of this study and have not been analyzed here.

4.1.1 Water level regulation defines the macrophyte development in lake level (I, III, IV, V)

Water level fluctuation is one of the most important factors controlling aquatic macrophyte growth (Quennerstedt 1958, Sculthorpe 1967, Rørslett 1988, Hellsten 2001). In this study, the water level fluctuation impacts were observed at the lake level (I, IV, V), at the vegetation population and communities level (I, III) and at the habitat and individual species level (III, IV, V). The aquatic macrophyte vegetation responses to altered water level fluctuation included changes in the vegetation coverage and zonation (I, III) and altered littoral paludification (V). Long-term exposure to modified water levels resulted in uniform changes within lakes with a similar hydrologically altered regulation pattern (I, III). Although the study sites varied greatly with geographical features, the coverage changes were constant within the study sites in all lakes under distinct regulation (I). No clear difference was obtained in the relative vegetation coverages from site data before the regulation. However, after the regulation the natural and regulated situations differed from each other (I). Regulated lakes showed a positive response to the paludification (V). In habitat level analysis, water level regulation was concluded to be the major determinant impacting the vegetation change in both lakes (IV).

With a **mean water level rise** and **decreased water level fluctuation range**, reduction in macrophyte vegetation cover was observed in the study lakes (I). Identical results have been documented in numerous other studies. In the investigations by Wilcox & Meeker (1991), a similar situation with raised water level and decreased fluctuation resulted in species alterations and structural vegetation changes. Macrophyte reduction after a water level increase has been observed in several other lakes (Sjörs & Nilsson 1976, Wallsten & Forsgren 1989, Hudon 1997, Hellsten 2001, 2002), and the littoral zone is reported to be less uniform and species rich (Quennerstedt 1958, Jonasson 1976, Sjörs & Nilsson 1976, Sjöberg & Danell 1983, Hellsten 2001). According to Hudon (1997), high summer water levels may eliminate the existing emergent vegetation and shift the distribution towards the upper part of the shore. If the regulated water levels maintain the previous upper water level, the littoral zone may become well defined (see Sjörs & Nilsson 1976). With decreased fluctuation range, the upper littoral zone can remain almost unaltered, whereas the lower zone may recede (Sjörs & Nilsson 1976).

The **mean water level drawdown** at the beginning of regulation resulted in increased vegetation cover in this study (I). In other studies, vegetation has been reported to increase under reduced water level (Hudon 1997, Åman 2000) and the emergent macrophyte vegetation cover has increased with decreasing water level (Egertson *et al.* 2004). Decreased summer water level creates suitable conditions for the germination and growth of taller emergent species (Coops *et al.* 2004). With reduced water levels macrophytes overcome the light limitation: more light penetrates to the sediment, favoring seed germination and growth (Wallsten & Forsgren 1989, Egertson *et al.* 2004). Permanent mean water level lowering will contribute to paludification (V), also discussed by Meriläinen & Toivonen (1979) and Rørslett (1991).

The **reduced spring flood** resulted in increased vegetation cover (I) and altered zonation (III) in this study. Moreover, the spring flood reduction had a positive effect on littoral paludification (V) in the study lakes. Several previous studies indicated that a lowering of the fluctuation induces an increase in the macrophyte vegetation (Weisner 1987, Rørslett & Johansen 1996, Hellsten *et al.* 2006). Reduction in the spring flood is reported to benefit the growth of several macrophyte species (Quennerstedt 1958). Combined with a decreased water level during the open water period, a rapid invasion of helophytes in the uppermost littoral can occur (Hellsten *et al.* 1996). On the other hand, lowering of the water level may dry the littoral zone and lead to tree species invasion and an unbalanced littoral (Sjörs & Nilsson 1976). In paludification, even small changes in the growing season or spring flood levels have accelerated hydrosere succession and the expansion of helophyte and nymphaeid vegetation (see Toivonen & Nybom 1989). Water level regulation changes the composition of the bottom substrate in the lakes and the stabilized shores can be replaced with a new, erodable shoreline (Hill *et al.* 1998). A lowered flood maximum leaves the dead vegetation remains in the lower littoral (Mäemets & Freiberg 2004, Hellsten *et al.* 2006), where they act as a growing medium for new vegetation. According to Hill *et al.* (1998), changes in the shoreline are predictable from the water level variation.

L. Kallavesi is the most **mildly regulated lake** and the differences in the vegetation abundance within the study sites were greatest (I). In a regulated lake with an atypical regulation pattern mimicking the natural spring flood the flora and the species numbers have not been reported to suffer from the regulation and thus resemble natural values (see Hill *et al.* 1998).

In general emergent species, compared to submergent, survive water level changes better due to their supporting and highly resistant below-ground structures (Hudon 1997). Emergent species also react to the water level changes more slowly than submergent species (Hudon 1997) and are thus good indicators of longer-term changes. In this study, individual helophyte species exhibited **species-specific responses** to water level fluctuation and regulation patterns (III).

Phragmites australis (common reed) dominated the areal coverage in most lakes (III). It was found to prefer delayed flood and low water levels during the early summer (III). Its relative proportion was smallest in lakes with stable water levels during the open water period (III). Previous results from large boreal lakes (Wallsten & Forsgren 1989, Naumenko *et al.* 2000, Andersson 2001, Mäemets & Freiberg 2004) confirmed the dominance of *Phragmites australis*. Its dominance over other species is based on several species-specific features, in which the influence of water level regulation is vital. It tolerates competition and stress well (Grime 1977, Rørslett 1989). As a generalist species it enjoys a wide distribution, dominating lakes from small, shallow and eutrophic (Weisner 1987), to alkaline (Duigan *et al.* 1999), large and shallow (Mäemets 2002), large and eutrophic (Andersson 1972) and deep and oligotrophic (Andersson 2001). Although it is reported to suffer from carbon and nutrient balance-related die-back in several

European countries (van der Putten 1997), in Fennoscandia it invades new biotopes with relatively low water levels. It is found to occur with a wide vertical range in relation to water level fluctuations (de Swart *et al.* 1994). Resulting from several years of low spring water levels, *Phragmites australis* expansions can be severe (Dienst *et al.* 2004). Delayed spring floods provide early establishment possibilities for young seedlings on the shore. During the first year larger rhizome biomass is produced and the following year the rate of emergence above the water surface as well as the height of the plant is dependant on the size and mass of the first-year growth. Plants which do not survive above the water die the following year (Weisner & Ekstam 1993).

Equisetum fluviatile (water horsetail) coverage proportions were highest in lakes with stable water levels during the open water period (III). Studies by Pearce & Cordes (1988) confirm that *Equisetum fluviatile* probably benefits from stable water levels. Anttonen-Heikkilä (1983) and Rintanen (1996) noted a marked decrease of *Equisetum fluviatile* after the water level had been raised in Finnish lakes. These observations are in accordance with the hypothesis of van den Brink *et al.* (1995) that *Equisetum fluviatile* cannot tolerate flooding during its growth period. On the other hand, it has also been reported to be unaffected by flooding (Sjöberg & Danell 1983). Based on the studies of Grime (1977) and Rørslett (1989), *Equisetum* is a strong competitor.

***Carex* sp.** (sedges) species were found to cover a marginal proportion of the total emergent vegetation in this study (III). According to Maristo (1941) and Sjöberg & Danell (1983) their growth is prevented by delayed floods and low water levels during early summer. In addition, stabilized and raised water levels have resulted in the disappearance of the *Carex* zone (Sjöberg & Danell 1983, Hellsten 2001). By comparison, flooding reduces the *Carex rostrata* (bottle sedge) populations compared to *Carex aquatilis* (water sedge), which is more tolerant to flooding effects (Sjöberg & Danell 1983).

Glyceria maxima (reed sweet-grass) occurrence was highest in lakes with clearly altered water level regulation (III, V). As an introduced species, it tolerates water level fluctuation by forming floating, partly extensive formations not dependent on the water level fluctuation (see Uotila 1971). Several other studies report that damming (Hill *et al.* 1998) and destabilization of established littoral communities by changing water levels (Hudon 1997) have a positive effect on the amount and colonization of exotic species.

4.1.2 Eutrophication has a site specific effect on aquatic macrophytes on the littoral (I, IV, V)

Eutrophication can be one of the most powerful agents changing the aquatic macrophyte ecology and the whole ecosystem in lakes (Hasler 1969, Wetzel 1983). Eutrophication means the acceleration of the base production and all biological activity in the lake ecosystem. The major causes of eutrophication are the construction of human settlements, agriculture, industrial activities and sewage inflow. Eutrophication is strongly related to land use changes in the lakeshores and catchments; forested catchments have been changed into farmlands, pastures and urban areas (Järnefelt 1952, Churski 1983, Dickman *et al.* 1983, Ozimek & Kowalczewski 1984, Wade 1999, Naumenko *et al.* 2000, Willén 2001, Egertson *et al.* 2004, Uuemaa *et al.* 2007).

Several chemical and physical water parameters control the distribution of aquatic macrophytes in lakes (Pip 1989, Rintanen 1996, Jeppesen *et al.* 2000, Vestergaard & Sand-Jensen 2000). In general, waste water loading includes increases in nutrients, organic substances and environmental toxins. Effluents from human populations and agriculture mainly contain phosphorus, nitrogen and organic particles, whereas industrial wastewaters are generally acidic and contain organic wastes (Kurimo 1970, Naumenko *et al.* 2000, Wilander & Persson 2001). On the other hand, waters running from forestry areas are humic and nutrient-rich. Eutrophication will affect the composition, amount, distribution and densities of species and growth forms (Best *et al.* 1984, Wade 1999, Vestergaard & Sand-Jensen 2000, Egertson *et al.* 2004) and the vegetation cover (Naumenko *et al.* 2000, Andersson 2001). Eutrophication along with water level decrease has been the major factor in lake overgrowth and even the complete disappearance of lakes (Churski 1983, Rørslett 1991). Most commonly the eutrophication of aquatic ecosystems have been studied with the use of primary production and planktonic organisms or in sets of smaller lakes with varying environmental conditions (Granberg 1973, Best *et al.* 1984, Hough *et al.* 1989, Gacia *et al.* 1994, Willén 2001, Squires *et al.* 2002).

In this study, eutrophication was studied at the lake level (I, V), at the habitat level (IV, V) and with individual species (IV) of emergent aquatic macrophytes. At the lake level, the amount of emergent vegetation cover was observed to either increase or decrease (I) in several lakes during the study period. Several previous studies conducted in the boreal zone and in large lakes have reported an increase in the lake vegetation cover along with eutrophication (Wallsten 1981, Naumenko *et* *al.* 2000, Andersson 2001, Valta-Hulkkonen *et al.* 2005). According to Kurimo (1970) several helophytes and nymphaeids are indifferent to eutrophication effects. Submergent species function better as indicators of eutrophication effects. They are dependent on light penetration and absorb nutrients from the water with their leaves. Submergent macrophytes cannot root in the soft bottom or resists increasing turbidity caused by phytoplankton production (Best *et al.* 1984, Ozimek & Kowalczewski 1984, Jeppesen *et al.* 2000, Sand-Jensen *et al.* 2000, Egertson 2004). The emergent vegetation tolerates eutrophic conditions rather better. These plants take up nutrients with their rhizomes and therefore reflect slower changes in the bottom sediment nutrient content and organic matter (Weisner 1991, Coops *et al.* 1996, Wade 1999, Jeppesen *et al.* 2000, Egertson 2004). On the other hand, increasing eutrophication has also been reported to decrease the emergent vegetation (Pieczynska *et al.* 1988, Weisner 1991, van der Putten 1997).

Eutrophication was discovered to affect aquatic macrophytes more locally (IV). The presence of incoming nutrients from the tributaries and from agricultural fields had a positive effect on vegetation occurrence and abundance, respectively (IV). At the species level, the occurrence of *Phragmites australis* had a strong positive response to agricultural fields (IV). Based on relatively recent studies, improvements in wastewater treatment have increased the proportion of non-point source pollution, mainly from agriculture (Vuorenmaa *et al.* 2001, Willén 2001). Although the emergent species have been found to suffer from eutrophication (Wade 1999) and not to respond to the incoming nutrients (Mäemets & Freiberg 2004), several studies suggest that eutrophication is one of the main factors behind the macrophyte expansion (Andersson 2001, Mäemets & Freiberg 2004). Wallsten (1981) found that enlargement of the vegetation areas occurring with farming and the increased nutrient content encouraged vegetation increase. On the other hand, the ceasing of cattle grazing, simultaneous application of new nitrogen- and phosphorus-rich fertilizers and intensive farming (see Meriläinen & Toivonen 1979) will increase the agricultural effects.

In this study eutrophication affected the paludification of the shores (V). At the lake level the total phosphorus content, and at the habitat level the abundance of eutrophy indicator species and *Glyceria maxima,* correlated positively with the paludification (V). Both the surface ward paludification and paludification within the water column were controlled by species indicating eutrophic conditions (V). The main paludification type was the bottom ward paludification in the studied lakes (V). Previous studies have reported a relationship between the nutrient content and overgrowth in northern European lakes (Churski 1983, Hellsten 2000, Andersson 2001, Mäemets & Freiberg 2004). Along with eutrophication, the amount of accumulated material on the shore increases. This accumulation combined with increased vegetation and a diminished spring flood creates favorable conditions for the paludification process. The introduced species *Glyceria maxima* is an aggressive spreader, favoring eutrophic conditions (Uotila 1971). It is immune to water level fluctuation and creates vegetation quickly, turning into peat by partly bottom ward and partly surface ward paludification.

The dramatic change in the land-use of shores (IV) and the improved water quality over the years (I) during the study period in all the lakes would suggest vegetation decrease. Large scale water monitoring has been conducted with common criteria since the 1960s–1970s, but without indicating the previous water quality and eutrophication trend (Vuoristo 1998, Wilander & Persson 2001). The water samples taken from the pelagic areas in the monitoring do not represent the situation in the littoral. Despite the recent improvements, decade-long nutrient loading of the lakes has increased nutrient availability. In regulated lakes with eutrophication effects, distinguishing the two from each other can be difficult (Andersson 2001, Mäemets & Freiberg 2004, Hellsten *et al.* 2006).

4.1.3 Geomorphology and other factors determine the vegetation development in a specific habitat (I, III, IV, V)

A number of other environmental factors also control aquatic macrophyte dynamics in large lakes. In this study, geomorphological factors were found to explain the vegetation development (I, IV, V). The physical and chemical conditions of the **substrate character** determine the distribution of aquatic macrophytes (Pearsall 1921, Lohammar 1965, Sculthorpe 1967, Spence 1967, Keddy 1982, Weisner 1991). In this study clay and clay-related deposits specified the spatial distribution of aquatic macrophytes (I, IV). Clay-dominated study sites were in proportion most abundant in conjunction with emergent vegetation (I). Clay soils were found to be one of the primary determinants in littoral paludification both at the lake level and at the habitat level (V). With clay occurrence, a majority of the vegetation was formed by *Equisetum fluviatile*, but with sand occurrence the emergent vegetation was dominated by *Phragmites australis* (III, IV). In sand-dominated, oligotrophic and open study sites the vegetation was abundant and the largest vegetation increase occurred (I). The results of this study are compatible with those of previous studies. In the previous studies fertile soils such as clay and silt have been found to increase the macrophyte growth (Sculthorpe 1967, Uotila 1971, Wisheu & Keddy 1989, Rintanen 1996). However, species-specific preferences vary between different emergent species. *Phragmites australis* is found to prefer open, sandy and oxygen-rich shores (Weisner 1991, Keto *et al.* 2002) and on the other hand it also favors the accumulation of organic sediment (Mäemets & Freiberg 2004). As a good competitor (Hellsten 2001) its occurrence is not necessarily related to the nutrient status. However, as an indifferent species, it cannot tolerate increased eutrophication but benefits from the nutrient addition in oligotrophic lakes. *Equisetum fluviatile* avoids hard bottom substrates and is erosion sensitive (Hellsten 2001) and therefore may favour clay bottoms. On the other hand, it has been found to have a wide tolerance range for the bottom substrate (Hellsten 2001). The dominant soil is only one factor in the bottom substrate development, which is a result of many environmental factors, mainly exposure (Hellsten 1997).

The **exposure** of the shore has been determined to be one of the most important factors controlling macrophyte distribution and growth (Segal 1971, Keddy 1982, Spence 1982, Weisner 1987). In the lake level study (I), the vegetation was found to be more abundant in sheltered sites compared to more exposed ones. On the other hand, exposure did not have a clear effect on the paludification (V). Furthermore, exposure did not affect the vegetation occurrence, abundance and change in the habitat level study (IV). According to Wallsten (1981), exposure can possibly restrict the potential vegetation expansion on the shores of a large lake. With the increased exposure, depending on the trophic state of the lake, the expansion of the emergent vegetation can benefit in eutrophic (Weisner 1987) or suffer in oligotrophic (Keddy 1983) conditions. As paludification also occurred on exposed shores, it may be connected with *Phragmites australis,* also preferring oligotrophic exposed conditions. Regarding the paludification, the exposure can function in various ways depending on the other conditions. According to Weisner (1987) the substrate at exposed sites around a small eutrophic lake consisted of a relatively thick layer of dead *Phragmites australis* parts, from the paludification on an exposed shore. On the other hand, at sheltered sites the bottom substrate can be too loose to provide anchorage for the vegetation (Weisner 1987).

In the habitat level study in two lakes, the **slope angle** had a negative response to vegetation occurrence and abundance, the occurrence of *Phragmites australis* and *Equisetum fluviatile* and the vegetation change (IV). The slope angle was negatively related to the paludification (V). The results of this study were confirmed by several previous studies. Slope has been reported to affect the vegetation biomass and dynamics (Wallsten 1981, Duarte & Kalff 1986, Rea *et al.* 1998). In regulated lakes, the water level dynamics strongly affect the conditions on the shore. On gently sloping shores the effects of water levels are more severe than on steeper shores (see Andersson 2001). Higher water level would reduce the spread of helophyte vegetation on gently sloping shores (Hellsten *et al.* 2006).

Direct human impact on aquatic macrophyte development includes restoration actions. The results of this study indicate that the presence of housing had a negative effect on vegetation occurrence and abundance in two lakes (IV). Studies by Mäemets & Freiberg (2004) support these results, as helophyte vegetation was weaker and the biomass was lower near villages. The effect of housing may also be related to increased free-time housing, which avoids shallow vegetated shore areas (Barkman 2003). According to Niemi *et al.* (1990), the human disturbance in aquatic macrophyte communities is not largely covered in reference studies.

In this study the notable increase of the emergent vegetation in intensive farming areas (I) is probably partly related to the decrease in **cattle grazing**. The disturbance by cattle grazing or by other species affecting macrophyte development was also observed in other studies (Lohammar 1965, Uotila 1971, Meriläinen & Toivonen 1979, Weisner 1987, Wade 1999). Cattle grazing was largely performed near lakeshores in the early 1900s (Luther & Munsterhjelm 1983) and over time it has been decreasing. The ceasing of cattle grazing was noted as one of the main reasons for the *Phragmites australis* expansion (Weisner 1987, Mäemets & Freiberg 2004).

4.2 Historic and multisource data in the spatiotemporal aquatic macrophyte studies

This study indicates the importance of **historic data** in understanding the environmental factors determining the littoral development. Historic aquatic macrophyte and environmental data sets were combined to indicate the aquatic macrophyte vegetation development during the second half of the 1900s (I, III, IV). The use of historic data is widespread in aquatic macrophyte studies (Hudon 1997, Dienst *et al.* 2004, Frederiksen *et al.* 2004). Several previous studies show that aquatic macrophyte communities were in a rather stable state until the mid 1900s. However, human impact began to affect the macrophytes during the second half of the century (Churski 1983, Kennison *et al.* 1998, Naumenko *et al.* 2000, Egertson *et al.* 2004). With the use of historic data slow changes exceeding decades and the interpretation of the cause and effect relations can be traced (Magnuson *et al.* 1991, Kennison *et al.* 1998). Naumenko *et al.* (2000) suggested that historic macrophyte data should always be combined with historic environmental data. Characteristic of the historical studies is that data extending to the early decades of the past century or earlier is rare (Egertson *et al.* 2004).

According to earlier studies (Alasaarela *et al.* 1989, Rørslett 1989, Wilcox & Meeker 1991, Hellsten & Riihimäki 1996) the water level regulation impacts are rather complex to detect. Comparison data prior to regulation seldom exists (Hellsten 2000). A majority of the regulation projects were initiated in the 1960s–1970s, although some were started in the early 1900s (Lindström 1973, Sjöberg & Danell 1983, Wilcox & Meeker 1991). According to Hudon (1997), the reference state should be validated with data based on historic environmental variables such as water level fluctuation. Based on the studies of Granberg (1973), material from the 1940s and 1950s provides a sound reference for human-induced changes in large boreal lakes. As suggested by Hudon (1997), the use of aerial photographs is often extendable only until the 1960s. In this study, historic aquatic macrophyte aerial photograph data before the regulation, from the 1940s–1960s, enabled analysis of the long-term effects of water level regulation (I, III, IV). The reference data, the measured historic water level variables, provided an excellent reference for the water level regulation impacts (I, III).

In this study, historic aquatic macrophyte cover changes in the large boreal lakes were mapped (I) and the species-specific aquatic macrophyte cover of emergent species was analysed (III). The historic cover changes in boreal lakes have previously been studied mainly in smaller lakes (Wallsten 1974, Meriläinen & Toivonen 1979, Wallsten 1981, Forsgren & Wallsten 1987, Weisner 1987, Mäkirinta 1991, Weisner 1991, Valta-Hulkkonen *et al.* 2005). Previous temporal and species-specific emergent macrophyte cover studies from the larger boreal lakes (Wallsten & Forsgren 1989, Naumenko *et al.* 2000, Andersson 2001, Mäemets & Freiberg 2004) confirm the importance of historic data in determining the major environmental factors, water level regulation and eutrophication, affecting aquatic macrophyte development in the littoral zone.

The use of **multisource data** proved to be successful in this study. Several methodological levels were applied, ranging from species specific (II, III, IV) to the habitat level (IV, V) and finally populations (III) and communities (I) in the whole lake. The use of aerial photographs provided hectare cover data from the emergent vegetation (I, II, III). The aerial photograph data was combined with environmental factor groups to examine the determining factors of occurrence and abundance of emergent vegetation at the habitat level (IV). Transect studies enabled analysis of the relationship between the horizontal and vertical vegetation populations and calculations of several indices from the data (III). Moreover, occurrence, types and main determinants of the littoral paludification were identified with the aid of vegetation transects (V). Traditionally, aquatic macrophyte research is carried out with floristic analysis (Wilson & Keddy 1985, Rintanen 1996, Sand-Jensen *et al.* 2000). With the increasing use of remote sensing methods, population, community and lake levels have been emphasized in the spatially located studies (Wallsten 1974, Malthus & George 1997) and traditional surveying methods have been combined with GIS and remote sensing (Lehmann 1998, Rea *et al.* 1998). Less emphasis has been given to the habitat level and environmental factors controlling the habitat level dynamics (Keddy 1982, Hellsten 1997). Studies combining multiple study levels or complementary methodology are less common (see Egertson *et al.* 2004, Davidson *et al.* 2005).

This study indicated the importance of the emergent vegetation in the littoral zone of large boreal lakes (II, III). Several previous studies have indicated the dominance of emergent vegetation in the littoral zone of boreal lakes (Andersson 2001, Valta-Hulkkonen *et al.* 2003, Mäemets & Freiberg 2004) and the large relative proportion of *Phragmites australis* (Wallsten 1981, Weisner 1987, Naumenko *et al.* 2000). The suitability of remote sensing in the study of emergent macrophytes has been demonstrated in several studies (Benton & Newnam 1976, Valta-Hulkkonen *et al.* 2003, Dienst *et al.* 2004). In a number of studies emergent vegetation is neglected, as it fails to indicate directly the environmental variables in the water, such as chemical content (Sand-Jensen *et al.* 2000, Vestergaard & Sand-Jensen 2000). However, emergent species form a vital part of the boreal littoral zone. Emergent macrophytes often form the highest standing crop or phytomass in lakes (Hudon 1997, Naumenko *et al.* 2000), and are responsible for creating the inherent character of the lake (Lohammar 1965, Hudon 1997).

Visual interpretation has been in use in several boreal macrophyte studies, mainly in earlier decades (Meriläinen & Toivonen 1979, Raitala *et al.* 1984, Wallsten & Forsgren 1989, Mäkirinta 1991) but also in recent studies (Frederiksen *et al.* 2004). Comparison of digital and visual classification has been performed before by Forsgren & Wallsten (1987), Wallsten & Forsgren (1989) and Marshall & Lee (1994). In this study, the visual and digital classifications were compared (II). The results demonstrated that visual interpretation is a successful method in the aquatic macrophyte mapping of emergent vegetation (II). The overall accuracy of the visual interpretation was relatively high (II). The macrophyte hectare area resulting from the visual interpretation was comparable with the digital classification (II). With the visual classification, emergent aquatic macrophyte vegetation classified the vegetation taxonomically better mainly at the species level, whereas digital classification produced categories according to life forms, phenotypes or the vegetation density (II). Visual classification was slower in time used per hectare (II) but in a lake with long shoreline and scarce vegetation the difference will not be so pronounced. This overall verification increases the validity of the obtained results in other lakes (I, III, IV).

4.3 Error sources and future aspects

In general, examination of the environmental factors and aquatic macrophyte vegetation offers several challenges, specifically in large lakes. Large lakes comprise a vast variety of habitats, and open lake conditions differ considerably from the littoral zone. Differences in the anthropogenic and other environmental conditions can be considerable (see Keränen 1985, Hill *et al.* 1998, Meriläinen *et al.* 2001). Larger lakes are few in number and large numbers of reference lakes with similar environmental conditions are not available. The scarcity of the historic reference data prevents sound comparison studies.

Several aspects must be considered when assessing the water level regulation and eutrophication impacts. The selection of an appropriate reference condition is rather complex. Small temporal variations in the selection of the reference condition may give dissimilar results. The regulation pattern can be altered over the decades (Hudon 1997) and the environmental conditions can vary considerably even between two years (see Wallsten 1981, Anttonen-Heikkilä 1983). The historical reference condition and the present-day results represent two individual moments and not a continuous phenomenon. In addition, several potential reference conditions may appear (see Swetnam *et al.* 1999). For an appropriate comparison of the regulation effects, an unregulated large study lake should have been included in the examination. Similar studies performed in different lakes are not directly comparable with each other (Sjörs & Nilsson 1976), as was observed in a study of regulation reservoirs with an annual fluctuation up to 20 meters or more (Lindström 1973, Bodaly *et al.* 1984, Rørslett 1988). Detailed spatially located environmental and historical data would allow new insights into the studied eutrophication, paludification and water level regulation processes. On the other hand, the distribution and abundance of macrophyte species is also affected by several other factors, even historical and stochastic (Shipley *et al.* 1989).

A number of details must be taken into account with multisource data. The number and the length of the study sites should be equal and the sites should be evenly distributed geographically. The transect data was not collected from randomly chosen habitats. The data sets were collected in the water regulation projects and habitats had to represent a full standing crop with typical zonation (see Wisheu & Keddy 1989). The maximization of the number of different study sites in lakes and the incorporation of historic and present day aerial photographs may have created uncertainty aspects. Data from the same study year both in the historic and current day situations should have been used in each study site, as the aerial photographs should represent the maximum aquatic vegetation during the growing season in July-August (see Valta-Hulkkonen 2005). Interpretation errors specifically due to sparse vegetation, bottom reflectance, turbidity, shadows, lake restoration and shoreline changes affect the results. Visual interpretation is a subjective method and a generalized study procedure is hard to develop (see also Wallsten 1974). The suitability of the remote sensing methods in mapping other growth forms than emergent and floating leaved is poor and other traditional methods should be used to achieve ecologically reasonable results. The availability of historic data limits the data in use. At the moment species-specific cover changes are only detectable using previous hectare coverage or field information from historic situation of the same site (see Maristo 1935). The traditional methods will continue to be in use along with the modern mapping means (see Vis *et al.* 2003). The visual and digital classification should be combined in order to obtain species-specific results. With transect or field data it is possible to detect changes back to the very late 1800s (Sand-Jensen *et al.* 2000, Egertson *et al.* 2004). If a longer time series is needed, aquatic macrofossils combined with other paleolimnological methods must be contrasted (Sand-Jensen 2000, Davidson *et al.* 2005). A holistic drainage basin level approach with climate, land use, soil and hydrology variables would add confidence to the studied historical aquatic macrophyte phenomenon.

In the future, the effects of global climatic change on aquatic macrophytes should be acknowledged. The altered precipitation and temperature patterns will change water levels and their dynamics, ice cover patterns and light penetration. Several other environmental factors such as eutrophication, land use changes and the spread of exotic species will interact with the climatic change (see Magnuson *et al.* 1998, Schindler 1998).

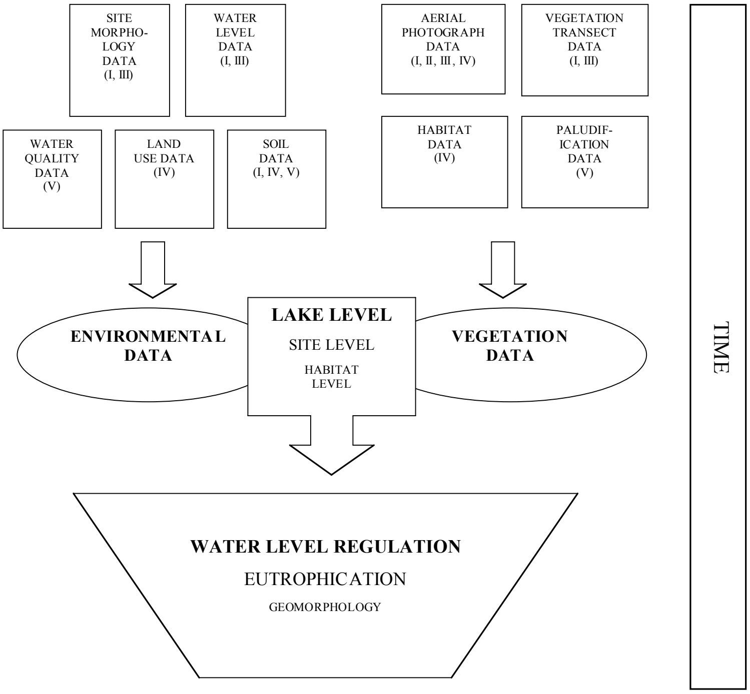

Fig. 2. Schematic diagram of the data and results in the examination of the main determinats of aquatic macrophytes in large boreal lakes during the second half of the 1900s. Different data in specific papers were categorized into vegetation and environmental data and into results in lake level, site level and habitat level.

5 Conclusions

The main aims of this thesis were to quantify the historical spatiotemporal changes of aquatic macrophytes in boreal lakes, to investigate aerial interpretation methodology in aquatic botany and to explore the relative importance of different environmental factors in aquatic macrophyte development.

A continual and patterned artificial water level regulation was the main factor determining the development of aquatic macrophyte vegetation at the lake level in the studied large boreal lakes. The major vegetation changes were induced by the mean water level rise or drawdown, decreased fluctuation range and reduced spring flood. Aquatic macrophyte response to the water level regulation was case- and lake-specific depending on the regulation amplitude. In a lake with water level regulation similar to natural fluctuation the aquatic vegetation response was determined by other factors than water level.

In large lakes eutrophication was a site-specific factor owing to the great differences in different parts of the lake in the eutrophication load. Aquatic macrophyte response to eutrophication was partly species-specific, however, the vegetation occurrence and abundance were both affected by the eutrophication. Eutrophication can reinforce the vegetation response to water level fluctuation.

Geomorphological factors such as openness, slope and bottom soil quality determined the actual vegetation development at a specific habitat. This is based on the major influence of water level regulation and eutrophication and defined by the species and growth form preferences. Clay and clay related deposits defined the distribution and abundance of aquatic macrophytes and the occurrence of paludification at both the lake and habitat level. The exposure and the slope were found to explain the vegetation dynamics.

Bottom ward overgrowth was the main paludification type in the studied lakes. Paludification, the permanent overgrowth of the littoral shoreline, was affected in the studied lakes by all major environmental factors, water level regulation, eutrophication and geomorphology.

Species-specific preferences play an important role in determining the vegetation development. *Glyceria maxima* as an invasive species favors eutrophic conditions and is immune to water level fluctuation. *Phragmites australis* is a strong competitor and generalist species that grows on many substrates. Due to their large size and high biomass, these species are capable of replacing previous vegetation.

The use of multisource aquatic macrophyte data combined with several environmental variables allowed examination of the data at different study levels from the lake to species level. The combination of multisource data provided new insights into environmental factors controlling the aquatic macrophyte development in boreal lakes over half a century.

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Original papers

This thesis is based on the following original papers, referred to in the text by their Roman numerals I–V

I Partanen S & Hellsten S (2005) Changes of emergent aquatic macrophyte cover in seven large boreal lakes in Finland with special reference to water level regulation. Fennia 183: 57–79.

II Valta-Hulkkonen K, Partanen S & Kanninen A (2003) Remote sensing as a tool in the aquatic macrophyte mapping of a eutrophic lake: a comparison between visual and digital classification. Proceedings of the 9th Scandinavian Research Conference on Geographic Information Science, 4.–6.6.2003, Espoo, Finland, 79–90.

III Partanen S, Keto A, Visuri M, Tarvainen A, Riihimäki J & Hellsten S (2006) The relationship between water level fluctuation and distribution of emergent aquatic macrophytes in large, mildly regulated lakes in the Finnish Lake District. Verhandlung Internationale Vereinigung Limnologie 29: 1160–1166.

IV Partanen S, Luoto M & Hellsten S Habitat level determinants of emergent macrophyte occurrence, abundance and change in two boreal lakes in Finland (submitted).

V Partanen S & Luoto M (2006) Environmental determinants of littoral paludification in boreal lakes. Limnologica 36: 98–109.

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