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Mechanisms regulating abundance of submerged vegetation in shallow eutrophic lakes

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Abstract Shallow eutrophic lakes tend to be either in a turbid state dominated by phytoplankton or in a clear-water state dominated by submerged macrovegetation. Recent studies suggest that the low water turbidity in the clear-water state is maintained through direct and indirect effects of the submerged vegetation. This study examined what mechanisms may cause a recession of the submerged vegetation in the clear-water state, and thereby a switch to the turbid state. The spatial distribution of submerged vegetation biomass was investigated in two shallow eutrophic lakes in the clear-water state in southern Sweden. Biomass of submerged vegetation was positively correlated with water depth and wave exposure, which also were mutually correlated, suggesting that mechanisms hampering submerged vegetation were strongest at shallow and/or sheltered locations. The growth of *Myriophyllum spicatum*, planted in the same substrate and at the same water depth, was compared between sheltered and wave exposed sites in two lakes. After 6 weeks the plants were significantly smaller at the sheltered sites, where periphyton production was about 5 times higher than at the exposed sites. Exclosure experiments were conducted to evaluate the effects of waterfowl grazing on macrophyte biomass. *Potamogeton pectinatus* growth was decreased by grazing, whereas *M. spicatum* was not affected. The effects were greater at a sheltered than at a wave-exposed site, and also negatively related to distance from the reed belt. These results suggest that competition from epiphytes and waterfowl grazing hamper the development of submerged vegetation at sheltered and/or shallow locations. An increased strength of these mechanisms may cause a recession of submerged vegetation in shallow eutrophic lakes in the clear-water state and thereby a switch to the turbid state.

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Introduction

By combining palaeoecological studies, tank experiments and field studies, Phillips et al (1978) showed that loss of submerged macrophytes in eutrophicated lakes is often due to increased growth of epiphytes and filamentous algae. However, the prevailing view among limnologists and lake managers still seems to be that shading by phytoplankton limits the distribution, and causes the disappearance, of submerged vegetation in eutrophic lakes (e.g. Chambers and Prepas 1988; Blindow 1992). The recent theory-building around alternative equilibria in shallow lakes (i.e. the tendency of shallow eutrophic lakes to be either in a state with a high phytoplankton production and very little submerged vegetation or in a state with clear water and abundant submerged vegetation) is in fact, at least partly, built on the assumption that the macrophyte state is stabilised by macrophyte growth being stimulated by a high light availability due to clear water (Scheffer 1990; Scheffer et al. 1993; Blindow et al. 1993). A self-stabilising effect is supposed to be obtained because the submerged vegetation has a positive influence on water clarity through a number of mechanisms, e.g. nutrient competition, improved possibilities for zooplankton to avoid fish predation (resulting in increased zooplankton grazing on phytoplankton) and decreased sediment resuspension (e.g. Timms and Moss 1984; Scheffer 1990; Scheffer et al. 1993; Blindow et al. 1993; Moss et al. 1994; Hargeby et al. 1994; Schriver et al. 1995). In the turbid state, establishment of submerged vegetation is hindered by low light penetration through the water column but may occur if water turbidity decreases drastically (e.g. due to biomanipulation) or the water level is lowered (e.g. Moss 1990, Blindow et al. 1993; Lauridsen et al. 1994). In the clear-water state in shallow lakes, however, it does not seem likely that light penetration through the water column is important in regulating submerged vegetation. This is not only because light penetrates to the lake bottom, but also because the established submerged vegetation exhibits an "escape effect" where the plants are able to reach to, or close to, the water surface (e.g. Scheffer et al. 1992).

In a shallow brackish lake, historical records suggested that appearance/disappearance of submerged vegetation was linked to fluctuations in epiphytic abundance caused by population changes in a periphyton grazer (Bales et al. 1993). Brönmark and Weisner (1992) proposed a conceptual model of mechanisms regulating submerged vegetation in shallow, eutrophic lakes involving changes in the shading by epiphytes caused by invertebrate grazing regulation of epiphytes and predation regulation of grazers. Field enclosure experiments in freshwater ecosystems have shown positive effects on macrophyte growth after reduction of fish predation on epiphyte-grazing snails (Martin et al. 1992; Underwood 1991; Underwood et al. 1992). Thus it seems that the competition from epiphytes is an important but often disregarded mechanism regulating submerged macrophytes.

Other mechanisms that may limit distribution of submerged vegetation in eutrophic shallow lakes include highly organic sediments that have been shown to limit growth of submerged macrophytes in experimental studies (Barko and Smart 1983, 1986; van Wijck et al. 1992). The importance of this relationship *in situ* in eutrophic lakes remains, however, unclear (Anderson and Kalff 1988; Barko et al. 1991). Earlier studies on effects of waterfowl grazing on submerged macrophytes indicated that effects were small because grazing occurred mainly during autumn when plant growth had decreased (Kiørboe 1980; Mitchell 1989). Recent studies, however, suggest that waterfowl grazing can have pronounced effects on submerged macrophytes in shallow eutrophic temperate lakes (Lauridsen et al. 1993; Søndergaard et al. 1996). Other grazers that may affect submerged macrophytes in temperate lakes include fish, crayfish and smaller invertebrates (e.g. Carpenter and Lodge 1986; Lodge 1991; Jacobsen and Sand-Jensen 1992, 1995). Vegetation mapping in the shallow eutrophic Lake Veluwe in The Netherlands over 20 years revealed that submerged vegetation was largely restricted to the slightly deeper, more wave-exposed, parts of the lake (Scheffer et al. 1994). It was proposed that explanations for this pattern could include influence of organic sediments, high epiphytic growth as well as waterfowl grazing (Scheffer et al. 1994).

The purpose of the present study was to identify what mechanisms that may cause a decline of submerged vegetation in shallow eutrophic lakes in the clear-water state and thereby a switch to the turbid state. This was done in two steps. First, we quantified within-lake differences in macrophyte biomass in relation to environmental variables in two shallow eutrophic lakes in the clear-water state. Within-lake distributions of macrophyte biomass in relation to environmental factors suggested that certain mechanisms were involved in regulating macrophyte abundance. Secondly, we performed field experiments to investigate if these mechanisms did contribute to the observed patterns.

Methods

The lakes

The investigations and field experiments were carried out in three eutrophic lakes in southern Sweden (Table 1). Krankesjön and Björkesåkrasjön are shallow eutrophic, at present macrophyte-dominated lakes in the clear-water state and with large waterfowl populations including the mainly herbivorous species coot (*Fulica atra*) and mute swan (*Cygnus olor*). Krankesjön shifted from a turbid state to a clear-water state between 1985 and 1987 (Hargeby et al. 1994). Björkesåkrasjön was in a turbid state around 1975 but has been in a clear-water state at least since 1986 (Karlsson et al. 1976; S.E.B. Weisner, personal observations). Finjasjön is a moderately deep lake, eutrophicated by municipal waste water. It is a phytoplankton-dominated lake, biomanipulated between 1992 and 1994 by removal of cyprinid fish. Water turbidity has decreased gradually since 1994 and a recovery of submerged vegetation has been observed (J.A. Strand and S.E.B. Weisner, unpublished work).

Field investigations

Field investigations were conducted during July-August in Krankesjön in 1993, 1994, 1995 and in Björkesåkrasjön in 1993 and 1995. In Krankesjön and Björkesåkrasjön, 37 and 16 localities, respectively, were sampled once per year. The localities were evenly distributed across the open water of the lakes. A global positioning system (GPS) was used in order to re-visit approximately the same localities each year. At each locality, the macrophytes were collected with a rake covering approximately 0.1 m^2 of the lake bottom. If no macrophytes were obtained within this area, a larger area (approximately 2 m^2) was also sampled. The samples were washed, determined to species, dried (85°C, 24 h) and weighed (DW). Ash free dry weight (AFDW) was measured by combustion at 550°C (4 h). Macrophyte biomass at different locations was ranked (within each lake and year separately) based on AFDW within the smaller area and also the larger area when no plants were obtained in the smaller area. At each locality, substratum softness was measured with a cone penetrometer (cone weight 500 g, cone diameter 10 mm, top angle of cone 30°), giving the cone penetration depth (CPD) at each site (Weisner 1991). Water depth was

Table 1 Morphological characteristics, nutrient mean summer concentrations and locations of the three lakes included in this study (data from management reports)

	Krankesjön	Björkesåkrasjön	Finjasjön
Area (km^2)	4.2	1.0	11.0
Mean depth (m)	1.5	0.9	2.5
Max depth (m)	3.0	1.6	13.2
Total-P (mg l^{-1})	0.06	0.10	0.23
Total-N (mg l^{-1})	1.6	1.6	1.4
Coordinates (lake centre)	55°42′N, 13°28′E	55°32′, 13°24′E	56°08′, 13°42′E

measured at each locality . The relative degree of wave exposure (WE) was calculated for each locality as:

$$\sum_{i=1}^{8} \text{exceedence}_i \times \text{fetch}_i$$

where exceedence is the proportion (%) of winds during summer exceeding 6 m s^{-1} for eight 45° wind direction intervals (data obtained from nearby weather stations) and fetch (km) is the mean distance to the reed border for each wind direction (measured as in Weisner 1991). The method for calculating wave exposure should be considered as a method for ranking localities with respect to wave exposure within lakes (Keddy 1982). Spearman rank correlations were used to analyse within-lake relationships between environmental variables, and between macrophyte biomass and environmental variables.

Growth experiments

Two growth experiments in order to asses growth of submerged macrophytes in relation to wave exposure independent of substrate conditions were conducted 1994 in Krankesjön (12 July to 23 August) and Finjasjön (13 July to 24 August). Non-flowering 10 cm apical shoots of *Myriophyllum spicatum* were planted in plastic buckets (height = 13 cm, width = 12 cm), one shoot in each bucket in 3 cm sand and 1.0 g of a commercial fertiliser (20% N; 2.2% P; 6.6% K; 1.2% Mg; 0.5% micronutrients). The buckets were attached to wooden floating frames (1.3 × 1.3 m) by ropes, at 0.2 and 0.5 m water depth. Frames were placed at one wave exposed site (in the middle of the lakes) and one sheltered site in each lake. The plants were placed 0.2 and 0.5 m below the water surface. Sixteen plants were placed at each water depth at each site in both lakes. Eight of the plants at each depth and site were protected from grazing from birds and large fish by metal net (mesh size = 19 mm). To assess the production of epiphyton during the experiment period, plastic bands (width 19 mm, length 100 mm) were used as artificial substrates. Five bands were fixed at 0.3 m water depth at each site.

When the experiments were terminated, the plants were collected and plant AFDW was determined as above. The periphyton bands were cut 3 cm from their attachments and placed separately in glass vials. In the laboratory, 10 ml ethanol was added to each vial. The vials were placed in an ultrasonic bath for 15 min prior to analysis of chlorophyll-*a* using a spectrophotometer (Jespersen and Christoffersen 1987).

Both final macrophyte and periphyton biomass exhibited a frequency distribution consistent with an exponential growth as can be expected in short-term growth experiments. Thus, to stabilise variances, all biomass values were log-transformed before analysing differences between treatments and sites using ANOVA or *t*-test.

Grazing experiments

Three grazing experiments were performed in Krankesjön in 1994 and 1995. Grazing experiment 1 was an attempt to evaluate the effect of grazing on spring growth of naturally occurring submerged vegetation in a shallow sheltered part of the lake. On 18 April 1994, four protected plots (exclosures) were placed randomly among eight unprotected plots in the open water along the reed belt, within a water depth range from 52 to 68 cm. The exclosures (1 m^2) were covered on tops and sides with metal net (mesh size 19 mm) and were all totally submerged. Plants were sampled on 21 June from 0.25 m^2 within each plot and sorted into species. AFDW was determined as above. Differences in plant AFDW between the exclosures and the unprotected plots were analysed by two-tailed Mann-Whitney *U*-test.

Grazing experiment 2 evaluated the influence of the distance to the reed belt on the effects of grazing on submerged macrophytes. Ten blocks, each containing an unprotected and a protected plot (exclosure), were located at the same water depth (50 cm) but between 3 and 36 m from the reed belt at a sheltered site. The exclosures used were 0.5 × 0.5 m wide, covered with metal net (mesh size 21 mm) on the sides. Plants of *Potamogeton pectinatus* (6 cm rhizomes with one green 50–80 cm shoot, of similar weight within each block, were planted in plastic 1-l containers (5 plants/container) with sand and 1 g fertiliser (same as above). One container in each plot was placed in the sediment on 15 June and collected on 6 July 1995. Plant AFDW was determined as above. The ratio between plant AFDW of unprotected and protected plots was calculated for each block and Spearman rank correlation was used for analysing the relationship between this ratio and the distance to reed belt.

In grazing experiment 3 we compared grazing effects at an exposed and a sheltered site during late summer / early autumn (9 August to 25 September). All plots were placed between 15 and 20 m from the reed belt to minimise the influence of distance to the reed belt. The exclosures were the same as in grazing experiment 2, and unprotected and protected plots were paired in blocks. The water was deeper at the exposed (mean 43 cm) than at the sheltered site (mean 28 cm). *P. pectinatus* plants (20 cm rhizome and three green shoots) and *M. spicatum* fragments (20 cm non-flowering apical shoots) were planted in 1-l containers with sand and 0.5 g fertiliser (two plants of each species in each container). Metal net screens were placed at the unprotected plots to resemble the effect of exclosures on wave action. Differences between final biomass (AFDW as above) of unprotected and protected plots were compared for each site and species separately with a two-tailed Wilcoxon signed-rank test based on the blocks of unprotected and protected plots. Differences in treatment effects between the wave exposed and the sheltered site was tested for each species separately with a two-tailed Mann-Whitney *U*-test on the within-block ratios between unprotected and protected plots.

Results

Field investigations

Median and range for the measured environmental variables in the field investigations differed somewhat between Krankesjön and Björkesåkrasjön (Table 2).

Table 2 Median value and range (minimum and maximum value) for the different measured environmental variables in 1993 of the 37 locations in Krankesjön and 16 locations in Björkesåkrasjön where submerged vegetation was investigated

	Krankesjön			Björkesåkrasjön		
	Median	Min	Max	Median	Min	Max
Water depth (cm)	94	18	217	61.5	15	96
Wave exposure (WE)	15.2	1.7	24.5	8.8	3.6	12.1
Substratum softness (CPD; cm)	37	2	67	53	35	76
Substratum organic content (%)	20.4	0.0	50.1	39.4	12.3	44.0
Distance to reeds (m)	80	15	430	85	25	220

Krankesjön is generally deeper and more wave exposed than Björkesåkrasjön. Björkesåkrasjön sediments are generally softer and have a higher organic content than Krankesjön sediments. The environmental variables were largely correlated to each other within the lakes, but patterns differed between the lakes (Table 3). Water depth and wave exposure were strongly positively correlated in both lakes. In Krankesjön, there were strong positive correlations also between substratum softness and substratum organic content and between wave exposure and distance to reeds. In Björkesåkrasjön, however, water depth as well as wave exposure were strongly negatively correlated with substratum softness.

Relationships between submerged macrophyte biomass and environmental variables were different between Krankesjön and Björkesåkrasjön, and also differed clearly between years in Krankesjön (Table 4; Fig. 1). In Krankesjön, no significant relationships were found in 1993. However, in 1994, macrophyte biomass was positively correlated to water depth, wave exposure and distance to reeds. In 1995, a strong correlation was found with wave exposure and the only other significant correlation was with distance to reeds. In Björkesåkrasjön, macrophyte biomass was strongly positively correlated to water depth and wave exposure, and negatively correlated to substratum softness and organic content, in both investigated years. Thus, the submerged macrophyte biomass in both lakes tended to be positively correlated with water depth and/or wave exposure which also were correlated with one another, although the deepest and also most exposed locality in Krankesjön lacked submerged macrophytes (Fig. 1).

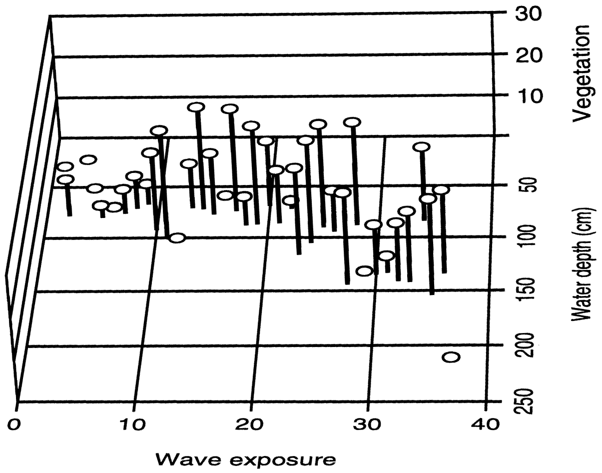

Fig. 1 The relationship between wave exposure, water depth and macrophyte biomass (vegetation) in Krankesjön in 1994 for 37 locations included in the field survey. Wave exposure and vegetation values represent rank order (lowest = 0)

The species composition also differed markedly between the lakes (Table 5). *Chara* sp. (mainly *Chara tomentosa*) dominated in Krankesjön, although it decreased during the 3 years, while *Myriophyllum spicatum* tended to increase and *Potamogeton pectinatus* was found in similar amounts each year. In Björkesåkrasjön, the submerged vegetation was dominated by

Table 3 Spearman's rank correlation coefficients (r_s) for the relationships between environmental variables in the lakes Krankesjön (n = 37) and Björkesåkrasjön (n = 16) in 1993. Bold type indicates significant relationships (P < 0.05)

Krankesjön	Wave exposure	Substratum softness	Organic content	Distance to reeds
Water depth	**0.773*****	0.278	**0.407***	**0.493****
Wave exposure		–0.195	–0.327	**0.693*****
Substratum softness			**0.778*****	0.076
Organic content				–0.022

Björkesåkrasjön	Wave exposure	Substratum softness	Organic content	Distance to reeds
Water depth	**0.692****	**–0.946*****	–0.282	0.347
Wave exposure		**–0.712****	–0.424	0.409
Substratum softness			0.387	–0.280
Organic content				–0.234

*P < 0.05, **P < 0.01, ***P < 0.001

Table 4 Spearman's rank correlation coefficients (r_s) for the relationships between submerged macrophyte biomass and environmental variables in Krankesjön (years 1993–1995) and Björkesåkrasjön (years 1993 and 1995). Bold type indicates significant relationships (P < 0.05)

	Krankesjön (n = 37)			Björkesåkrasjön (n = 16)	
	1993	1994	1995	1993	1995
Water depth	0.207	**0.340***	0.286	**0.709****	**0.711****
Wave exposure	0.126	**0.364***	**0.564*****	**0.773****	**0.645***
Substratum softness	0.145	0.048	0.270	**–0.672****	**–0.655***
Substratum organic content	0.041	0.049	0.071	**–0.628***	**–0.513***
Distance to reeds	0.053	**0.384***	**0.359***	0.247	0.156

*P < 0.05, **P < 0.01, ***P < 0.001

Table 5 Proportion (%) of the locations in Krankesjön (years 1993–1995) and Björkesåkrasjön (years 1993 and 1995) that had a well-developed submerged vegetation dominated by *Chara* sp., *Potamogeton* sp., *Myriophyllum spicatum* or *Ceratophyllum demersum*

	Krankesjön (n = 37)			Björkesåkrasjön (n = 16)	
	1993	1994	1995	1993	1995
Chara	54.0	43.2	21.6	0	0
Potamogeton	0	5.4	2.7	6.3	12.5
Myriophyllum	5.4	8.1	10.8	31.2	12.5
Ceratophyllum	0	0	0	6.3	18.8
All species	59.5	56.8	35.1	43.8	43.8

Table 6 Analysis of variance of the 1994 growth experiments with *Myriophyllum spicatum* in the lakes Krankesjön and Finjasjön using a two-way ANOVA, performed on log-transformed values of final plant weight (ash-free dry weight, AFDW). Replicates missing plants have been excluded

Krankesjön					
Source of variation	*df*	SS	MS	*F*	*P*
Site (exposed-sheltered)	1	0.165	0.165	15.655	0.0002
Depth (0.2–0.5 m)	1	0.000	0.000	0.010	0.921
Site × depth	1	0.001	0.001	0.139	0.711
Error	57	0.601	0.010		
Finjasjön					
Source of variation	*df*	SS	MS	*F*	*P*
Site (exposed-sheltered)	1	0.072	0.072	25.938	0.0001
Depth (0.2–0.5 m)	1	0.009	0.009	3.076	0.085
Site × depth	1	0.004	0.004	1.453	0.233
Error	55	0.153	0.003		

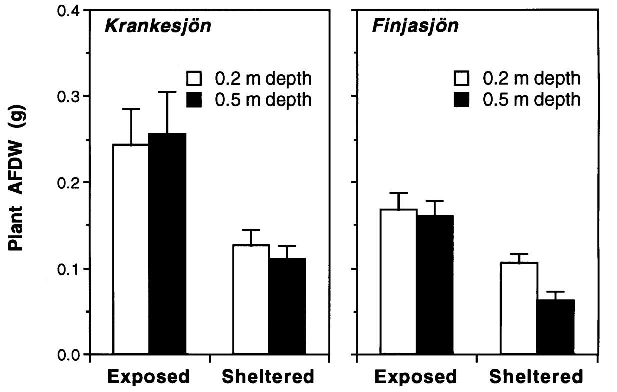

Fig. 2 Final macrophyte (*Myriophyllum spicatum*) biomass (ash-free dry weight, AFDW) at the wave-exposed and sheltered sites at two depths in the growth experiments in Krankesjön and Finjasjön. *Thin vertical bars* represent SEs

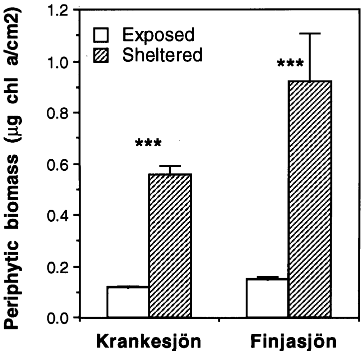

Fig. 3 Periphytic biomass on artificial substrates after 6 weeks of growth at the wave exposed and sheltered sites in the growth experiments in Krankesjön and Finjasjön. *Thin vertical bars* represent SEs. ***$P < 0.001$; significance of difference between wave exposed and sheltered sites tested with a two-tailed t-test on log-transformed values

angiosperms (mainly *P. pectinatus, M. spicatum* and *Ceratophyllum demersum*).

Growth experiments

In the growth experiments, a three-way ANOVA (site-water depth-protection from grazers) showed that there were no differences in AFDW between protected and unprotected plants ($P > 0.68$ and $P > 0.88$ in Krankesjön and Finjasjön, respectively) and no interaction between protection from grazers and site and/or water depth in any of the lakes (P varied between 0.16 and 0.73). Therefore, data for unprotected and protected plants were not separated (Fig. 2), and the data was analysed with a two-way ANOVA (site-water depth; Table 6). In both lakes, macrophyte growth was lower at the sheltered site than at the wave exposed site ($P < 0.001$ in both lakes). There was no significant influence of water depth (Table 6). Periphyton growth was approximately 5 times higher at the sheltered than at the exposed site in both lakes (Fig. 3).

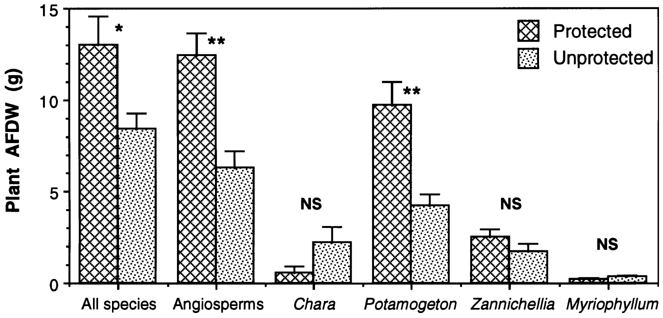

Fig. 4 Final macrophyte biomass (AFDW; divided into different groups/species) in grazing experiment 1 comparing establishment of natural vegetation in unprotected and protected plots. *Thin vertical bars* represent SEs $*P < 0.05$, $**\ P < 0.01$, *NS* not significant ($P > 0.1$); significance of difference between unprotected and protected plots tested with a two-tailed Mann-Whitney *U*-test

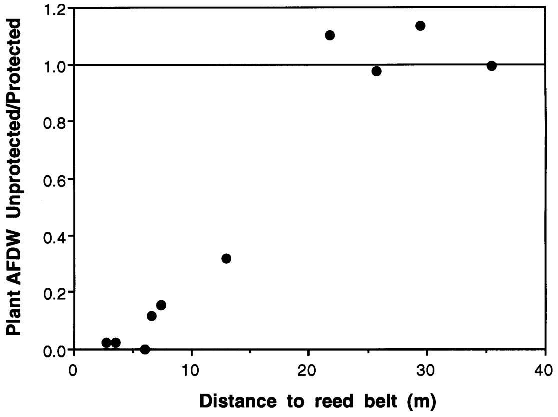

Fig. 5 Relationship between distance to reed belt and ratio between final biomass (ash-free dry weight) of unprotected and protected *Potamogeton pectinatus* plants in grazing experiment 2 in Krankesjön. Spearman rank correlation: $r_s = 0.891$, $P < 0.01$

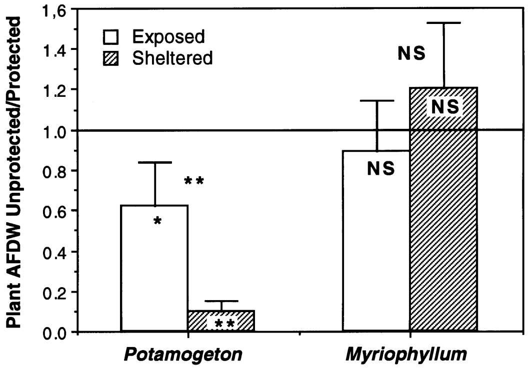

Fig. 6 Ratio between final biomass (AFDW) of unprotected and protected *P. pectinatus* and *M. spicatum* plants in grazing experiment 3 comparing grazing effects at a wave exposed and a sheltered site in Lake Krankesjön. *Thin vertical bars* represent SEs. $*P < 0.05$, $**P < 0.01$, *NS* not significant ($P > 0.1$); significance of difference between unprotected and protected plants was tested with a two-tailed Wilcoxon signed-rank test (the experiment was designed with unprotected and enclosed plants in pairs) for each species and site separately (*asterisks or NS within bars*); difference between wave-exposed and sheltered site (for each species separately) was tested with a two-tailed Mann-Whitney *U*-test (*asterisks or NS above bars*)

Grazing experiments

Final macrophyte biomass was higher in protected than in unprotected plots in grazing experiment 1 at a sheltered site in Krankesjön (Fig. 4). The most pronounced effects ($P < 0.01$) were obtained for angiosperms (excluding *Chara* sp.) and *Potamogeton* sp. (*P. obtusifolius* and *P. pectinatus*) but the total biomass of submerged vegetation was also significantly affected ($P < 0.05$).

In grazing experiment 2, grazing effects decreased significantly with increased distance from the reed belt (Spearman rank correlation between distance from reeds and ratio between AFDW of unprotected and protected plots, $n = 10$, $r_s = 0.891$, $P < 0.01$; Fig. 5). The ratio between unprotected and protected plots in blocks placed more than 20 m outside of the reeds was around 1, indicating that grazing did not affect these plants.

Grazing experiment 3 showed that *P. pectinatus* but not *M. spicatum* was affected by grazing, and the effects on *P. pectinatus* were greater at the sheltered than at the exposed site (Fig. 6). Differences in plant AFDW between protected and unprotected plots within blocks (Wilcoxon signed-rank test) were significant for *P. pectinatus* both at the wave-exposed ($P < 0.05$) and the sheltered site ($P < 0.01$). The ratio between final dry weight of unprotected and protected *P. pectinatus* plants differed significantly ($P < 0.01$) between the wave-exposed and the sheltered site according to a Mann-Whitney *U*-test.

Discussion

The traditional view on submerged macrophytes in lakes is that they grow out to a certain depth and that distribution can be predicted from their maximum depth penetration in a lake, which is largely dependent on water turbidity (e.g. Chambers and Kalff 1985). The field investigations in the shallow lakes Krankesjön and Björkesåkrasjön revealed a pattern that differs completely from this view since abundance of submerged vegetation was positively correlated with water depth and wave exposure. It is obvious that these positive relationships can only occur in relatively shallow lakes and within certain degrees of wave exposure, as indicated by the lack of submerged vegetation in the deepest and also most wave-exposed locality in Krankesjön. Thus, in deeper lakes the maximum depth penetration will be more important for the distribution of the vegetation.

The strongest correlations between macrophyte biomass and environmental variables within the lakes were obtained with wave exposure. However, because wave exposure and water depth were closely related in the lakes, it is not certain which factor is most important in determining submerged macrophyte occurrence. Submerged vegetation tended to be less developed at sheltered and shallow sites compared to wave-exposed, deeper sites. We suggest three different mechanisms that may cause, or contribute, to this pattern: differences in competition from epiphytes, different grazing pressures and different sediments. It has been suggested that effects of higher epiphyton growth at sheltered sites compared to exposed sites may cause a decreased growth of macrophytes at sheltered sites (Scheffer et al. 1992, 1994; Strand and Weisner 1996). It has also been suggested that a more intense waterfowl grazing at sheltered than at exposed sites may be the cause (Scheffer et al. 1992, 1994). Sediments at sheltered sites are often more organic with a lower density (higher softness) than at more exposed sites. Such sediments can affect macrophyte growth negatively (Barko and Smart 1983, 1986; van Wijck et al. 1992). However, macrophyte growth was not correlated to sediment variables in Krankesjön, and in Björkesåkrasjön correlations were strongest with water depth and wave exposure. Thus, we conclude that the field investigations suggest two mechanisms limiting macrophyte growth in Krankesjön and Björkesåkrasjön: epiphyton competition and waterfowl grazing. The field experiments aimed at finding out if one or both of these mechanisms could explain the macrophyte distribution patterns found in the lakes.

The growth experiments showed that macrophyte growth was lower at the sheltered sites than at the exposed sites although plants were growing in the same substrate. The higher periphyton growth at the sheltered sites strongly suggests that influence of epiphytes is important, probably mainly by decreasing light availability for the macrophytes (van Dijk 1993; Sand-Jensen and Borum 1991). It is possible that stronger boundary layer effects at sheltered sites also contributes to a decreased macrophyte growth. Both epiphytes and boundary layers may have an impact on macrophytes by limiting transfer of mineral nutrients and inorganic carbon from the water to the macrophyte leaves (Sand-Jensen 1977, 1989; Sand-Jensen and Borum 1991). An increase in wave exposure leads to a subsequent shift from loosely attached chlorophytes and cyanobacteria to a reduced epiphytic layer consisting of more firmly attached diatoms (Blenkinsopp and Lock 1994).

The grazing experiments show that activities of larger animals (excluded by the exclosures) does affect growth of the macrophytes, at least *P. pectinatus*. This conclusion is strengthened by effects being obtained both on plants re-growing naturally from the sediment and on transplanted plants growing in containers. It seems likely that birds prefer sheltered sites compared to wave exposed sites and that macrophytes may be more exposed to waterfowl grazing in shallow water since the plants are easier to reach for the birds (Scheffer et al. 1992). Thus, effects of waterfowl grazing are likely to be more pronounced in shallow, sheltered localities compared to deeper, wave exposed localities. This suggests that the large grazing effects at sheltered, shallow sites were caused by waterfowl grazing. The reason for large grazing effects close to the reed belt in grazing experiment 2 may be that coot prefer the protection from predators in the reed, and particularly so in breeding season. It is also possible that predation by waterfowl on invertebrates causes a decreased grazing on epiphytes and thereby a reduced macrophyte growth.

Since macrophytes occurred naturally in unprotected plots (grazing experiment 1), waterfowl grazing did not completely prevent macrophyte growth at the sheltered site. However, we do not agree with the commonly cited conclusion of Kiørboe (1980) that the negative influence of waterfowl grazing is limited even in areas with great concentrations of waterfowl, because the greatest grazing pressure comes outside the main growing season. Our results show that grazing effects on *P. pectinatus* at sheltered sites were pronounced. *Chara* sp. and *M. spicatum* were however not significantly affected by grazing (grazing experiments 1 and 3). This shows that grazing sensitivity differs among submersed macrophytes, and might explain the dominance of *Chara* sp. (Blindow et al. 1993), and the increase in *M. spicatum* during this study, in Krankesjön. It has been proposed that selective grazing affects species composition and even succession (Crawley 1983). The reason for *P. pectinatus* to be more sensitive is unknown, but it is well documented that waterfowl often exploit this species (Anderson and Low 1976; Beekman et al. 1991).

The field investigations indicate an ongoing development in Krankesjön resulting in a stronger exclusion of submerged vegetation from sheltered sites. The causes behind such a development could include an increased nutrient load to the lake, changes in the fish community resulting in increased predation on epiphyte grazers and thus increased epiphyte growth, or increased numbers of herbivorous waterfowl. If these mechanisms increase further in strength it may result in a decrease in lake area colonised by submerged macrophytes. This will cause the feedback mechanisms stabilising the lake in the clear-water state to be weakening. Ultimately, the lake will shift from the clear-water to the turbid state, where a new set of feedback mechanisms will preserve the lake in that state.

Our conclusion is that competition from epiphytes and grazing by waterfowl may both contribute to regulating the distribution of submerged vegetation in shallow eutrophic lakes in the clear-water state. Consequently we suggest that if these mechanisms increase in strength, due to internal ecosystem events or external forces, a switch to the turbid state may be initiated by a recession of submerged vegetation.

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