

# ROLE OF MACROPHYTES IN A CLAY-TURBID LAKE

## IMPLICATION OF DIFFERENT LIFE FORMS ON WATER QUALITY

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## ABSTRACT

The littoral zone is a very important component taking part in forming the food web structure and the prevailing ecology of a lake. Especially in shallow lakes, continuous biotic and abiotic interactions in the littoral also reflect to the pelagic zone, having a bearing on the whole ecosystem. An important structuring force in the littoral is macrovegetation. The role of macrophytes is linked to their spatial distribution and biomass, which in turn is a result of various environmental factors (e.g. trophic status, light, substrate character, competition). Submerged macrophytes have been shown in various studies to be important in lake restorational aspects as they decrease sediment resuspension and remobilisation of nutrients, as well as provide refuge for zooplankton, resulting in decreased turbidity and increased water quality.

Hitherto, investigations on the role of macrophytes have been mostly focused on submerged species as they most promptly respond to eutrophication through light limitation and provide profitable refuge for zooplankton due to structural complexity. But in lakes with inherently low submerged vegetation, other functional groups, e.g. emergent and floating-leaved species, may play an important role in determining the ecological status of a lake. In this thesis, the role of the emergent life form was studied in the two important functions of macrophytes: 1) refuge for zooplankton and 2) effect on resuspension. Also, importance of fish herbivory on the restricted submerged flora of a turbid lake was evaluated.

This thesis shows that in clay-turbid eutrophicated lakes, emergent vegetation may play an important role in seasonal and diurnal regulation of zooplankton by providing refuge, especially for free swimming cladocerans. In addition, in eutrophic and turbid conditions, lacking submergent flora, emergent and also floating-leaved vegetation may harbour considerable densities of plant-attached cladocerans. These plankters in turn hold considerable phytoplankton filtering capacities, which may result in positive water quality effects through algal control.

The results also underline the importance of emergent vegetation in regulating turbidity caused by resuspended sediment. The results demonstrate that during the growing season, sediment resuspension and consequently the increase in inorganic turbidity and internal P-loading may be substantially reduced by emergent, as well as submerged, vegetation. Due to a longer growing season, emergent vegetation may therefore have considerable water quality effects in a shallow lake.

This study also revealed that in turbid and eutrophicated conditions with low submerged biomass and few dominating species, herbivory by fish may have an influence on the dominance proportions and species composition of the restricted submerged flora.

To conclude, in turbid lakes, other functional forms of macrophytes, besides submergents, should not be overlooked. This thesis has highlighted the importance of emergent macrophytes in the ecosystem of clay-turbid lakes. In the future, more detailed studies on the floating-leaved species, often abundant in turbid circumstances, have to be conducted. In all, more thorough investigations of interactions and processes linked with macrophytes related to phytoplankton-caused and inorganic turbidity should be performed. The establishment of submerged macrophytes is traditionally considered essential in the restoration of eutrophicated lakes. This thesis underlines the importance of other life forms on water quality. In this respect, emergent and floating-leaved species may be a more profitable tool in restoration of lakes not only when removed- but also when retained. In general, the comprehensive function of macrophytes should be taken into more thorough account in lake restoration schemes: recreational expectations and water quality aspects should be weighed – and preferably combined.

## List of papers

This thesis is based on the following articles referred to in text by Roman numbers (I-VI).

- I 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.
- II Nurminen, L., Horppila, J. & Tallberg, P. 2001: Seasonal development of the cladoceran assemblage in a turbid lake: the role of emergent macrophytes. - Arch. Hydrobiol. 151: 127-140.
- III Nurminen, L. & Horppila, J. 2002: A diurnal study on the distribution of filter feeding zooplankton: Effect of emergent macrophytes, pH and lake trophy. - Aquat. Sci. 64: 198-206.
- IV Horppila, J. & Nurminen, L. 2001: The effect of an emergent macrophyte (*Typha angustifolia* L.) on sediment resuspension in a shallow north temperate lake. - Freshwat. Biol. 46: 1447-1455.
- V Horppila, J. & Nurminen, L. 2003: Effects of submerged macrophytes on sediment resuspension and internal phosphorus loading in Lake Hiidenvesi (southern Finland). -Wat. Res. 37: 4468-4474.
- VI Nurminen, L., Horppila, J., Lappalainen, J. & Malinen, T. 2003: Implications of rudd (*Scardinius erythrophthalmus*) herbivory on submerged macrophytes in a shallow eutrophic lake. -Hydrobiologia (in press).

## Author`s contribution

- I LN planned and conducted the study and wrote the paper.
- II LN and JH planned the study and conducted the sampling jointly, PT helped in data analysis. LN conducted the microscope work, data analysis and wrote the paper.
- III Both authors (LN, JH) designed the study and conducted the sampling. LN analysed the data, conducted the laboratory work and wrote the paper.
- IV Both authors designed the study and conducted the fieldwork jointly. LN did the laboratory analyses and JH wrote the paper.
- V Both authors designed the study and conducted the fieldwork. LN did the laboratory analyses and JH wrote the paper.
- VI LN and JH designed the study and collected the fish data. JL and TM helped interpret the data. LN analysed the data and wrote the paper.

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# 1. INTRODUCTION

## 1.1 Littoral zone – a link to the pelagic

The littoral zone of the lake can be regarded as a very complex area with multiple interactions between zooplankton-fish, predator-prey, biotic and abiotic factors forming a continuous cycle, changing in time and space, that influences the entire lake ecosystem. Food web interactions within littoral habitats and links between littoral and pelagic areas are inadequately understood. Animal movements (e.g. migration of fish and zooplankton) link the littoral and pelagic habitats both in terms of predator-prey interaction and translocation of nutrients (Carpenter et al. 1992, Schindler et al. 1996). In this puzzle, vegetation is an important component in regulating the biological structure of a lake via the littoral zone, especially in shallow eutrophic lakes (Timms & Moss 1984). In addition, abiotic factors, e.g. turbidity, bottom texture and light, reflect particularly on submerged vegetation.

The quantitative role of macrophytes in lake ecology is closely linked to their spatial distribution and biomass, which in turn is a result 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, temperature, pH, substrate characteristics, lake morphology, intra- and interspecific competition, herbivory and epiphyte loading (Dale 1986, Duarte et al. 1986, Vant et al. 1986, 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 (Schulthorpe 1967, Toivonen & Huttunen 1995). The role of macrophytes as stabilizing and structuring components in lakes of differing trophicity have been emphasized in the stable state theory by Scheffer et al. (1993) and in the cascading hypothesis by Jeppesen et al. (1998).

## 1.2 Theoretical background

The alternative stable state theory by Scheffer et al. (1993), underlining the stabilizing effect of vegetation, is based on the interaction between submerged macrophytes and phytoplankton-induced turbidity in a shallow lake (**Fig. 1**). This

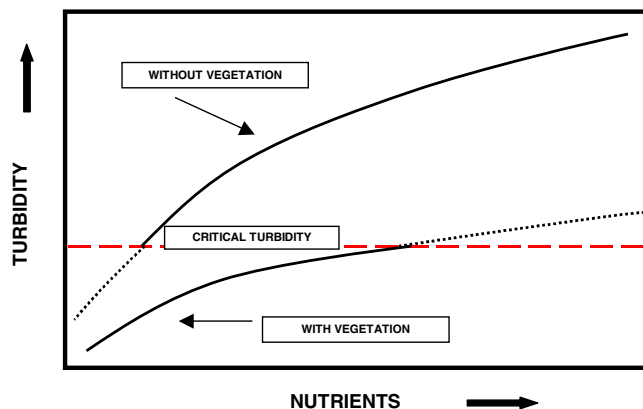


Figure 1. Stable-state theory by Scheffer et al. (1993) (modified) based on alternative equilibrium turbidities caused by disappearance of submerged vegetation.

theory is grounded on assumptions that turbidity increases concomitantly with nutrient level, increase of vegetation results in reduced turbidity, and vegetation vanishes when a critical level of turbidity is exceeded. Existence of submerged vegetation stabilizes the water quality of a shallow lake to a certain threshold. Even a rather considerable rise in nutrient loading cannot affect the turbidity level due to stabilizing effects of vegetation. Thus, the critical level of nutrient loading, causing phytoplankton turbidity, is lifted. However, in a *vice versa* situation of a high turbidity level and scanty vegetation, a much lower nutrient status should be attained in order to reach the same desired turbidity level. Thus, according to this theory, submerged vegetation performs as both positive (high biomass) and negative (low biomass) buffer in the altering stable states of shallow lake ecosystems.

The other background assumption related to the structuring role of vegetation in lakes is the hypothesis by Jeppesen et al. (1998) which is based on the cascading effect of submerged vegetation in lakes of differing trophicity (**Fig. 2**). The theory emphasizes the importance of structural complexity of submerged plants in providing refuge for zooplankton against fish predation. The biomass and seasonality of zooplankton is connected to lake trophicity, in turn reflecting the vegetation density. In eutrophic lakes with high macrophyte density, the zooplankton peak follows plant biomass, coinciding in late summer. On the contrary, in hypertrophic and oligotrophic waters with more scanty vegetation, the zooplankton biomass peak takes place in the beginning of summer or autumn, as no adequate refuge by vegetation is present.

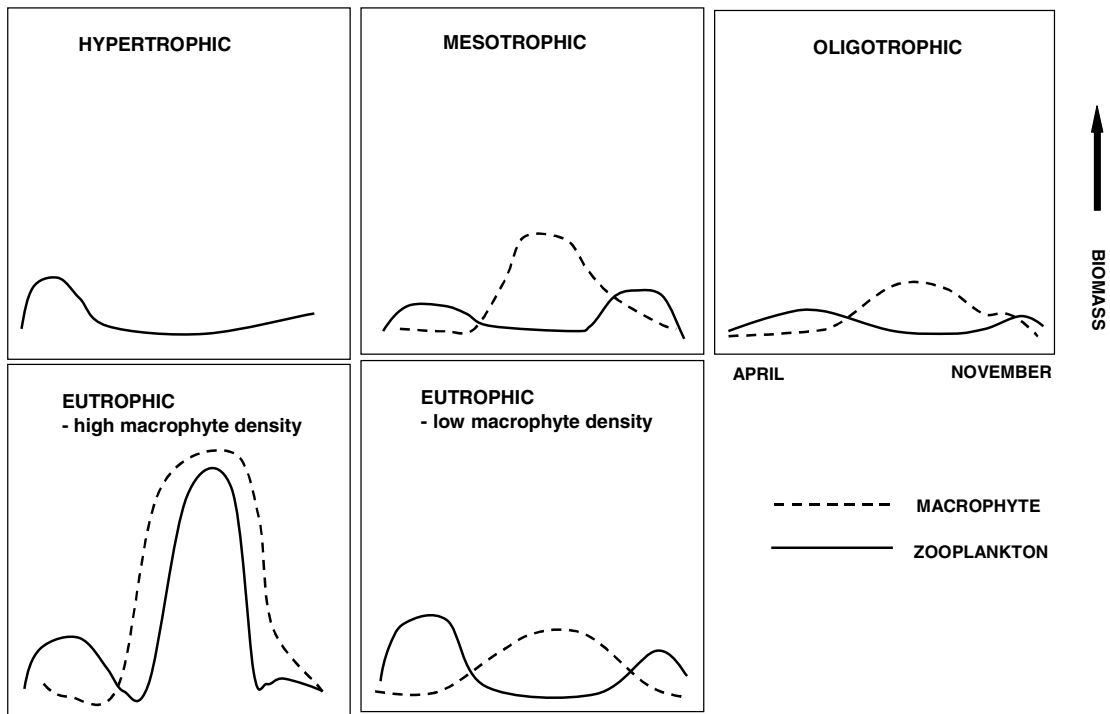


Figure 2. Conceptual model by Jeppesen et al. (1998) (modified) illustrating the change in zooplankton seasonality and biomass in various nutrient levels and the relationship with submerged vegetation.



### 1.3 Abiotic factors connected with macrophytes

#### 1.3.1 Light climate

The biological nature of each lake, reflecting also on macrophyte diversity and biomass, is strongly ruled by the euphotic depth, beyond which light level falls below 1% of surface irradiation (the critical level for photosynthesis) (Wetzel 1983). The light photon can either absorb or scatter – the proportions of which differ according to water quality and are very lake-specific. Scattering is caused by inorganic suspended particles and does not remove light from the water as absorption does, but changes direction (Kirk 1994). On the contrary, dissolved organic substances absorb light and phytoplankton both scatter and absorb. Also different wavelengths (blue, green, red) absorb in variable depths in different types of lakes (Kirk 1985). Understanding the differences between absorption, scattering and light attenuation is fundamental since different relative concentrations of phytoplankton, suspended solids and detritus effect the entity of light under water. Since algae and submerged vegetation depend on light availability, these causal links in the light climate are very important.

#### 1.3.2 Sediment resuspension

In lakes, water movement leading to resuspension of sediment depends on wave velocity, sediment properties, lake shape, and depth profile (Håkanson & Jansson 1983). In lakes with variable depth profile, sediment in exposed shallow areas are resuspended and concentrated to deeper parts. But in shallow lakes, resuspension can be continuous due to lack of deeper areas acting as sediment traps (Evans 1994). In addition to lake profile, the type of sediment is fundamental to resuspension frequency; organic substances and clay have low settling rates, whereas coarser material such as sand is not easily resuspended (Håkanson & Jansson 1983).

In addition to wave action, sediment can also be resuspended by animals (Andersson et al. 1988). Especially in shallow lakes, large part of the fish community feed on invertebrates dwelling on the bottom. As a whole, resuspension by benthivores can be quite substantial, e.g. bream (*Abramis brama* (L.)) can suspend 5 times its body weight per day (Breukelaar et al. 1994). Generally, main causes for turbidity in shallow lakes are suspended solids and algae, which tend to sink in lack of resuspension (Barko & James 1998). Aquatic macrophytes have been observed to reduce sediment resuspension by depressing wave velocity and hindering fish tampering (Dieter 1990, Madsen et al. 2001). The effect of aquatic vegetation appears to correlate with the vegetation structure and density.

#### 1.3.3 Nutrient dynamics

In shallow lakes, mostly due to the intense sediment-water contact nutrient dynamics is a continuous process (Evans 1994). One of the most important nutrients is phosphorus that correlates positively with eutrophication. The sediment-water interaction is very important, as a great deal of usable phosphorus can be stored in the sediment to be readily released. In general, sediment acts as a phosphorus buffer, but some mechanisms such as oxygen and iron, turbulence, decomposition and resuspension may enhance phosphorus release (Scheffer 1998).

Many biotic components have a significant role in nutrient cycling. Fixation of atmospheric nitrogen by e.g. cyanobacteria may cause influx of nitrogen to water. In general, phytoplankton obtain much of the required nutrients from the water column (Barko & Smart 1980). Aquatic animals have their own input in the ongoing nutrient circulation. Zooplankton and fish uptake nutrients in feeding and release nutrients back to water column by excretion (Taylor 1984, Kraft 1992). Also, benthivorous

invertebrates excrete mineral nutrients and enhance mixing of sediment surface, and phosphorus release tends to increase in concert with increasing invertebrate biomass (Wiśniewski & Planter 1985). The role of benthivorous fish is two-sided as they on one hand, may reduce the release of phosphorus from sediment by decreasing the invertebrate densities, but on the other hand act as nutrient pumps, causing resuspension while foraging and excrete nutrients into water column.

Effect of macrophytes on the phosphorus cycle is ambiguous (Granéli & Solander 1988). Vegetation beds reduce turbulence, which enhances possible anaerobic conditions at sediment surface but at the same time prohibits resuspension and limits phosphorus release from sediment. Macrophytes mobilize nutrients from sediment directly through root uptake and decayal and indirectly by causing fluctuations in pH and oxygen through metabolic activities (Barko & Smart 1980, Barko & James 1998). In general, aquatic vegetation can be considered as a phosphorus sink during growth and as a potential source during senescence (Carpenter & Lodge 1986). The emphasis of vegetation on phosphorus availability depends on both macrophyte species and density (Van Donk et al. 1993, Christensen & Andersen 1996). In shallow water bodies, potential negative effects by macrophytes on water quality (i.e. enhanced nutrient cycling) may be overshadowed by the ability of plant beds to moderate wave velocity (i.e. turbidity and suspended particle concentrations in the water) (Barko & James 1998).

#### **1.4 Biological components interlinked to macrophytes**

##### *1.4.1 Phytoplankton*

Phytoplankton is an important indicator of water quality (e.g. algal biomass, species formation, nutrient uptake) and coinciding with nutrient loading often has a dominant

role as the main primary producer in shallow lakes. Macrophytes and their symbiotic epiphytes, which especially in shallow eutrophic lakes may play a considerable role in nutrient dynamics, compete for the same available nutrients (Kufel & Ozimek 1994). Nevertheless, phytoplankton, in addition to epiphyton, has been proven to be instrumental (directly or indirectly) in many processes taking place in the littoral zone related to macrophytes. The volume of sedimentation and resuspension (in turn modified by macrophyte beds), influences phytoplankton communities, as most species tend to sink in still water (Barko & James 1998). Macrophytes also have a shading effect on phytoplankton leading to reduced intensity (Ozimek et al. 1990). The total shading effect depends on the biomass and surface area of plant species (Sher-Kaul et al. 1995).

Very crucial linkage having a substantial bearing on the water quality is phytoplankton grazing by zooplankton, to which macrophytes provide refuge from predators. Therefore, plant beds enable increased grazing, influencing the chlorophyll *a* concentrations (phytoplankton-caused turbidity) of the lake. Macrophytes apparently have a certain threshold after which they have a substantial effect on phytoplankton biomass. Plant threshold levels suggested to be adequate vary between 20-50% PVI (percent volume infested) (Canfield et al. 1984, Schriver et al. 1995). On the whole, studies on the relative importance of top-down control of phytoplankton by zooplankton or bottom-up control through nutrients in macrophyte beds are scarce. Fish modify the influence of macrophytes on phytoplankton through zooplankton predation in different plant densities. Therefore, phytoplankton variables may change along nutrient, macrophyte and fish gradients.

### 1.4.3 Zooplankton

Zooplankton grazing has been recognized to be an indisputable factor regulating phytoplankton in lakes (e.g. Kerfoot et al. 1988). Particularly *Daphnia*, as predominant cladoceran, can play a major role in the seasonality and biomass of phytoplankton. Biomass, average individual size and structure of the zooplankton community are largely determined by predation pressure. In shallow eutrophic lakes, fish predation can induce a shift from *Daphnia*-domination to a zooplankton community with smaller cladocerans, e.g. *Bosmina*, coinciding with rotifers and cyclopoid copepods (Jeppesen et al. 1992). Predation pressure increases in concert with lake trophy due to shift to a higher proportion of zooplanktivores and change in age composition towards younger fish, preying more selectively on zooplankton (Cryer et al. 1986).

Zooplankton seek refuge against predation, and in shallow lakes, where shelter provided by a depth gradient is absent, zooplankton resort to horizontal migration among macrophytes for refuge (Walls et al. 1990). Horizontal distribution of zooplankton varies diurnally and seasonally, mostly due to the spatial and temporal variation of predation by e.g. young-of-the-year fish (YOY) and invertebrate predators (Cryer & Townsend 1988). Reverse migration caused by predation of YOY fish or plant-associated predators such as odonates has also been reported, although diurnal horizontal migration (DHM) induced by invertebrate predators is probably most important in lakes with low fish densities (Lauridsen et al. 1996). Also diurnal microvertical migration, e.g. pH-induced, is reported in many studies (e.g. Hansen et al. 1991). According to Ivanova and Klekowski (1972), high lake pH may impair the survival of grazing zooplankton, influencing the respiration and filtration rate of cladocerans. Large cyanobacteria may, in addition of elevating pH, affect the

filtration capacity of zooplankton by interference and be less edible and even toxic (Dawidowicz 1990, Gliwicz 1990).

Migration by zooplankton into vegetation is a trade off between predation risk and optimal feeding conditions since macrophytes (e.g. *Myriophyllum*) produce repellants suppressing zooplankton (Lauridsen et al. 1997). Additionally, filtration among plants and macrophyte shading, causing a lower phytoplankton biomass, result in smaller littoral zooplankters, such as *Ceriodaphnia* and *Diaphanosoma* (Lauridsen et al. 1996). Despite unfavourable conditions, especially large zooplankton aggregate within the vegetation beds during daytime (Timms & Moss 1984, Davies 1985, Lauridsen & Buenk 1996). Refuge effect and relative zooplankton composition and abundance among vegetation depends on plant density (Schriver et al. 1995) and fish composition (Persson 1991). In larger stands, especially free-swimming, often pelagic, cladocerans are more scarce (Lauridsen et al. 1996), but plant-associated species may be very abundant (Paterson 1994). Cladocerans fixed to plants (e.g. *Sida crystallina* (O.F. Müller)) may be crucially underestimated, and they may possess a considerable filtration capacity (Irvine et al. 1990, Jeppesen et al. 1997). Plant density affects the predation capability of fish, the denser the bed the better the refuge (Schriver et al. 1995, Jeppesen et al. 1997), although, high fish predation have been shown to suppress zooplankton communities even in dense vegetation (Kairesalo et al. 1998). In general, sparse plant beds allow efficient foraging for some juvenile fish (poor protection for pelagic zooplankton) but plant-associated cladocerans appear to escape predation and can be abundant even at high fish densities.

#### 1.4.4 Fish

Fish in a shallow lake play an indispensable role in structuring the lake community. In addition to direct predation, fish may influence both bottom-up and top-down control via their search for food at the bottom. While searching for food, fish stir up sediment, causing a rise in concentrations of suspended solids (Breukelaar et al. 1994). Increase in turbidity reduces hunting by visual predators (e.g. perch; *Perca fluviatilis* L.), which in turn increases the number of planktivorous prey fish, resulting in a negative impact on large zooplankton (Jeppesen et al. 1997).

Many factors influence the structure of fish community. High pH has a negative influence on fish recruitment and fry survival (Timmermann 1987). Increase in lake trophy leads to a change in fish community structure where vegetation plays a significant role; in turbid waters lacking vegetation, dominating species are cyprinids and pikeperch (*Stizostedion lucioperca* (L.)) (Lammens 1989), whereas in vegetated water, percids and small pikes (*Esox lucius* L.) prevail (Grimms 1983). Predator efficiency declines in concord with macrophyte structural complexity (Heck & Crowder 1991), but reversely prey density and diversity increases, therefore, fish presumably grow best in intermediate vegetation density (Crowder & Cooper 1982). The structuring role of vegetation on the fish community is based on food availability and predation risk leading to macrophyte density mediating predator-prey interactions. Foraging efficiency among vegetation is discovered to be species-specific; zooplankton consumption by juvenile roach (*Rutilus rutilus* (L.)) decreased with vegetation density, whereas capture rates of rudd (*Scardinius erythrophthalmus* (L.)) and perch can be enhanced by vegetation when not too dense (Winfield 1987, Persson et al. 1993). Vegetation does not influence fish communities only by predator-prey

interactions; herbivory of macrophytes by cyprinids (rudd and roach) has been observed to play an important role in structuring macrophyte species composition in lakes (Van Donk 1998).

The protective importance of macrophytes against predation from larger piscivores is crucial for juvenile fish (Venugopal & Winfield 1993, Persson & Eklöv 1995). This results in higher densities of juvenile fish in macrophyte rich lakes (Carpenter & Lodge 1986). Importance of YOY fish is far more prominent in lake ecosystems than expected (e.g. Cryer et al. 1986; Whiteside 1988). In meso-eutrophic lakes, juvenile fish may be responsible for the mid summer zooplankton biomass decline (**Fig. 2**) (Luecke et al. 1990).

#### 1.5 Macrophytes in turbid water – diverse causal connection

The formation and existence of macrophytes has a duplex causal connection with turbidity (**Fig. 1**; Scheffer et al. 1993). Vegetated lakes are more transparent as vegetation has a decreasing effect on turbidity. The cascading power over phytoplankton-induced turbidity is clearly seen in temperate lakes where the macrophyte biomass peak is in mid summer and the chlorophyll peak appears in spring and fall. In Dutch lakes, wintergreen submerged plant, *Elodea*, kept phytoplankton biomass generally low, whereas *Ceratophyllum* and *Potamogeton* oming shorter growing seasons, allowed phytoplankton blooms in spring and autumn (Van Donk & Gulati 1995). As previously discussed, in addition to influencing algal growth and seasonality, macrophytes may buffer sediment resuspension by wave action (inorganic turbidity), affect nutrient availability and harbour filter feeding cladocerans. However, the weighting of these various mechanisms on water quality varies considerably in different lakes.

As vegetation has a major function in controlling turbidity, also turbidity among other factors regulates macrophyte growth (Scheffer 1998). Maximum depth for plant growth is inversely related to attenuation of light (Chambers & Kalff 1985). More important than the light that reaches the bottom is the amount of light reaching the plant canopy. Therefore, the effect of turbidity on submerged vegetation depends on the growth form as canopy-forming species prevail when nutrient level increases (Chambers 1987, Moss 1998). In turbid waters, also species overwintering in vegetative form have a competitive advantage, since they hold the energy to start spring growth and do not require bottom-reaching light (Scheffer et al. 1992). Periphyton growth together with nutrient loading increases turbidity affecting plant growth. Periphyton can reduce light by 80%, limit diffusion of carbon and other nutrients and also mechanically suppress plants (Sand-Jensen & Borum 1984). Other important factors effecting formation of vegetation is wave action and herbivory. Water movement enhances nutrient uptake but can also increase uprooting and turbidity, due to resuspension, resulting in inhibition of plant settlement (Van Donk & Otte 1996, Scheffer 1998). Herbivory, via grazing and uprooting of plants, can be very substantial leading up to over 50% reduction in vegetation (Lodge 1991). Herbivorous fish in temperate lakes (e.g. rudd and roach) have not been witnessed to reduce plant biomass but may have a potential effect on plant species composition through selective grazing (Van Donk et al. 1998). As an indirect effect, bottom foraging of these grazers stir up sediment, leading to inhibition of plant growth.

## 2. OBJECTIVES OF THE STUDY

The discussion on the manifold causal role of macrophytes in littoral ecosystems and their stabilizing effect on water quality are mostly confined to submerged species (e.g. Hanson and Butler 1994, Jacobsen et al. 1997, Stansfield et al. 1997). This is due to their alert response to eutrophication through changing light climate, and ability to provide profitable refuges for zooplankton due to structural complexity (Dionne & Folt 1989). The stable state theory by Scheffer et al. (1993) as well as the refuge hypothesis by Jeppesen et al. (1998) are both founded on submerged species. However, the role of other macrophyte life forms needs to be specified, especially in lakes, where the water quality is not solely regulated by the development of phytoplankton biomass, but also by inorganic suspended solids. Such lakes may be inherently quite turbid and have scanty submerged vegetation. Therefore, the role of emergent and floating-leaved species should be taken under more careful scrutiny.

The study area of this thesis, Lake Hiidenvesi, resembles an inherently clay-turbid eutrophicated lake with relatively scarce submerged vegetation. In these settings, I aimed to clarify the role of the emergent life form on the two important functions of macrophytes: 1) refuge for zooplankton and 2) effect on sediment resuspension. In addition, the importance of fish herbivory on the restricted submerged vegetation was investigated. This thesis therefore hypothesizes that in clay-turbid circumstances, in the absence of submergents, other life forms e.g. emergent and floating-leaved, play a significant role in the important structural and stabilizing functions of vegetation stated.

The thesis is composed of six studies of which paper **I** is a vegetation mapping and life form structure study in the different basins of Lake Hiidenvesi with divergent water quality. In paper **II**, the role of emergent vegetation on the seasonal distribution of littoral zooplankton (refuge effect) in turbid water is evaluated. This study aimed to clarify whether the seasonal development of zooplankton follows the hypothesis by Jeppesen et al. (1998) in clay-turbid circumstances where emergent macrophytes dominate instead of submerged species. The same theme is continued in paper **III** where diurnal horizontal migrations of zooplankters among emergents in basins of differing water quality (eutrophic and mesotrophic) is studied. In addition, in this paper (**III**) the effects of mass occurrence of phytoplankton, common in eutrophic conditions, on littoral zooplankton composition and diurnal distribution are discussed.

The importance of different macrophyte life forms, in this study emergent (**IV**) and submerged (**V**) macrophyte stands, on sediment resuspension and phosphorus dynamics is investigated and compared. Finally, the effect of fish, in this case rudd, herbivory on the species composition and abundance of inherently scanty submerged vegetation is studied in paper **VI**.

However, as discussed in previous sections the littoral ecosystem is a linkage of abiotic and biotic factors jointly affecting the processes. Therefore, in addition to these main research subjects, this thesis also aims to discuss some of the causal links and processes in the manifold field of research related to macrophytes in clay-turbid lakes (Fig. 3).

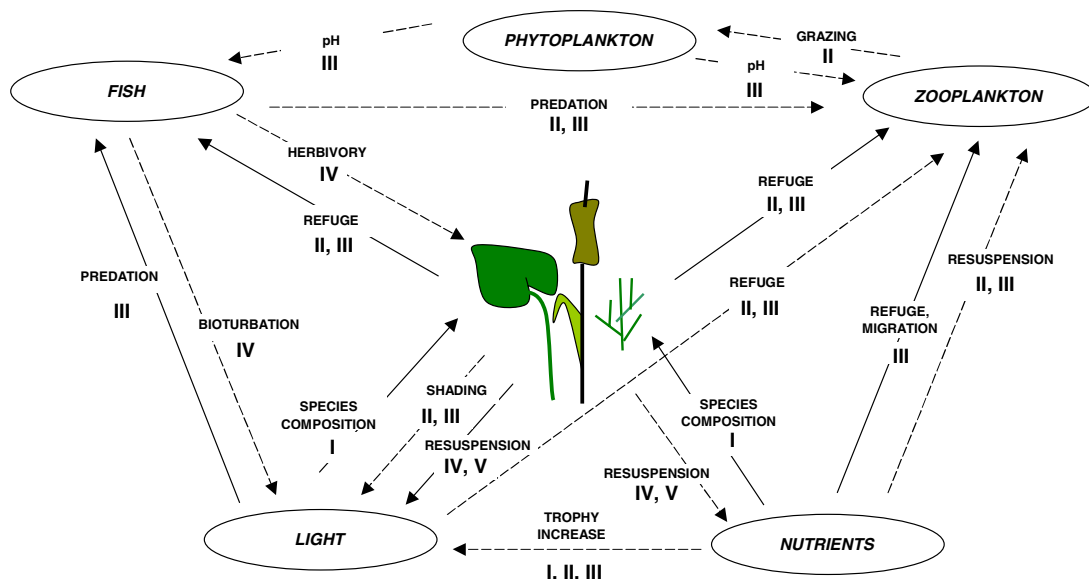


Figure 3. Schematic illustration of the different abiotic and biotic links related to macrophytes discussed directly and indirectly in this thesis (bold Roman numbers indicate articles) (solid line - positive effect; broken line - negative effect).

### 3. STUDY AREA AND METHODS

#### 3.1 Study lake

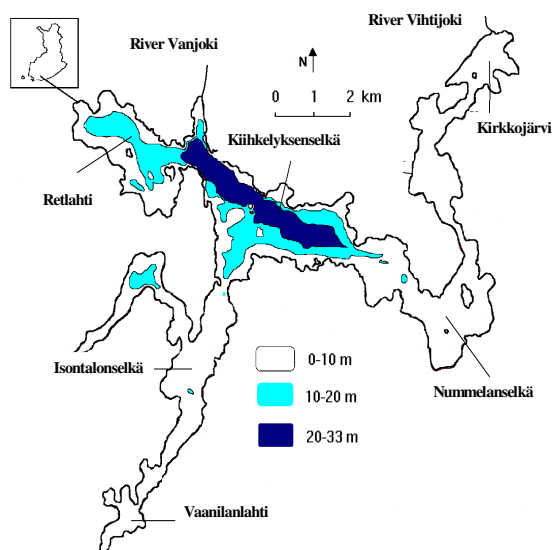


Figure 4. Map of Lake Hiidenvesi; study areas (indicated as basins) are shown. Main characteristics and water quality variables of basins are indicated in Table 1.

Lake Hiidenvesi is the second largest lake (30.3 km<sup>2</sup>) on the southwestern coast of Finland (60° 24' N, 24° 18' E).

Due to heavy point and non-point loading, the lake has a long eutrophication history with severe cyanophyte blooms occurring since 1960s (Tallberg et al. 1999). Almost 90% of the annual external phosphorus loading (0.5-1 g m<sup>2</sup> P) to the lake comes from the two rivers Vihtijoki (51%) and Vanjoki (38%) (Ranta & Jokinen 1998).

Altogether, Lake Hiidenvesi is inherently considerably turbid, due to the composition and resuspension of the bottom material (inorganic matter e.g. clay). The lake is a flow-through system, consisting of several separate basins quite different in their morphology and trophic status (**Table 1**), the basins being as follows: Kirkkojärvi (northeastern part), Nummelanselkä, Kiihkelyksenselkä, Retlahti, Isontalonselkä and Vaanilanlahti (southwestern part) (**Fig. 4**).

Due to high turbidity, the biomass of submerged macrophytes is relatively low and restricted to shallow sheltered bays. Emergent vegetation in the lake is relatively abundant especially in shallow Kirkkojärvi and Vaanilanlahti basins. Floating-leaved life form is common throughout the lake with wide zones of *Nuphar lutea* (L.) prevailing in every basin.

Table 1. Main characteristics and environmental variables of the interconnected basins of Lake Hiidenvesi (measured 8<sup>th</sup> August) (**I**). (bottom type; 1 \*semi-hard, 2 \*semi-soft, 3 \*soft)

Basins	Tot-N (µg l <sup>-1</sup> )	Tot-P (µg l <sup>-1</sup> )	Secchi (cm)	Turbidity (NTU)	Conductivity (mS m <sup>-1</sup> )	Mean depth (m)	Bottom type
Kirkkojärvi	1400	100	30	58	10.1	1.9	3
Nummelanselkä	1100	50	60	25	8.7	2.6	2
Kiihkelyksenselkä	1100	40	100	16	8.2	11.2	1
Retlahti	850	30	120	8	8.1	7.9	1
Isontalonselkä	730	30	110	11	8.2	3.3	1
Vaanilanlahti	890	140	110	6	10.3	1.3	2

## 3.2 Sampling and analyses

### 3.2.1 Macrophytes

The aquatic vegetation mapping (I) was conducted with an aquascope and sampling rakes (modified garden rake and Luther-rake; Luther 1951). Simultaneously with mapping, macrophyte abundance (modified 3-degree Norrlin scale method; Luther 1951, Munsterhjelm 1997) and growing depths were charted. Chemical water quality samples (total P, total N) were analysed according to the standards of Finnish Environment Institute. Turbidity and conductivity were analysed with YSI 6600 sonde. The mappings were roughly compared to earlier vegetation mappings from the 1950's (K. Aura, pers. comm). To evaluate the weighing of each environmental variable on the species occurrence, each measured parameter was independently tested with the macrophyte life forms using 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).

### 3.2.2 Seasonal and diurnal zooplankton distribution

The sampling for zooplankton was conducted with a tube sampler (h = 1 m, V = 7.5 l); fortnightly during the summer (seasonally) from three different zones of emergent vegetation (5 m inside and outside the stand and at the edge) (II) and diurnally (5 samples in total; 3 times at noon and 2 at midnight) from three different zones (same as above) of emergent stands in two basins (*Typha angustifolia* in Kirkkojärvi basin; *Phragmites australis* in Isontalonselkä basin) of differing water clarity and quality (III). The cladoceran samples (5 replicates, II; 3 replicates consisting 3 pooled subsamples, III) were enumerated using an inverted microscope and identified to genus or species level. Dense samples were

subsampled and 30 individuals from each species were measured (*Daphnia* spp. using eye-length) and individual numbers were converted to carbon biomass, using length-carbon- regressions (e.g. Luokkanen 1995). Cladoceran biomasses and densities in the different vegetation zones were compared using analysis of variance for repeated measurements and the mean lengths of different cladocerans with analysis of variance (II). Paired comparisons were conducted with Bonferroni t-tests (II). Cladoceran biomass, densities and individual lengths during day and night in the different zones were compared using the Mann-Whitney U-test (III).

The daily phytoplankton consumption rate of zooplankton (II) was calculated using the equation of Lampert (1988), according to which the daily amount of carbon eliminated =  $83 \text{ mg g}^{-1} \text{ d}^{-1} \text{ DW}$ , and by method of Jeppesen et al. (1994), according to which cladocerans ingest an amount of phytoplankton equivalent to 100% of their own biomass per day. Consumption rates were compared with phytoplankton biomass, taken from the epilimnion (0-2 m) with tube sampler.

Physical and chemical water characteristics (e.g. temperature, pH) (II, III) were taken during every sampling and the density of stands was measured with a 0.25 m<sup>2</sup> frame. The photosynthetic photon flux density at 400-700 nm from 10 cm below the water surface and 10 cm above the bottom in each zone was measured by a LI-COR quantum meter. Phosphorus, nitrogen and chlorophyll *a* were measured in the beginning of the study (III).

### 3.2.3 Sediment resuspension

The sediment resuspension studies related to macrophytes were conducted in three different zones (5 m inside and outside and at the edge) of emergent (IV) macrophytes and two zones (30 m inside and outside) related to submerged (V) vegetation. The



stem densities of emergents and PVI (percent volume infested) of submerged vegetation were measured during every sampling. The rate of sediment resuspension was estimated using the method by Gasith (1975), applicable especially to shallow water bodies, based on the assumption that the organic matter content of the bottom sediment is different from that of suspended seston. The method uses the equation

$$R = S \frac{(f_S - f_T)}{(f_R - f_T)} \quad (\text{Gasith 1975, Bloesch 1994}), \text{ where}$$

R= resuspended bottom sediment (dry mass)

S= entrapped settling flux (dry mass)

$f_S$  = organic fraction of S

$f_R$  = organic fraction of R (surface sediment)

$f_T$  = organic fraction of seston (T) suspended in the water

Gross sedimentation rate was determined by placing sedimentation traps (5 replicates) in each zone. The traps (height : width ratio of 6 : 1) were lifted at 14-day intervals. The content of traps was dried and the organic fraction ( $f_S$ ) was determined by ignition at 550 °C. Seston samples from each zone were taken with a tube sampler, filtered through a GF/C filter and, following filtration, analyzed for suspended solids (SS) and loss on ignition ( $f_T$ ), total P and SRP (soluble reactive phosphorus). In addition, three replicate surface sediment samples were also lifted from each zone with a corer and analyzed for loss on ignition ( $f_R$ ). The rate of P resuspension in each zone was estimated using the calculated resuspension rates and the P content of surface sediment, determined on each date from the surface sediment samples. Following the recommendations of Gasith (1975), the values of gross sedimentation rate (S) were corrected by subtracting the dry mass of suspended matter, contained by the water volume in each trap, from the gross dry mass per trap. Between-zone differences in the values of  $f_S$ ,  $f_R$ ,  $f_T$ , as well as in the

sedimentation rate, were tested using analysis of variance for repeated measurements (IV,V). Paired comparisons were conducted with Bonferroni t-tests (IV,V).

### 3.2.4 Fish diet

Rudd (*Scardinius erythrophthalmus*) data for diet analysis were collected among macrophyte vegetation with gillnets (mesh sizes 10-45 mm from knot to knot) placed in water depths of 1-1.5 m (VI). Gillnettings were conducted during the day with nets held in the water for 1-2 h. The gut content (anterior third) was analysed for volume proportions of different food items (Rask 1989). The fish (n = 516) were measured to nearest mm and weighted to nearest g. The age was determined using both scales and cleithra (Horppila & Nyberg 1999). The growth rate was back-calculated using Fraser-Lee method (Bagenal & Tesch 1978).

Food consumption of rudd (age groups 3-7) was estimated using bioenergetics model (Kitchell et al. 1977, Hewett & Johnson 1992). Existing roach parameters (Horppila & Peltonen 1997) were applied to rudd. The calorimetric values were obtained from literature (Cummins & Wuycheck 1971, Horppila & Peltonen 1997). Back-calculated yearly growth rates were used in calculating macrophyte consumption of each age group. Back-calculated lengths were converted to weight using the length-weight equation  $w = 0.00003 L^{3.305}$  ( $r^2 = 0.99$ ). Total macrophyte consumption by rudd was estimated using a scenario of different combinations of biomass and age group distributions.

## 4. RESULTS AND DISCUSSION

### 4.1 Macrophyte species composition

The macrophyte vegetation in Lake Hiidenvesi (**I**) was different in the divergent areas of the lake, conceivably due to the disparity of water chemistry, substratum and morphological features of the connected basins (Smith & Wallsten 1986, Bailey 1988). The overall rather low light penetration 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 conditions, are practically absent (**I**) (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, substratum characters and exposure gradients (**I**) (**Table 2**), which are concomitantly the most important features determining the formation of emergent vegetation (Bailey 1988, Toivonen & Huttunen 1995). Eutrangent species such as *Typha latifolia* L., *Typha angustifolia* L.,

*Sparganium erectum* Rehman, *Glyceria maxima* (Hartm.) Holmberg and *Acorus calamus* L., tolerating loose loam substrata (Toivonen & Bäck 1989), thrive in the shallow waters of the northern and northwestern basins of Lake Hiidenvesi (**I**).

Indifferent *Phragmites australis* (Cav.) Trin. Ex Steudel and *Equisetum fluviatile* L. requiring more exposed sites with coarser substrata, dominate the less eutrophicated western and southern basins (**I**). Floating-leaved species, e.g. nymphaeids, and *Polygonum amphibium* L. are well represented in Lake Hiidenvesi (**I**), due to an allegedly advantageous life form in turbid waters.

As light attenuation and depth are most important factors explaining submerged vegetation abundance, the species abundance and overall biomass of submerged flora in turbid Lake Hiidenvesi is mainly restricted to rather few low light-tolerant species (**I**). However, the somewhat differing species composition of the basins reflects the changing light conditions and nutrient status (**Table 2**). Prevailing “turbidity tolerant“ flora, in addition to *Potamogeton obtusifolius* Mert. & Koch, are pleustophytes, which are rootless byonants, (*Ceratophyllum demersum* L., *Ranunculus circinatus* Sibth.) and canopy-forming submerged plants (*Myriophyllum verticillatum* L.) (**I**).

Table 2. 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) (**I**).

	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

The species assemblage in Lake Hiidenvesi indicated 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 (I). Tall reedy 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 (I). 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*, thriving from sheltered soft habitats and having a high tolerance for low light conditions (Uotila 1971, Meriläinen & Toivonen 1979), have plagued parts of the shallow northern basins, especially Kirkkojärvi basin (I). In addition, nutrient level increase induces macrophyte competition with phytoplankton, as well as shading by phytoplankton blooms and periphyton (Sand-Jensen & Søndergaard 1981). Sand-Jensen & 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.

## 4.2 Role of emergent macrophytes as zooplankton refugia

### 4.2.1 Influence on seasonality of zooplankton community

In north temperate lakes, the most frequently observed seasonal pattern of littoral zooplankton includes a spring peak followed by a steep decline in mid summer, being usually explained by increased predation of underyearling fish (Cryer et al. 1986, Whiteside 1988). This is true especially in lakes with low submerged macrophyte density and consequently low refuge availability for zooplankton (Jeppesen et al. 1998). In eutrophic lakes with high submerged macrophyte coverage, the refuge effect is high and zooplankton biomass follows the macrophyte biomass, peaking in mid summer (Fig. 2; Jeppesen et al. 1998). In this study related to emergent species (*Typha angustifolia*) (II), although the zooplankton biomass was quite low, the seasonal pattern followed the one resembling high macrophyte biomass lakes, zooplankton peak taking place in mid summer, even though coinciding with the highest consumption rate of fish. In the beginning of summer as no refuge for cladocerans was found (II), predation probably suppressed zooplankton biomass. Through the summer as emergent stands developed, the cladoceran abundance increased accordingly (II) (Fig. 5). Among the vegetation, the biomass of especially free-swimming filter feeders (*Diaphanosoma brachyurum* (Lieven), *Bosmina longirostris* (O. F. Müller), *Ceriodaphnia quadrangula* (O. F. Müller) and chydorids) increased, while at the edge and outside the stands, the free-swimming cladoceran biomass remained low (II) (Fig. 5). This seasonal succession resembled the trend observed by e.g. Lehtovaara & Sarvala (1984).

The pattern observed was conceivably a consequence of concomitant changes in predation pressure and refuge availability

provided by emergents, as predation pressure in the studied Kirkkojärvi basin is high, indicated by high catches of small cyprinids as well as perch and small average size of cladocerans with high share of cyclopoid copepods and cladocerans in the crustacean assemblage (Tallberg et al. 1999, Olin et al. 2002). The fish assemblage of the Kirkkojärvi basin is dominated by cyprinids, different species spawning in sequence in spring. The YOY fish inhabit the vegetation, feeding at first on algae and rotifers and switching to cladocerans (Hammer 1985). Thus, predation pressure provided by small fish is considerable.

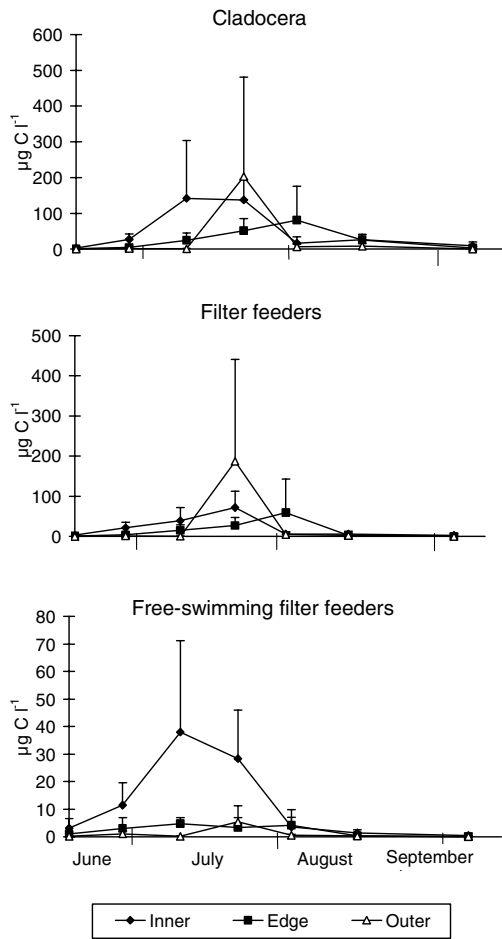


Figure 5. Total cladoceran carbon biomass (top), biomass of filter feeding cladocerans (middle) and biomass of free-swimming filter feeding cladocerans (bottom) in the different zones of the *Typha angustifolia* stands (vertical bars indicate SD values) (II).

The effects of emergent macrophytes on the grazing pressure of cladocerans can be considerable (II). Even though low at the edge and outside the stands, the grazing pressure of free-swimming filter feeders within the vegetation (II) (Fig. 6) reached the 80% daily grazing considered to be sufficient to balance growth rates of algae (Reynolds 1984). In the outer zone of the emergent stand, the grazing pressure of the rather large-sized plant-associated cladoceran, *Sida crystallina* (O. F. Müller), was higher than of the free-swimming species together (II) (Fig. 6). In our sampling, due to methodology, the density of *Sida crystallina* (mostly fixed to plants e.g. floating-leaved) was allegedly underestimated.

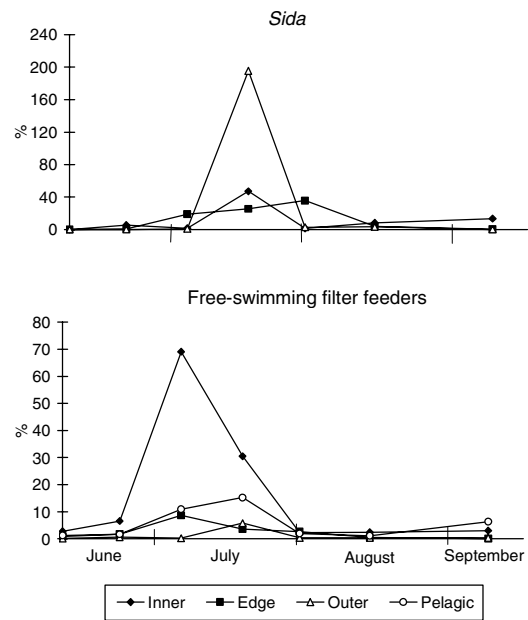


Figure 6. Consumption rate (as percentage of phytoplankton biomass) by *Sida crystallina* and by littoral and pelagic free-swimming filter feeders in the different zones of the *Typha angustifolia* stand (II). The calculations follow the method introduced by Jeppesen et al. 1994.

Another clear effect on zooplankton provided by emergent macrophytes in turbid conditions is reduced concentrations of suspended solids, indicated by the enhanced light conditions among the vegetation (II). Emergent macrophytes can

reduce resuspension to one fifth compared to unvegetated areas (IV). This is remarkable since high concentrations of suspended solids can reduce fecundity and survivorship of cladocerans via reduced ingestion rates of phytoplankton cells (Gliwicz & Rybak 1976).

#### 4.2.2 Importance of lake trophy in diurnal distribution of zooplankton

To avoid predators, many cladocerans seek refuge during the day, i.e. perform horizontal migration within macrophyte beds (Walls et al. 1990). As previous studies showed clear refuge providance of emergent vegetation in turbid conditions (II), the effect of lake trophy (turbid hypertrophic and less turbid, mesotrophic) (Table 1) on diel migration patterns of zooplankton (III) was further studied. The two areas studied, Kirkkojärvi basin and Isontalonselkä basin, had different cladoceran assemblages, both in respect of species composition and diel community structure. In the turbid Kirkkojärvi basin, diel changes in cladoceran assemblages were observed in the form of nocturnal peaks both in density (III) (Fig. 7) and biomass (Fig. 8).

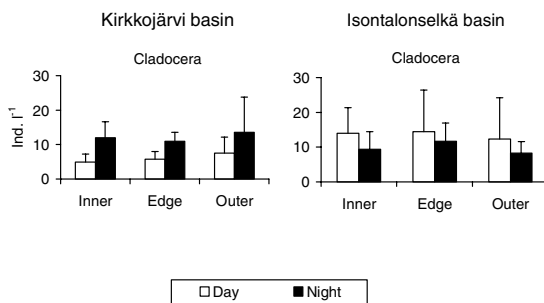


Figure 7. Mean total cladoceran densities during the day and night sampling in the three zones of the emergent vegetation stands of Kirkkojärvi and Isontalonselkä basins (vertical bars indicate SD values) (III).

These day-night differences were primarily due to the prevailing cladocerans, *Limnosida frontosa* (Sars), *Diaphanosoma*

*brachyurum*, *Sida crystallina*, and mostly plant-associated chydorids (III). In Isontalonselkä basin, with distinctively clearer water, the emergent stand seemed insufficient to provide refugia for zooplankton or induce diel migration, indicated by highest cladoceran densities during the day (III) (Fig. 7). This being mostly due to the daytime peak in free-swimming filterers (Fig. 8), namely, *Daphnia* spp. (III).

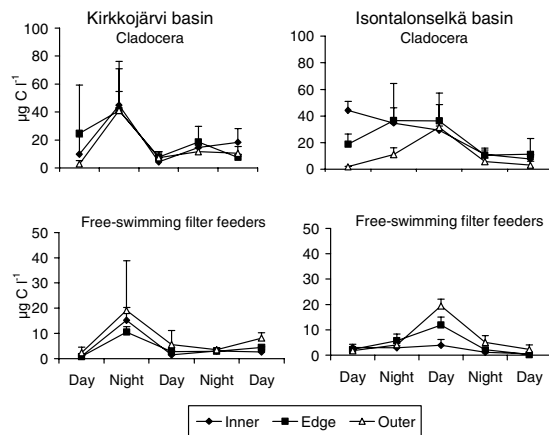


Figure 8. Total cladoceran carbon biomass (top) and biomass of free-swimming filter feeders (bottom) in the three zones of the emergent stands of Kirkkojärvi and Isontalonselkä basins (vertical bars indicate SD values) during three sequential days (III).

According to the study by Smiley and Tessier (1998), YOY fish, congregating within the vegetation during the day, may result in opposite diurnal migration, i.e. cladocerans moving into open water during the day and into vegetation during night. The reverse horizontal migration (nocturnal aggregation among vegetation) among the large-sized cladocerans, *Limnosida frontosa* and *Sida crystallina*, in Kirkkojärvi basin (III) (Fig. 9) suggested that even in turbid lakes fish may have a significant role in regulating zooplankton communities (Gliwicz 1986).

Since in Kirkkojärvi basin dense schools of small fish seek refugia within the vegetation from piscivores during the day

(unpublished), large-sized zooplankton may reciprocally concentrate into the pelagic (Walls et al. 1990). *Sida crystallina* was the only cladoceran in which night-time density peaks were observed in both Kirkkojärvi and Isontalonselkä basins (III). These coinciding peaks, with highest densities at the edge zone (III), support previous findings that *Sida crystallina* actively uses the edge of macrophyte beds, staying attached to plants during the day, but is free-swimming at night, performing diel horizontal movement (Fairchild 1981, Vuille 1991). In Kirkkojärvi basin, *Limnosida frontosa*, on the contrary to *Sida crystallina*, migrated from the inner zone out into the pelagic (III) (Fig. 9), this being in harmony with the more limnetic nature of the species.

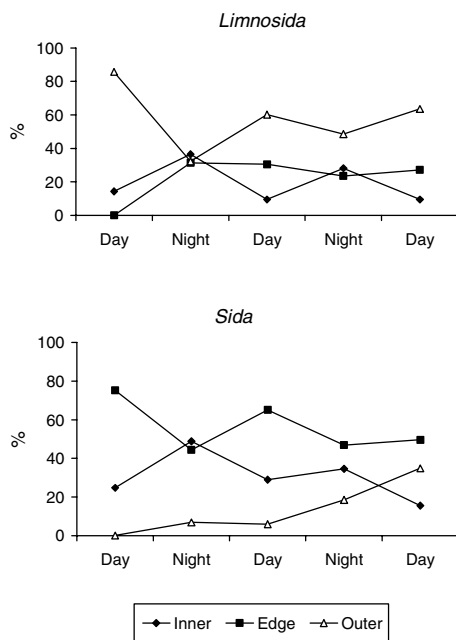


Figure 9. Percentage of the (a) *Limnosida frontosa* and (b) *Sida crystallina* populations during day-night sampling in the three zones of the emergent vegetation stand of Kirkkojärvi basin during three sequential days (III).

In Isontalonselkä basin, the clearly predominating cladoceran was *Daphnia* sp., showing 'shore avoidance' (Hutchinson 1967) by aggregating in the open water both night and day (III). This behaviour of

cladocerans may be induced by several different mechanisms. Macrophytes serve as a habitat for invertebrate predators (Kornijów & Kairesalo 1994) and several fish species (Boikova 1986, Lauridsen et al. 1999) that constitute a predation risk to large-bodied zooplankton, inducing concentration in open water. Furthermore, YOY fish, feeding primarily on zooplankton, may be aggregated within macrophyte stands either on a diel (Gauthier & Boisclair 1997) or a seasonal basis (Whiteside 1988, Hall & Rudstam 1999). The daytime cladoceran density peak, observed in the outer zone of Isontalonselkä basin (III) (Fig. 8), is in contrast with findings in the Kirkkojärvi basin and other shallow eutrophic lakes (Lauridsen & Buenk 1996, Lauridsen et al. 1996, Jeppesen et al. 1997), where cladocerans aggregate near macrophyte stands during day and are pelagic during night, but again in harmony with observations by Lauridsen et al. (1999) from mesotrophic lakes. According to Jeppesen et al. (1997) and Stansfield et al. (1997), macrophyte density is a critical factor for the efficiency of the beds as zooplankton refuge. Since there was no notable difference in the macrophyte densities between the two basins (III), the distinctively more transparent water in Isontalonselkä basin may abate the sufficiency of emergent macrophytes as refugia for zooplankton.

#### 4.2.3 Effect of a phytoplankton bloom on zooplankton assemblage

Contradictory to preceding observations in Kirkkojärvi basin (II), no clear refuge effect, i.e. aggregation within the emergent stand was detected in the diurnal distribution study (III), conceivably due to the ongoing cyanobacterial bloom. The suppressing impact of phytoplankton, leading to cladocerans avoiding unpropitious conditions clearly overruled the refuge effect. In Kirkkojärvi basin, typical small-sized "midsummer"

cladocerans *Diaphanosoma brachyurum*, *Ceriodaphnia quadrangula* and *Chydorus sphaericus* (O.F. Müller) (Manuljova 1964), benefiting together with *Bosmina longirostris* from high concentrations of small-sized suspended material in the water (Gliwicz 1977), normally compose most of the biomass of the free-swimming filter feeders (II). High concentrations of filamentous phytoplankton can largely explain the scarcity of cladocerans, e.g. *Daphnia* spp. is known to decline during algal blooms as filamentous algae mechanically inhibit the filtration processes (Gliwicz 1990).

In addition, the low density of filter feeding zooplankton (III) can be the consequence of elevated pH (Fig. 10) (Jeppesen et al. 1990), since most, particularly small cladocerans, i.e. *Bosmina longirostris* (Hansen et al. 1991) and *Ceriodaphnia quadrangula* (O'Brien & De Noyelles 1972), are noted to suffer from pH values approaching 10. Furthermore, a typical littoral predator, *Polyphemus pediculus* (L.), normally abundant among the emergent stands in Kirkkojärvi basin (II), was absent during the study (III), being concomitant with the species vulnerability to high pH (Beklioglu & Moss 1995). The role of a dominant cladoceran in cyanophyte-plagued Kirkkojärvi basin (III) indicates that *Diaphanosoma brachyurum*, besides being better adapted to mineral turbidity than other crustacean zooplankters (Hart 1988, Koenig et al. 1990) and able to utilize organically enriched, suspended clay as food resource (Cuker & Hudson 1992) is comparatively tolerant to the mechanical inhibition by filamentous algae. On the other hand, stressed increase in the free-swimming filter feeder densities, coinciding with the decreased pH (III), suggests sensibility to high pH. A smaller difference in the two nocturnal density peaks in differing pH environments, compared with other filtrating cladocerans (III), suggests that *Sida crystallina*, is conceivably not as sensitive to elevated pH.

However, due to widespread nymphaeid stands, *Sida crystallina* is one of the dominating cladocerans in Kirkkojärvi basin, and the notably smaller densities compared to previous studies (II) therefore stress the overall suppressing effect of the phytoplankton bloom (III), as large filter feeders are noted to be most vulnerable to filamentous algae (Dawidowicz 1990). In addition, pH values above 9.5 or 10 may impair fish activity whilst the activity of large filter feeding cladocerans may continue up to pH values about one unit higher (Beklioglu & Moss 1995). Underlined reverse movement by *Limnosida frontosa* and *Sida crystallina* during our study when pH dropped to 6 (III) supports the argument of simultaneously increased predation by small fish.

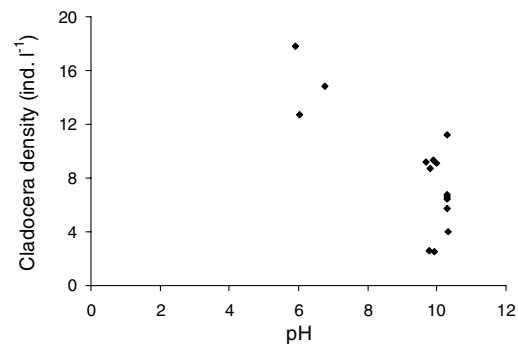


Figure 10. Effect of increased pH on cladoceran density in Kirkkojärvi basin, during a cyanophyte bloom (III).

### 4.3 Role of emergent and submerged species in sediment dynamics

#### 4.3.1 Impact on sediment resuspension

The importance of macrophytes in sediment resuspension of a shallow turbid lake was studied by investigating submerged and emergent life forms and comparing the obtained resuspension results. The resuspension values in Kirkkojärvi (5 - 37 g m<sup>-2</sup> d<sup>-1</sup>) fell within the limits reported from other lakes (Evans 1994). In our studies, on average, the submerged vegetation (mixed

stand of *Ranunculus circinatus*, *Ceratophyllum demersum* and *Potamogeton obtusifolius*; PVI max. 30%) (V) reduced resuspension rate by 10.9 g m<sup>-2</sup> DM and the nearby stand of the emergent *Typha angustifolia* (IV) (10-22 stems m<sup>-2</sup>) was estimated to be on the same level (9.7 - 16.4 g m<sup>-2</sup> DM).

The resuspension rate measured during the study conducted among the submerged macrophytes (V) (83 d) constituted to 1701 g m<sup>-2</sup> DM of sediment in the outer zone and 793 g m<sup>-2</sup> DM in the inner zone. The difference between the two zones increased in the course of the summer together with the growing macrophyte density. During June, the resuspension rate in the inner zone was >60% and in August <20% of that in the outer zone (V) (Fig. 11). Corroborating the conclusions by Dieter (1990), the results from Kirkkojärvi demonstrated that the rate of resuspension can also be substantially reduced by emergent macrophytes (IV). During 12-26 May, the resuspension rates in the inner zone and at the edge were 76% and 93% of that in the outer zone, respectively. In the course of the summer, the differences increased and, during 21 July - 3 August, the corresponding numbers were 18% (IV) (Fig. 11) and 51%.

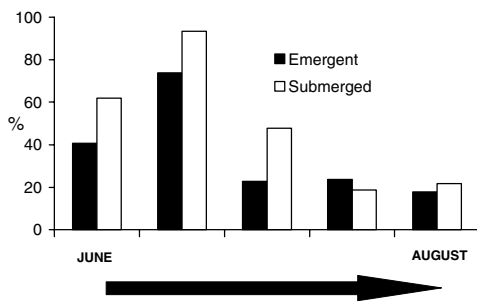


Figure 11. Percentage of resuspension (g m<sup>-2</sup> d<sup>-1</sup> DM) in the inner zone from the resuspension of the outer zone of both submerged and emergent vegetation stands.

During 9 - 23 June, the resuspension rate in the inner zone was temporarily elevated. This was due to a peak in the effects of waves originating from wind blowing exceptionally from the north-east, a direction having the highest effective fetch. During the study period, 2210 g m<sup>-2</sup> DM of sediment was resuspended in the outer zone of emergent macrophytes, whereas at the edge and in the inner zone, the corresponding numbers were 1414 and 858 g m<sup>-2</sup> DM (IV), respectively.

Both macrophyte life forms, submerged (V) and emergent (IV), remarkably reduced the concentration of suspended solids within the vegetations. The close agreement of resuspension values and suspended solid concentrations suggests that in Kirkkojärvi resuspension was a continuous process, as is common in shallow water areas, except for periods of ice cover (Evans 1994). No clear dependence of resuspension rate on wind speed or wave height was observed, suggesting that moderate wave heights were enough to cause resuspension (Bengtsson et al. 1990) and that resuspension was caused by multiple factors including benthivorous fish (Breukelaar et al. 1994) and waves generated by boat traffic (Yousef et al. 1980). In Kirkkojärvi, boat traffic is frequent and benthivorous fish species make up 65% of the catches of experimental nettings (Vinni et al. 2000).

Measurement of sediment resuspension is difficult even at favorable conditions (Bloesch 1994, Evans 1994). In the littoral zone of Kirkkojärvi, the organic content of seston and surface sediment differed significantly, facilitating the use of the method by Gasith (1975). The close agreement with the resuspension rates obtained in emergent (IV) and submerged (V) studies also emphasize the good repeatability of the measurements. Because of the decreased water turbulence within the traps, studies with sediment traps usually result in higher sedimentation



compared with mass balance calculations (Kozerski 1994). Traps measure the upper limit of the average resuspension rate during the exposure time of the trap (Kozerski 1994). Thus, the present results probably represent maximum values of sedimentation and resuspension in Kirkkojärvi. The exposure time of the traps was within the limits recommended for experiments on settling fluxes for organic material (Bloesch & Burns 1980).

#### 4.3.2 Importance in phosphorus reduction

From the resuspension study conducted among submerged and emergent vegetation, calculations for phosphorus resuspension and retention were also performed. In the study conducted among submerged vegetation (V), with the resuspended sediment,  $2.0 \text{ g m}^{-2} \text{ P}$  was brought into the water column in the outer zone and  $0.98 \text{ g m}^{-2} \text{ P}$  in the inner zone. Submerged plants thus reduced the internal loading of total P by  $12 \text{ mg m}^{-2} \text{ per day}$ . In the emergent vegetation investigation (IV),  $3.3 \text{ g m}^{-2} \text{ P}$  was brought to the water column in the outer zone,  $1.9 \text{ g m}^{-2} \text{ P}$  at the edge and  $1.1 \text{ g m}^{-2} \text{ P}$  in the inner zone. Thus, compared with open water areas, the stem density at the edge reduced the internal loading of total P by  $16.7 \text{ mg m}^{-2} \text{ d}^{-1}$  and the density in the inner zone by  $26.2 \text{ mg m}^{-2} \text{ d}^{-1}$ .

In Kirkkojärvi, the present area of submerged stands is *ca.* 15 ha and of emergent macrophytes (mainly *T. angustifolia* and *T. latifolia*) approximately the same *ca.* 16.6 ha (unpublished). Thus, during the study period submerged vegetation retained approximately 150 kg (V) and emergent macrophytes 232 kg (edge) -365 kg (inner zone) (IV) of phosphorus, adding up to a total of *ca.* 747 kg phosphorus, which would otherwise have been transported into the water column. The helophytes do not senesce until late September. By applying the observed average daily P resuspension values in each emergent zone for a six-

month open-water season, the emergent stands in Kirkkojärvi can be estimated to annually retain 510-800 kg P, which corresponds to 6-10 % of the current external P loading (Tallberg et al. 1999).

The inverse relationship between suspended solids and SRP in the inner zone of submerged macrophytes (V) suggested that resuspended particles adsorbed phosphorus from the water. In the outer zone, no sign of such an effect was found. In all the zones of the emergent investigation (IV), the effect of SS on SRP was non-significant, corroborating the results by Søndergaard et al. (1992). Thus, SRP release from resuspended sediment is not governed by the amount of suspended solids in the water but rather by SRP concentration in the water during resuspension. Resuspended particles can either adsorb phosphorus from the water or release it, depending on their P saturation level. The concentration of SRP in the pelagic zone of Kirkkojärvi increased steeply in late July (from below  $10 \mu\text{g l}^{-1}$  to above  $40 \mu\text{g l}^{-1}$ , unpublished), suggesting an increased availability of P towards late summer. It can be concluded that when the concentration of SRP in the water of Kirkkojärvi is low, resuspension releases SRP from the sediment to the water, the release rate being (due to higher resuspension rate) substantially higher in open water areas than in areas covered by macrophytes.

#### 4.4 Implications of fish herbivory

The gut content of rudd during the macrophyte growing season was studied to investigate the volume of plant grazing. The diet of all studied rudd (VI) contained animal remains, plant material and detritus (Fig. 12), being congruent with the species omnivorous feeding habits (Niederholzer & Hofer 1980). The highest macrophyte consumption in the beginning and end of summer (VI) was related to the biomass peak of macrophytes in late summer, but also to the absence of animal food. Rudd is

not very active in selecting food, and on the contrary, utilizes majority of the suitable-sized submerged species, occurring in adequately high densities (Prejs & Jackowska 1978). In Kirkkojärvi, the submerged macrophyte community is compounded of a mixed vegetation of e.g. *Potamogeton obtusifolius*, *Sparganium emersum*, *Ranunculus circinatus*, bryophytes and also occasional mass occurrences of filamentous algae (I), all being well represented in the rudd diet (VI) (Fig. 12). Some species, such as submerged *Myriophyllum verticillatum*, pleustophytic *Ceratophyllum demersum*, and nymphaeids, forming high biomasses in the littoral of Kirkkojärvi (I), were nevertheless absent in rudd guts (VI).

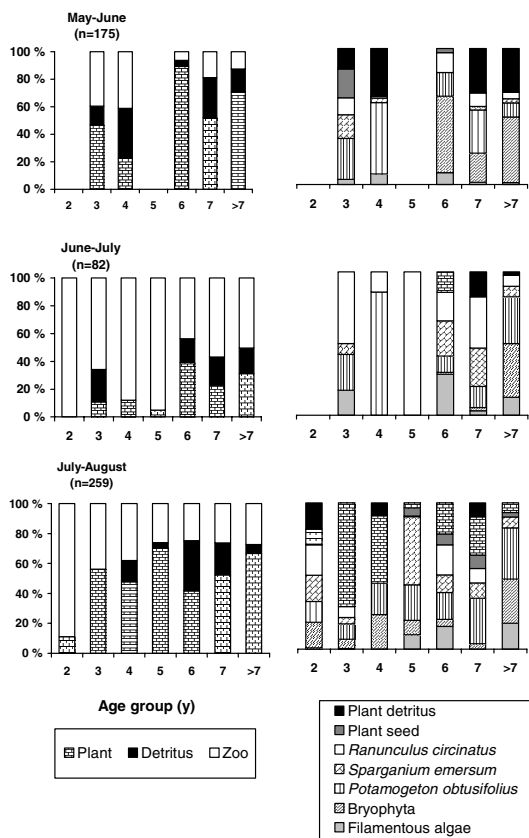


Figure 12. Volume percentage composition of the diet of different rudd age groups. Total number of analysed fish in each time period is shown in parentheses. On the left hand side, rudd diet divided into plant material, detritus and animal material (zoo). On the right, plant material divided into more specific categories (VI).

Also, Prejs & Jackowska (1978) and van Donk & Otte (1996) found a high preference of rudd for *Elodea* and *Potamogeton* but avoidance of, chemically and mechanically inconvenient, *Myriophyllum* and *Ceratophyllum*. The feeding habits observed were, therefore, rather due to the distribution and densities of edible macrophytes.

The ability to consume alternate low-energy food sources, such as detritus and plant material, is one of the characteristics of cyprinids (Michelsen et al. 1994). Fish utilize the majority of animal tissue but considerably less of the plant material ingested, therefore, a relevant amount of macrophytes must be consumed (Prejs 1976, Prejs & Jakowska 1978). Also, feeding rate of rudd has been established to increase concurrently with vegetation density (Peirson et al. 1985). The biomass of rudd stock in the littoral area of the Kirkkojärvi basin is not known, but falls probably within the range of 50-100 kg ha<sup>-1</sup>. The annual plant consumption by the stock would thus be 45-115 kg ha<sup>-1</sup> (VI).

Herbivorous fish, such as rudd, harvest plant biomass and may influence the macrophyte species formation (van Donk & Otte 1996), but also grazing of benthic food remobilises nutrients stored in the sediment and plant biomass, accelerating internal loading (Hansson et al. 1987, Horppila 1999). In addition, the effect of a strong rudd population in a shallow lake may have antagonistic effects; on the other hand, accelerating turbidity by bottom dwelling, but also enhancing macrophyte growth by consumption of young shoots (Prejs 1984, van Donk & Otte 1996), which in turn reduce resuspension (V). In the studied Kirkkojärvi basin, partly selective grazing and partly upholding of turbidity and high nutrient levels by bottom dwelling, conceivably promotes the inedible and pleustophytic macrophyte growth form, which has increased in Kirkkojärvi during the past decades (I).

## 5. CONCLUSIONS

In a clay-turbid water body, an inherently scarce submerged macrophyte composition may prevail, therefore drastic changes in the species and life form composition due to decrease in the trophic state of the lake or increase of (phytoplankton-induced) water transparency are not necessary likely. In such lakes, the stabilizing and structural role of other life forms besides submerged vegetation, e.g. emergent and floating-leaved, may be seriously overlooked. The environmental premiss provided by high background concentrations of suspended inorganic particles may provide a new perspective for the function of vegetation in turbid lakes.

As detected in this thesis, in clay-turbid eutrophic conditions emergent vegetation appears to play an important role in the seasonal regulation of zooplankton by providing refuge for especially free-swimming cladocerans. The aggregation among the vegetation resembles the trend observed with submerged vegetation in eutrophic lakes. In addition, emergent vegetation appear to provide prominent refuge also for large-sized plant-associated species, such as *Sida crystallina*. These cladocerans, occurring in considerable densities and holding remarkable phytoplankton filtering capacities, must have considerable water quality effects through algal control. In eutrophic and turbid lakes, with scarce submerged vegetation the refuge function of emergent and, also floating-leaved, life forms may therefore be prominent. In such lakes, with high predation pressure by fish and the quite low total zooplankton biomass, the importance of these life forms may be emphasized.

The differences in total cladoceran density and behaviour, as well as dissimilar species composition, in the study areas of differing trophic suggest that emergent stands in mesotrophic conditions, in contrast to

eutrophic and more turbid circumstances, might not provide adequate refuge for filter feeders to induce diurnal horizontal migration among the vegetation.

Although the studies in this thesis detected that emergents encourage zooplankton aggregation within vegetation in turbid and eutrophic conditions, it appears that heavy phytoplankton blooms overshadow this effect directly, through mechanical enhancement, as well as indirectly, via elevated pH, influencing the proportional composition and diurnal distribution of littoral zooplankton.

Wind-induced water movements may determine whether the littoral zone acts as a sink or a source of nutrients for the pelagic system. The results in this thesis demonstrated that sediment resuspension and the consequent increase in inorganic water turbidity and internal loading of phosphorus may be substantially reduced by macrophytes, both submerged and emergent life forms. In clay-turbid lakes with low submerged vegetation density, emergent macrophytes were discovered to be substantial in reducing phosphorus cycling from the sediment. In addition, owing to a longer growing season than submerged species, emergent vegetation contribute to considerable water quality effects.

In turbid and shallow eutrophicated lakes with low submerged biomass and few dominating species, herbivory by fish may have an influence on the species composition of submerged vegetation. Fish, as rudd in this study, is a quite omnivorous feeder, grazing on any edible and suitable-sized plants. A rudd population alone is not likely able to consume adequate quantities to alter the proportions of different species since herbivory also enhances growth of new shoots. However, as this thesis indicates, partly selective grazing and partly upholding of turbidity and high nutrient levels by bottom dwelling, conceivably

promotes the inedible and pleustophytic macrophyte growth form.

The establishment of submerged macrophyte stands is often considered to be crucial for restoration of shallow lakes but the effects of e.g. emergents are not so often recognized. On the contrary, emergent and floating-leaved life forms are often considered less important in the lake restoration viewpoint, in fact they are often recommended to be harvested, to remove nutrients or to improve the recreational possibilities of the lake. This thesis however, highlights the importance of these undermined macrophytes to water quality. They are important in many aspects of restoration - not only when removed - but also when retained. In this thesis, emergent vegetation has been shown to reduce sediment-induced turbidity and nutrient cycling, as well as to provide refuge for phytoplankton grazing zooplankton (phytoplankton-induced turbidity). In this respect, emergent and presumably also floating-leaved stands are important factors in terms of water quality, especially in clay-turbid lakes with inherently scanty submerged vegetation. In general, the comprehensive function of macrophytes should be taken into more thorough account in lake restoration schemes: recreational expectations and water quality aspects should be weighed – and preferably combined.

## 6. FUTURE STUDY OUTLOOKS – Resonance of floating-leaved species

Hitherto, few studies on the food web effects of floating-leaved species, that are often very abundant in turbid lake circumstances, have been conducted (e.g. Moss et al.1998). Preliminary studies in Lake Hiidenvesi have demonstrated the importance of floating-leaved *Nuphar lutea* as refugia for *Sida crystallina*, as the large-sized zooplankton are found fixed to the leaves in considerable densities, with

cladoceran abundance increasing in concordance with leaf area (Fig. 13).

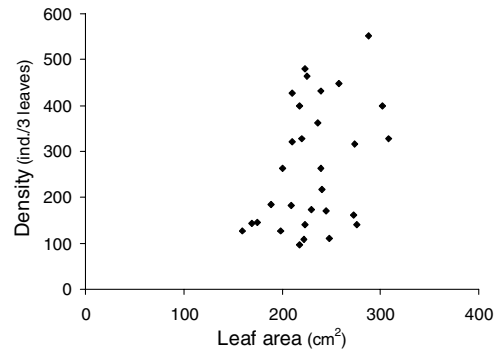


Figure 13. Relationship between leaf area of floating-leaved macrophytes (*Nuphar lutea*) and density of cladocerans (*Sida crystallina*) attached to leaves in Kirkkojärvi basin.

Therefore, our investigations underline the need to study the potential refuge effect of floating-leaved macrophytes, especially for plant-associated cladocerans, in turbid conditions. According to our findings, diurnal migration on/off the leaves by *Sida*, is very pronounced and regular, suggesting predator avoidance behaviour (Fig. 14).

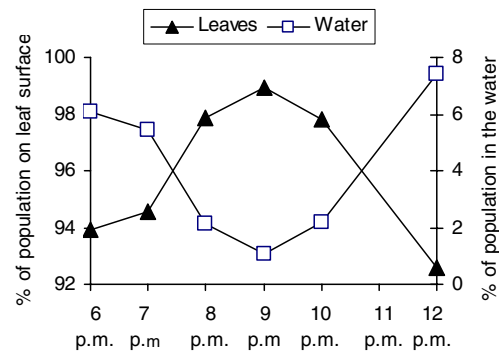


Figure 14. Diurnal changes in the proportion of plant-attached cladoceran, *Sida crystallina*, on the leaves of floating *Nuphar lutea* and adjacent open water of Kirkkojärvi basin.

Floating-leaved stands are potential harbours for prominent plant-associated zooplankton communities (e.g. *Sida*), possessing considerable phytoplankton consumption rates as indicated also in the studies of this thesis. In this light, floating-

leaved stands may have considerable whole-lake water quality effects. Therefore more detailed investigation on the role of floating-leaved life form especially in turbid lakes should be conducted: both the importance as refugia for zooplankton and impact on resuspension should be clarified. In all, more thorough investigation of interactions and processes linked with macrophytes related to phytoplankton-caused and inorganic turbidity should be conducted.

## 7. FINAL WORDS

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Finally

- the final drop.

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