Ann. Bot. Fennici 40: 199–208 ISSN 0003-3847
Helsinki 19 June 2003

Macrophyte species composition reflecting water quality changes in adjacent water bodies of lake Hiidenvesi, SW Finland

Leena Nurminen

Department of Limnology and Environmental Protection, Section of Limnology, P.O. Box 65, FIN-00014 University of Helsinki, Finland

Received 25 June 2002, revised version received 27 Jan. 2003, accepted 27 Jan. 2003

Nurminen, L. 2003: Macrophyte species composition reflecting water quality changes in adjacent water bodies of lake Hiidenvesi, SW Finland. — *Ann. Bot. Fennici* 40: 199–208.

The manifold role of aquatic macrophytes in lake ecology is closely linked to their distribution and biomass, which in turn is a synergy of various environmental factors. The implication of different environmental variables on macrophyte speciation and life form structure in lake Hiidenvesi, with an uneven eutrophication history, was studied. The persisting life forms reflected the somewhat inherently turbid water: emergent and floating-leaved species were common, whereas submerged species were scarce and low-light tolerant dominated. Effects of uneven nutrient loading were noticeable amongst the interconnected basins of the lake: the shallow, northernmost basins are most turbid and eutrophic, and the steeper westerly basins are in turn less eutrophicated and more clear-water. Increased nutrient level and turbidity together with softening of bottom substrate have emphasized the speciation to more eutraphent species and pleustophytes, especially in the most eutrophic Kirkkojärvi basin.

Keywords: aquatic macrophytes, eutrophication, floristic change, DCA, turbidity

Introduction

Aquatic vegetation plays an essential role in the function of the ecosystems of shallow lakes. Macrophytes are involved in several feed-back mechanisms that tend to keep the water clear even in relatively high nutrient loadings (Moss 1990) and are therefore crucial for the shallow water areas. The composition of aquatic flora influences the littoral phytoplankton, epiphyton, zooplankton and invertebrate communities, and has therefore a bearing also on the abundance and composition of the fish communities (Duarte *et al*. 1986). In addition, macrophyte stands have been reported to notably affect lake nutrient status, resuspension of bottom material and water turbidity (James & Barko 1990, Sand-Jensen & Borum 1991, Horppila & Nurminen 2001).

The quantitative role of macrophytes in lake ecology is closely linked to their areal distribution and biomass, which in turn is a synergy of various environmental factors (Duarte *et al.* 1986, Middelboe & Markager 1997). Besides lake trophic status, other important factors impinging on macrophyte occurrence are light transmission, water colour, temperature, pH,

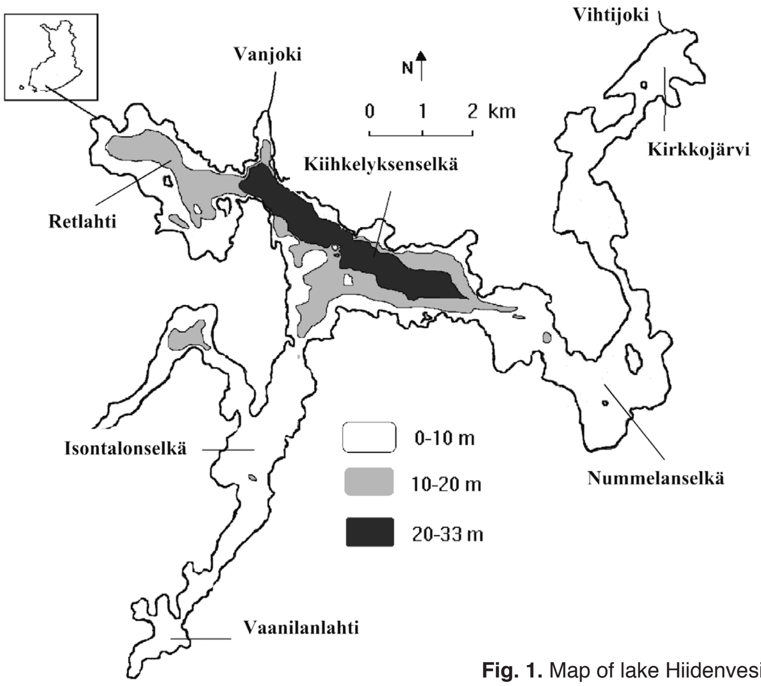

Fig. 1. Map of lake Hiidenvesi with the studied basins indicated.

substrate characteristics, lake morphology, intra- and interspecific competition, herbivory and epiphyte loading (Iversen 1929, Dale 1986, Duarte *et al.* 1986, Vant *et al.* 1986, Chambers & Prepas 1988, Lodge 1991). Different macrophyte life forms require nutrients from different sources and vary in exposure tolerance (Toivonen & Huttunen 1995). Therefore, macrophyte species richness and proportions of various growth forms closely reflect the trophic state of lakes, with meso-eutrophic and eutrophic lakes supporting significantly more species than oligotrophic ones (Schulthorpe 1967, Toivonen & Huttunen 1995).

Aquatic vegetation reflects the nutrient status of their immediate habitat by presence/absence and abundance (Suominen 1968, Uotila 1971). As mostly sessile organisms, macrophytes react slowly to changes in nutrient conditions and can be used as long-term indicators and have therefore been widely used to reveal water quality or habitat characteristics (e.g. Pietsch 1972, Kohler 1982, Arts *et al.* 1990, Melzer 1999). However, predicting the change in macrophyte abundances in response to variation of nutrient loading is considerably difficult (Chambers & Kalff 1985). Also, comparison of the role of macrophytes along lake size and depth gradients is complicated and less clear a subject (Gasith & Hoyer 1998).

In this present paper, the macrophyte flora of a single large water body, lake Hiidenvesi, was investigated. The study focus was on comparing the vegetation disparity in connected basins of differing trophy and morphology and additionally, revealing possible changes in the speciation due to uneven nutrient loading. The hypothesis of the study was that the areal distribution of species reflect the different prevailing environmental variables. This investigation wanted, in more detailed scrutiny, to focus on the individual environmental factors and their implication on macrophyte dispersion and the relative significance of different life forms.

Study area

Lake Hiidenvesi is the second largest lake (30.3 km^2) on the southwestern coast of Finland. Due to heavy point and non-point loading, the lake has a long eutrophication history with severe cyanophyte blooms occurring since the 1960s (Tallberg *et al.* 1999). Almost 90% of the yearly external phosphorus and nitrogen loading to the lake comes from the two rivers Vihtijoki (Tot-P 6–15 tonnes; Tot-N 140–210 tonnes) and Vanjoki (Tot-P 10–20 tonnes; Tot-N 210–320 tonnes) (Marttila 2002). Altogether, lake Hiidenvesi is inherently considerably turbid, due to the composition and resuspension of the bottom material (inorganic matter i.e. clay). The lake is a flow-through system, consisting of several separate basins quite different in reference to their morphology and trophic status, the studied basins being as follows; Kirkkojärvi (northeastern part), Nummelanselkä, Kiihkelyksenselkä, Retlahti, Isontalonselkä and Vaanilanlahti (southwestern part) (Fig. 1).

Materials and methods

The study was performed during the summer of 1998 within the months of June to September. The basic macrovegetation mapping was conducted from a boat using an aquascope (when possible due to turbidity), a modified garden rake (used at depths 0.5–2 m) and a "Luther-rake" (hoe attached to long rope; Luther 1951). The latter was thrown in random sites to every direction (north, south, west, east) to get a broader view of the species distribution in relatively turbid conditions. Simultaneously, abundance and growing depths were charted, and vegetation maps drawn for each species. The relative abundance was estimated according to a 3-degree scale (sparse-relatively abundant-abundant) modified from the Norrlin scale method (Luther 1951, Munsterhjelm 1997). Most of the species were specified on the spot. Part of the material was pressed and identified to species later in the laboratory. To reveal possible changes in the macrophyte vegetation, the mappings of 1998 were roughly compared to previous floral observations from the 1950s (K. Aura, pers. comm.). However, due to different used methodology and relatively non-systematic mapping (focusing more on only few basins) the earlier data is more suggestive in nature. The composition of the bottom material was roughly approximated; mud–clay (soft), sand–mud–clay (semi-soft), sand–clay (semi-hard).

Water quality samples were taken from every study site (six basins in total). Samples for chemical analyses (total P, total N) were analysed according to the standards of Finnish Environmental Agency. Turbidity, conductivity and pH were measured with YSI 6600 sonde. Secchi depths for each basin were measured. To evaluate the weighting of each environmental variable on the species occurrence, each measured parameter was independently tested with the macrophyte life forms using the Mantel test (McCune & Mefford 1999).

The ordinations for species data of different life forms in the basins were performed with the program PC-ORD, using detrended correspondence analysis (DCA) (McCune & Mefford 1999). The DCA-analyses were performed separately for (1) helophytes (2) submerged and floating-leaved plants.

Results

Macrovegetation in adjacent basins

The macrophyte vegetation of lake Hiidenvesi reflects the trophic characteristics of the lake (Table 1). The shallow and turbid Kirkkojärvi basin is characterized by beds of emergent macrophytes (*Typha angustifolia*, *T. latifolia*, *Glyceria maxima*) up to 1–1.5 m depth accompanied by widespread zones of floating-leaved species (*Nuphar lutea*, *Nymphaea* spp. and *Polygonum amphibium*) between the emergent plants and the open water. Restricted stands of submerged species, such as *Myriophyllum verticillatum*, *Potamogeton obtusifolius*, are found mainly confined to shallow protected bays. Elodeids, *Ceratophyllum demersum* and *Ranunculus circinatus*, in places form relatively large widespread vegetations. Bryophytes and the green algae, *Nitella flexilis*, form dense mats in the shallow areas together with *P. obtusifolius*. Also filamentous algae (e.g. *Spirogyra* spp., *Mougeotia* spp. and *Rhizoclonium* spp.) are very common in the Kirkkojärvi basin, occasionally forming dense mats in late summer. Amongst the helophytes, lemnid species (e.g. *Hydrocharis morsus-ranae*, *Lemna minor*, *Spirodela polyrhiza*) are common. The emergent, *Acorus calamus*, forms sparse stands evenly around the basin.

The second basin, going north to south, is the Nummelanselkä basin with transitional vegetation, partly resembling the vegetation of the Kirkkojärvi basin and partly less turbid water. The helophyte dominance changes here from *Glyceria maxima* to *Carex* spp. and *Equisetum fluviatile*, with also a few *Schoenoplectus lacustris* -stands existing. Prevailing submerged and elodeid species are *Potamogeton perfoliatus*, *P. obtusifolius*, *Ceratophyllum demersum* and *Ranunculus circinatus*. Floating-leaved *Nuphar lutea* forms broad zones and also *Sparganium emersum* and *Polygonum amphibium* are common in the Nummelanselkä basin.

The macrophyte vegetation of the Kiihkelyksenselkä basin differs considerably from the previous basins introduced due to its rockier and steeper shores. All in all, the vegetation is rather scarce, dominating species being *Polygonum amphibium, Nuphar lutea*, *Potamogeton perfoliatus* and *P. natans*. The dominating helophytes are *Phragmites australis*, *Equisetum fluviatile* and *Carex* spp. Due to the steeper shores, macrophyte vegetation is mostly concentrated in the more shallow bays and there is no continuous line of vegetation as in the previous basins. Also *Polygonum amphibium* and *Sagittaria sagittifolia* are common, but less frequent than in the eastern and northern parts of the lake. In the southwestern bays of the basin, species such as *Potamogeton alpinus, P. gramineus, P. berchtoldii* and *Myriophyllum alterniflorum* exist.

The vegetation in the Retlahti basin reflects the clearer water and harder bottom texture of

Table 1. The life forms and macrophyte species in lake Hiidenvesi. In the columns are the trophic states (o, oligotraphent; o-m, oligo- and mesotraphent; m, mesotraphent; M-e, meso-eutraphent; e, eutraphent; i, indifferent; Toivonen & Huttunen 1995) and abbreviations of indicator species used in DCA-ordination.

	Trophy	Abbreviation
Helophytes		
Sedges		
Carex rostrata	i	
Carex acuta	m-e	
Carex pseudocyperus	e	
Carex sp.	–	carsp
Reeds		
Equisetum fluviatile	i	efluv
Phragmites australis	i	paust
Alisma plantago-aquatica	m-e	aplan
Typha latifolia	m-e	tlati
Iris pseudacorus	m-e	
Sagittaria sagittifolia	m-e	
Schoenoplectus lacustris	i	slacu
Sparganium erectum	m-e	
Eleocharis palustris	i	
Hippuris vulgaris	m	
Butomus umbellatus	e	
Typha angustifolia	e	tangu
Sparganium erectum	e	
Glyceria maxima	e	gmaxi
Acorus calamus	e	acala
Rhizophytic hydrophytes		
Floating-leaved		
Nuphar lutea	i	nlute
Sparganium emersum	i	semer
Nymphaea candida	i	
Nymphaea tetragona	i	nymsp
Nymphaea alba	i	
Sparganium gramineum	m	sgram
Polygonum amphibium	m-e	pamph
Sparganium angustifolium	o	
Sparganium sp.	–	
Potamogeton natans	i	pnata
Elodeids		
Callitriche cophocarpa	m	
Callitriche hermaphroditica	e	
Potamogeton alpinus	i	palpi
Potamogeton obtusifolius	m-e	pobtu
Potamogeton berchtoldii	m-e	pberc
Potamogeton perfoliatus	m	pperf
Potamogeton gramineus	o-m	pgram
Potamogeton lucens	e	
Elodea canadensis	m-e	ecana
Myriophyllum alterniflorum	o-m	malte
Myriophyllum verticillatum	e	mvert
Isoetids		
Ranunculus reptans	o-m, i	
Eleocharis acicularis	o-m, i	
Pleustophytes		
Ceratophyllids		
Ceratophyllum demersum	e	cdeme
Ranunculus circinatus	e	rcirc
Utricularia vulgaris	i	
Lemnids		
Lemna minor	m-e	
Hydrocharis morsus-ranae	e	
Spirodela polyrhiza	e	
Ricciocarpus natans	m-e	

the area. Occasionally rather large stands of *Phragmites australis* and *Equisetum fluviatile* prevail in the basin, with only a few restricted *Glyceria maxima* vegetations in more protected locations. Also a few hard-bottom, more oligo-mesotrophic species, such as *Myriophyllum alterniflorum* and *Sparganium gramineum*, form extensive stands in the northernmost bays. In the southern bays related to some brooks, some more eutrophic species such as *Ceratophyllum demersum*, *Potamogeton obtusifolius* and *P. berchtoldii* and *Myriophyllum verticillatum*, are found. Also floating-leaved *Potamogeton natans* and *Nuphar lutea* are common in this basin.

The Isontalonselkä basin has, due to its greater depth and rocky and steep shores, a relatively scarce macrophyte vegetation. The shoreline is mostly colonized by patchy emergent stands formed by *Phragmites australis*, *Typha* spp. and *Carex* spp. The emergent species are accompanied by zones of floating-leaved nymphaeids. The submerged vegetation is very scarce consisting mainly of *Potamogeton* spp.

The most southwesternly basin, Vaanilanlahti, is again very shallow and covered with macrovegetation. Large helophyte stands of *Typha angustifolia*, *T. latifolia*, *Carex* spp., and also *Glyceria maxima* and *Phragmites australis* exist. The bay is covered with submerged macrophytes; mostly *Myriophyllum verticillatum*, also quite a few *Potamogeton* species (e.g. *P. lucens*) and *Utricularia* spp. As in other sheltered areas, amongst the helophytes many lemnids prevail. In Vaanilanlahti, as in Kirkkojärvi, filamentous algae form large patchy mats.

During the last 50 years, there has been a slight change in the macrovegetation of lake Hiidenvesi towards a more eutrophic speciation (K. Aura, pers. comm.). During the summer of 1998, the very common and widespread pleustophyte species, *Ceratophyllum demersum* and *Ranunculus circinatus*, especially in the Kirkkojärvi basin, were practically absent in the 1950s as only scarce vegetations of *C. demersum* existed. There has occurred a clear change in helophyte vegetation as well; *Phragmites australis* and *Equisetum fluviatile* have declined, and *Glyceria maxima* and *Typha* species, on the other hand, have spread considerably compared to the observations from the 1950s. *Acorus calamus* has spread within the Kirkkojärvi basin. Pondweed species, such as *Potamogeton gramineus* and *P. alpinus*, have declined in 50 years.

Analysis of environmental variables and speciation

The measured environmental parameters are very characteristic to each basin, clearly manifesting the disparity of the interconnected water bodies (Table 2). Secchi depth was lowest (0.3 m) and turbidity highest (58 NTU) in the most eutrophic (total N > 1400 μg l^{-1}; total P around 100 μg l^{-1}) Kirkkojärvi basin, with lowest mean depth (1.9 m) and softest bottom substrate. Counter to this basin, representing the shallow areas of the lake, was Kiihkelyksenselkä basin (representing the deeper, less eutrophic basins) with Secchi depth of 1 m and considerably clearer water (turbidity 16 NTU), total N being > 1000 μg l^{-1}, total P around 40 μg l^{-1}, mean depth 11 m and bottom substrate hard clay–sand.

The Mantel test showed significant relationships between some environmental parameters

Table 2. Main characteristics and environmental variables of the interconnected basins of lake Hiidenvesi. Bottom types: 1 = semi-hard, 2 = semi-soft, 3 = soft).

Basins	Tot-N (μg l^{-1})	Tot-P (μg l^{-1})	Secchi (cm)	Turbidity (NTU)	Conductivity (μS cm^{-1})	Mean depth (m)	Bottom type	pH
Kirkkojärvi	1438	98	30	58	0.101	1.9	3	9.1
Nummelanselkä	1118	51	60	25	0.087	2.6	2	8.0
Kiihkelyksenselkä	1113	41	100	16	0.082	11.2	1	8.3
Retlahti	850	33	120	8	0.081	7.9	1	8.4
Isontalonselkä	730	26	110	11	0.082	3.3	1	7.7
Vaanilanlahti	890	137	110	6	0.103	1.3	2	8.0

(conductivity, bottom type, phosphorus and turbidity) and different life forms in the basins (Table 3). The Mantel test was performed to all variables shown in Table 2 except pH, due to the nature of the parameter. Although lake pH is a principal determinant of macrophyte species richness (Iversen 1929), it can show great variation during the growing season, this being the case also in lake Hiidenvesi, as during the measurements a heavy phytoplankton bloom governed in the Kirkkojärvi basin. Therefore, conductivity was considered a more usable parameter for trophic status (Toivonen & Huttunen 1995).

In the emergent vegetation ordination (Fig. 2) the basins on the left side of axis 1 (eigenvalue = 0.256) (axis 2; eigenvalue = 0.049), Retlahti, Isontalonselkä and Kiihkelyksenselkä, are rather deep, less eutrophic (mesotrophic) and larger and clearer than the other basins, also the bottom type is harder (more clay–sand). On the right side are the three smaller, more shallow eutrophic basins with softer bottom substrate; Kirkkojärvi, Nummelanselkä and Vaanilanlahti. The emergent species on the left side of the axis (*Phragmites australis* and *Equisetum fluviatile*) are indifferent species typical in considerably large-sized, hard-bottomed water areas. Whereas, on the right side of the axis are placed many eutraphent species thriving from soft bottom substrate and small, sheltered water areas (*Acorus calamus*, *Typha angustifolia*, *Glyceria maxima*).

In the ordination containing submerged and floating-leaved vegetation no similar clear differences are detectable, conceivably due to many indifferent species (Fig. 3). The eutrophic basins Kirkkojärvi and Nummelanselkä have settled on the left side of the axis 1 (eigenvalue = 0.152) (axis 2; eigenvalue = 0.024). In accordance, many eutraphent and turbidity-tolerant species have oriented in this section; *Ranunculus circinatus*, *Ceratophyllum demersum*, *Potamogeton obtusifolius* (submerged) and *Nuphar lutea* and *Nymphaea* spp. (floating-leaved). Species such as *Polygonum amphibium* and *Sparganium emersum* are indifferent, nevertheless thriving from increase in nutrient level. On the right side of the axis, in the clearer, less eutrophic, hard-bottom basins (Retlahti, Kiihkelyksenselkä and Isontalonselkä) are indifferent (e.g. *Potamogeton perfoliatus*) and more meso-oligotrophic (*Myriophyllum alterniflorum*, *Potamogeton gramineus*, *P. alpinus* and *Sparganium gramineum*) species common.

Discussion

Macrophyte speciation

In lake Hiidenvesi, the macrophyte vegetation differs in the divergent areas of the lake. This is conceivably due to the disparity of water quality, substrate and morphological features of the connected basins (Smith & Wallsten 1986, Bailey 1988, Toivonen & Huttunen 1995). As a quite large lake, Hiidenvesi potentially provides a wider array of habitats than smaller lakes, and therefore a more polymorphic macrophyte flora could be expected (Toivonen & Huttunen 1995). Nevertheless, regardless of size the overall rather low light penetration ascribed to clay as the determining bottom substrate of the lake, constrains the flora to turbidity tolerant species and life forms. The macrophyte vegetation is biased towards eurycoic (wide amplitude) emergent and floating-leaved species, with a fairly small biomass of truly submerged plants, and e.g. rosette types (isoetids), demanding relatively good light

Table 3. The statistically significant ($p < 0.05$) environmental variables (rows) influencing the distribution of different macrophyte life forms (columns) in the basins of lake Hiidenvesi (Mantel test).

	Emergent	Submerged	Floating-leaved	Pleustophyte	All forms
Turbidity	0.05	–	–	–	–
Conductivity	0.01	0.04	0.02	0.03	0.03
Bottom type	0.03	–	–	0.04	0.03
Phosphorus	0.05	0.02	0.03	0.03	0.03

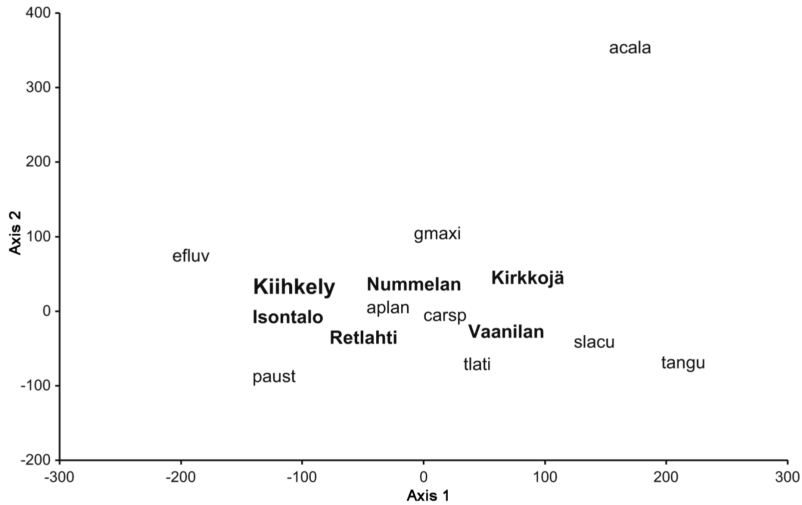

Fig. 2. DCA-ordination diagram of the distribution of helophyte species in the different basins (in bold) of lake Hiidenvesi. Abbreviations of species explained in Table 1.

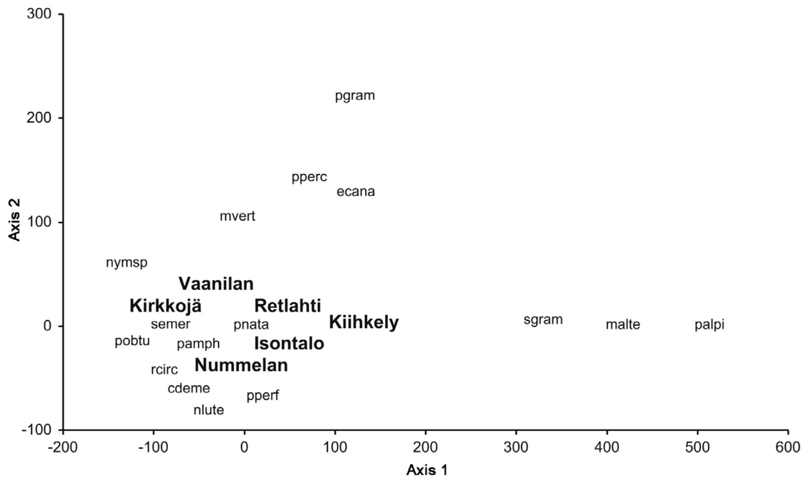

Fig. 3. DCA-ordination diagram of the distribution of floating-leaved and submerged species in the different basins (in bold) of lake Hiidenvesi. Abbreviations of species explained in Table 1.

conditions, are practically absent (Toivonen & Huttunen 1995).

The diversity of helophytes in lake Hiidenvesi is engrossing, as the species richness, (increasing with lake trophy) resembles local variation of trophic state, substrate characters and exposure gradients, which are concomitantly the most important features determining the speciation of emergent vegetation (Chambers 1987, Bailey 1988, Røslett 1991, Toivonen & Huttunen 1995). Soft, organic substrate inhibits the anchorage of emergent roots, especially in exposed sites with wave and wind movement (Weisner 1987, Weisner 1991). Therefore, eutraphent species such as *Sparganium erectum*, *Typha angustifolia*, *T. latifolia*, *Acorus calamus* and *Glyceria maxima*, tolerating loose loam substrate (Toivonen & Bäck 1989), thrive in the shallow waters of the northern and northwestern basins of Hiidenvesi. Indifferent *Phragmites australis* and *Equisetum fluviatile*, requiring more exposed sites with coarser substrata, dominate the less eutrophicated western and southern basins. *Carex* spp. is found throughout the lake in sheltered bays, with frequency increasing westward concomitantly with *Glyceria maxima* decreasing as the lake bottom converts to harder substrate.

Floating-leaved species, e.g. nymphaeids and *Polygonum amphibium*, are well represented in lake Hiidenvesi, due to an allegedly advantageous life form in turbid waters. Water-lilies, especially *Nuphar lutea*, an indifferent species tolerating well wave stress, are numerous throughout the lake; *Nymphaea* spp. being restricted to more sheltered sites (Sculthorpe 1967). Also, *Potamogeton natans*, the only truly floating-leaved pondweed, occurs throughout the lake, with frequency increasing in the less eutrophic western basins.

As light attenuation and depth are most important factors explaining submerged vegetation abundance (maximum colonization depth is usually ascribed to light transparency in the water column and the minimum light requirement for growth; Chambers & Kalff 1985, Smith & Wallsten 1986, Blindow 1992), the species abundance and overall biomass of submerged flora in turbid lake Hiidenvesi is mainly restricted to rather few low light-tolerant species. However, the somewhat differing species composition of the basins reflects the changing light conditions and nutrient status. Prevailing "turbidity tolerant" flora are pleustophytes and canopy-forming submerged plants. Pleustophytes, as rootless byonants living in the water column or just below the surface, are not restricted by the amount of light penetrating to the lake bottom (Toivonen 1985). Therefore, especially in the most turbid and eutrophicated northeastern basins, species such as *Ceratophyllum demersum* and *Ranunculus circinatus*, form high dominating biomasses, together with the low-light tolerant pondweed, *Potamogeton obtusifolius* (Hutchinson 1975). In the most turbid Kirkkojärvi basin, submerged bryophytes (e.g. *Fontinalis* and *Drepanocladus*), well tolerating diminished light penetration, form large uniform mats in greater depths than rooted angiosperms (Sculthorpe 1967).

In turbid conditions, macrophytes can still grow at 1 m at Secchi depths of 0.2 m and less, as is also the case in lake Hiidenvesi. If tubers and rhizomes contain enough energy to enable vigorous growth in spring up to the water surface, the plant can survive under low irradiance levels and overcome the effect of turbidity ("escape effect") (Scheffer *et al*. 1992). Such canopy-forming species is, *Myriophyllum*, with an extensive capacity to elongate and concentrate photoreceptive biomass at the water surface (Barko *et al*. 1981). The eutraphent *M. verticillatum* prevails in the shallow protected bays, with soft bottom, especially in the northeastern basins. The other *Myriophyllum* species, *M. alterniflorum*, being more oligo-mesotrophic, forms extensive stands in the hard substrates of the less eutrophic western areas. Despite the competitive advantage of high overwintering standing crop, *Elodea canadensis* has strikingly low densities in lake Hiidenvesi, forming scattered and sparse populations within mixed submerged vegetation. As a result from the relatively limited ability to elongate to the water surface under low light conditions and the dependence of light penetration through ice in winter time, the species may be disadvantaged in water bodies of low clarity (Barko *et al*.1981).

Floral change — implications of nutrient increase

The floral development in lake Hiidenvesi indicates a clear eutrophication process, leading to transition toward a more eutraphent vegetation. It seems that during the past 50 years, the contrast between the interconnected basins has broadened and culminated with the northernmost basins, Kirkkojärvi and Nummelanselkä, becoming manifestly more eutrophic.

Tall ready helophytes and nymphaeids, favoring eutrophication (Toivonen & Bäck 1989), are the life forms thriving in lake Hiidenvesi. Many of which have expanded their distribution in the lake, such species are *Typha latifolia*, *T. angustifolia*, *Glyceria maxima* and *Nuphar lutea*. From the cattails, *T. angustifolia* grows in much deeper water than *T. latifolia*, nonetheless, both thrive from softening of bottom and are superior competitors against *Phragmites australis* (Toivonen & Bäck 1989), which consequently has, together with *Equisetum fluviatile*, decreased in lake Hiidenvesi. The findings of Toivonen (1985) are in concert with the eradication of *P. australis* and *E. fluviatile* in lake Hiidenvesi. The reason for the deterioration of these two emergent species is presumably manifold; the species require relatively coarse bottom substrate for anchoring of roots, and therefore the capacity of these species to expand towards deeper water at sheltered sites is probably negatively affected by a combination of a loose substrate and a low below-ground biomass (Weisner 1987). As a consequence, the softening of bottom material combined with water level fluctuation and ice erosion in shallow waters may partly be responsible for the diminishing of *P. australis* and *E. fluviatile* stands (Munsterhjelm 1997). Forming coherent vegetations, *Glyceria maxima* is a vigorous competitor that thrives from soft loam substrate, and is probably a prominent reason in displacing the two former species, especially in the most eutrophicated northeastern basins (Kirkkojärvi & Nummelanselkä).

Likewise the emergent vegetation, the main cause for change in the naturally low-light resistant submerged flora is the rise of nutrient level and softening of bottom material. Byonant pleustophytes, such as *Ceratophyllum demersum* and *Ranunculus circinatus*, with thriving from sheltered soft habitats and high tolerance for low light conditions (Uotila 1971, Meriläinen & Toivonen 1979), have plagued parts of the shallow northern basins, especially Kirkkojärvi basin. Both deteriorated pondweeds, *Potamogeton gramineum* and *P. alpinus*, require a relatively hard substrate, and the softening of bottom material with increased nutrient level has lead to disappearance of the species from most former growing places, e.g. *P. alpinus* has disappeared from the mouths of the rivers Vihtijoki and Vanjoki. In addition, nutrient level increase induces macrophyte competition with phytoplankton, as well as shading by phytoplankton blooms and periphyton (Sand-Jensen & Søndergaard 1981, Toivonen & Bäck 1989, Karttunen & Toivonen 1995). Sand-Jensen and Borum (1991) found periphyton coverage to be the major problem for diminishing of submerged plants in eutrophic lakes, reducing the light level at the leaf surface up to 80%. Thus, heavy periphyton vegetation, plaguing the submerged flora, especially in shallow Kirkkojärvi and Vaanilanlahti basins, cannot be overlooked as a cause, if not reducing, at least partly regulating especially the rooted submerged vegetation.

Lake Hiidenvesi is a typical meso-eutrophic and relatively turbid water body with inherently a quite low macrophyte abundance and species composition, therefore drastic changes in floral speciation due to clearance of water transparency are not likely. In attempting to compare habitats of different nutrient status, it is fundamental to bear in mind lake morphometry (Toivonen 1985). Decrease of nutrient level in lake Hiidenvesi would be most significant in the shallow, turbid northeastern basins, particularly Kirkkojärvi, whereas impacts on the vegetation of the deep basins would be quite minor as lake morphometry overrules the effects of decreasing turbidity, as in deep wave exposed water bodies the vegetation in characterisingly more scarce (Spence 1982). Clearly, the deep basins will never be vegetated (Scheffer 1998), whereas shallow sheltered water bodies can form completely different prospects for formation of aquatic vegetation.

Acknowledgements

The financial support provided by the Finnish Environmental Center enabled this study. I also thank Jukka Horppila and Janne Soininen who gave invaluable comments on this manuscript.

References

Arts, G. H. P., van der Velde, G., Roelofs, J. G. M. & van Swaay, C. A. M. 1990: Successional changes in the soft water macrophyte vegetation of (sub) atlantic, sandy, lowland regions during this century. — *Freshw. Biol.* 24: 287–294.

Bailey, R. C. 1988: Correlations between species richness and exposure: freshwater molluscs and macrophytes. — *Hydrobiologia* 162: 183–191.

Barko, J. W., Hardin, D. G. & Matthews, M. S. 1981: Growth and morphology of submersed freshwater macrophytes in relation to light and temperature. — *Can. J. Bot.* 60: 877–887.

Blindow, I. 1992: Decline of charophytes during eutrophication: comparison with angiosperms. — *Freshw. Biol.* 28: 9–14.

Chambers, P. A. 1987: Nearshore occurrence of submerged macrophytes in relation to wave action. — *Can. J. Fish. Aquat. Sci.* 44: 1666–1669.

Chambers, P. A. & Kalff, J. 1985: Depth distribution and biomass of submerged aquatic macrophyte communities in relation to Secchi depth. — *Can. J. Fish. Aquat. Sci.* 42: 701–709.

Chambers, P. A. & Prepas, E. E. 1988: Underwater spectral attenuation and its effect on the maximum depth of angiosperm colonization. — *Can. J. Fish. Aquat. Sci.* 45: 1010–1017.

Dale, H. M. 1986: Temperature and light: the determining factor in maximum depth distribution of aquatic macrophytes in Ontario, Canada. — *Hydrobiologia* 133: 73–77.

Duarte, C. M., Kalff, J. & Peters, R. H. 1986: Patterns in biomass and cover of aquatic macrophytes in lakes. — *Can. J. Fish. Aquat. Sci*. 43: 1900–1908.

Gasith, A. & Hoyer, M.V. 1998: Structuring role of macrophytes in lakes: Changing influence along lake size and depth gradients. — In: Jeppesen, E., Søndergaard, Ma., Søndergaard, Mo. & Christofferson, K. (eds), *The structuring role of submerged macrophytes in lakes*: 381–392. Springer Verlag, New York.

Horppila, J. & Nurminen, L. 2001: The effect of an emergent macrophyte (*Typha angustifolia*) on sediment resuspension in a shallow north temperate lake. — *Freshw. Biol*. 46: 1447–1455.

Hutchinson, G. E. 1975: *A treatise on limnology. III. Limnological botany*. — John Wiley & Sons, New York, London.

Iversen, J. 1929: Studien über die pH — Verhältnisse dänischer Gewässer und ihren Einfluss auf die Hydrophyten-Vegetation. — *Bot. Tidskr.* 40: 277–326.

James, W. F. & Barko, J. M. 1990: Macrophyte influences on the zonation of sediment accretion and composition in a north-temperate lake. — *Arch. Hydrobiol*. 20: 129–142.

Karttunen, K. & Toivonen, H. 1995: Ecology of aquatic bryophyte assemblages in 54 small Finnish lakes, and their changes in 30 years. — *Ann. Bot. Fennici* 32: 75–90.

Kohler, A. 1982: Wasserpflanzen als Belastungsindikatoren. — *Dechenia-Beih.* (Bonn) 26:31–42.

Lodge, D. M. 1991: Herbivory on freshwater macrophytes. — *Aquat. Bot*. 41: 195–224.

Luther, H. 1951: Verbreitung und Ökologie der höheren Wasserpflanzen im Bracwasser der Ekenäs-Gegend in Südfinnland. I. Allgemeiner Teil. — *Acta Bot. Fennica* 49: 1–231.

Marttila, J. 2002: *Hiidenveden kunnostussuunnitelma*. — Dept. Limnol. Env. Prot., Univ. Helsinki.

McCune, B. & Mefford, M. J. 1999: *PC-ORD. Multivariate analysis of ecological data*, *version 4*. — MjM Software Design, Gleneden Beach, Oregon.

Melzer, A. 1999: Aquatic macrophytes as tools for lake management. — *Hydrobiologia* 395/396: 181–190.

Meriläinen, J. & Toivonen, H. 1979: Lake Keskimmäinen, dynamics of vegetation in a small shallow lake. — *Ann. Bot. Fennici* 16: 123–139.

Middelboe, A. L. & Markager, S. 1997: Depth limits and minimum light requirements of freshwater macrophytes. — *Freshw. Biol*. 37: 553–568.

Moss, B. 1990: Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. — *Hydrobiologia* 200/201: 367–379.

Munsterhjelm, R. 1997: The aquatic macrophyte vegetation of flads and gloes, S coast of Finland. — *Acta Bot. Fennica* 157: 1–68.

Pietsch, W. 1972: Ausgewählte Beispiele für Indikatoreigenschaften höherer Wasserpflanzen. — *Arch. Naturschutz Landschaftsforsch*. 12: 121–151.

Røslett, B. 1991: Principal determinants of aquatic macrophyte richness in northern European lakes. — *Aquat. Bot*. 39: 173–193.

Sand-Jensen, K. & Søndergaard, M. 1981: Phytoplankton and epiphyte development and their shading effect on submerged macrophytes in lakes of different nutrient status. — *Int. Rev. Ges. Hydrobiol*. 66: 529–554.

Sand-Jensen, K. & Borum, J. 1991: Interaction among phytoplankton, periphyton and macrophytes in temperate freshwater and estuaries. — *Aquat. Bot*. 41: 137–175.

Scheffer, M., de Redelijkheid, M. R. & Noppert, F. 1992: Distribution and dynamics of submerged vegetation in a chain of shallow eutrophic lakes. — *Aquat. Bot*. 42: 199–216.

Scheffer, M. 1998: *Ecology of shallow lakes*. — Popul. Commun. Biol. Ser. 22. Chapman & Hall, London.

Sculthorpe, C. D. 1967: *The biology of aquatic vascular plants*. — St. Martin's Press, New York.

Smith, V. H. & Wallsten, M. 1986: Prediction of emergent and floating-leaved macrophyte cover in Central Swedish lakes. — *Can. J. Fish. Aquat. Sci*. 43: 2519–2523.

Spence, D. H. N. 1982: The zonation of plants in freshwater lakes. — *Adv. Ecol. Res*. 12: 37–125.

Suominen, J. 1968: Changes in the aquatic macroflora of the polluted Lake Rautavesi, SW Finland. — *Ann. Bot. Fennici* 5: 65–81.

Tallberg, P., Horppila, J., Väisänen, A. & Nurminen, L. 1999: Seasonal succession of phytoplankton and zooplankton along a trophic gradient in a eutrophic lake — implications for food web management. — *Hydrobiologia* 412: 81–94.

Toivonen, H. 1985: Changes in the pleustic macrophyte flora of 54 small Finnish lakes in 54 years. — *Ann. Bot. Fennici* 22: 33–44.

Toivonen, H. & Bäck, S. 1989: Changes in aquatic vegetation of a small eutrophicated and lowered lake (southern Finland). — *Ann. Bot. Fennici* 26: 27–38.

Toivonen, H. & Huttunen, P. 1995: Aquatic macrophytes and ecological gradients in 57 small lakes in southern Finland. — *Aquat. Bot*. 51: 197–221.

Uotila, P. 1971: Distribution and ecological features of hydrophytes in the polluted lake Vanajavesi, S. Finland. — *Ann. Bot. Fennici* 8: 257–295.

Vant, V., Davies-Colley, R., Clayton, J. Coffey, B. 1986: Macrophyte depth limits in North Island (New Zealand) lakes of differing clarity. — *Hydrobiologia* 137: 5–60.

Weisner, S. 1987: The relation between wave exposure and distribution of emergent vegetation in a eutrophic lake. — *Freshw. Biol*. 18: 537–544.

Weisner, S. 1991: Within-lake patterns in depth penetration of emergent vegetation. — *Freshw. Biol*. 26: 133–142.