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Effects of grazing by fish and waterfowl on the biomass and species composition of submerged macrophytes

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Abstract

Biomanipulation improved water transparency of Lake Zwemlust (The Netherlands) drastically. Before biomanipulation no submerged vegetation was present in the lake, but in summer 1987, directly after the measure, submerged macrophyte stands developed following a clear-water phase caused by high zooplankton grazing in spring. During the summers of 1988 and 1989 *Elodea nuttallii* was the most dominant species and reached a high biomass, but in the summers of 1990 and 1991 *Ceratophyllum demersum* became dominant. The total macrophyte biomass decreased in 1990 and 1991. In 1992 and 1993 *C. demersum* and *E. nuttallii* were nearly absent and *Potamogeton berchtholdii* became the dominant species, declining to very low abundance during late summer. Successively algal blooms appeared in autumn of those years reaching chlorophyll-*a* concentrations between 60–130 μg l^{-1}. However, in experimental cages placed on the lake bottom, serving as exclosures for larger fish and birds, *E. nuttallii* still reached a high abundance during 1992 and 1993. Herbivory by coots (*Fulica atra*) in autumn/winter, and by rudd (*Scardinius erythrophthalmus*) in summer, most probably caused the decrease in total abundance of macrophytes and the shift in species composition.

Introduction

Submerged vegetation is of great importance to the functioning of shallow lakes, affecting both abiotic and biotic processes (Carpenter & Lodge, 1986). Macrophytes play a key role in several feed-back mechanisms that tend to keep the water clear at relatively high nutrient loadings (Moss, 1990), e.g. by reducing nutrient levels in the water (Van Donk et al., 1993), providing a refuge for herbivorous zooplankton (Timms & Moss, 1984), and preventing resuspension of the sediment by wind and benthivorous fish (Meyer et al., 1990).

With increase of lake trophy, the area occupied by submerged macrophytes may decrease. The disappearance of submerged macrophytes from eutrophic waters has been attributed mainly to poor light availability due to shading by epiphyton and phytoplankton (Phillips et al., 1978). Recently, it has been suggested that top-down effects, like herbivory by vertebrate and invertebrate grazers, are also important in structuring and lowering the macrophyte biomass (e.g. Lodge, 1991). Often an increase in herbivorous birds has been observed when submerged macrophyte communities were restored (Hanson & Butler, 1990; Hargeby et al., 1994; Lauridsen et al., 1994a; Schutten et al., 1994; Van Donk et al., 1994).

Disappearance of submerged macrophytes in shallow eutrophic lakes can lead to an alternative stable turbid state dominated by phytoplankton (Scheffer, 1990). Restoration by means of nutrient reduction seems often to be retarded or even prevented by strong buffering mechanisms (Moss, 1990; Scheffer et al., 1993). Return of aquatic vegetation is crucial for a successful restoration of such lakes (Moss, 1990). Reduction of the planktivorous fish stock ('biomanipulation') has been recently applied successfully to several turbid shallow lakes to induce a switch from the phytoplankton-dominated state to a clear-water state with submerged macrophytes (e.g. Jeppesen et al., 1990; Lauridsen et al., 1994b; Meijer et al., 1994; Hanson & Butler, 1994). Some of these lakes tended to return abruptly to the turbid state during the summer months, some five years after restoration (Meyer et al., 1994). These changes started with a decline of submerged macrophytes (Van Donk et al., 1993; Meijer et al., 1994).

In this paper we present the results of a study in Lake Zwemlust analysing the factors causing changes in submerged macrophyte biomass and species composition after restoration by biomanipulation. Especially the impact of herbivory by waterfowl and fish is discussed.

Study area

Lake Zwemlust is a small water body (1.5 ha), with a mean depth of 1.5 m and a maximum depth of 2.5 m. It is located in Nieuwersluis in the Province of Utrecht, The Netherlands. The water quality in the lake had deteriorated until the biomanipulation measures in 1987, due to nutrient-rich seepage water from the polluted River Vecht running about 50 m from the lake. Besides precipitation, seepage water is the main source of the lake's water input. Prior to biomanipulation, the lake was highly turbid, especially in summer (Secchi-depth, 0.3 m), primarily because of high biomass of the cyanobacterium *Microcystis aeruginosa*. The recurrent and persistent blooms of algae led to deterioration of the light climate and a complete disappearance of submerged macrovegetation. Only small strips of emerged and floating plants (*Phragmites australis* and *Nuphar lutea*) were present in the littoral zone of the lake (Van Donk et al., 1989). Consequently, an alteration in the structure of the fish community occurred: the piscivore pike (*Esox lucius*) vanished and the planktivore bream (*Abramis brama*) became dominant.

In March 1987 biomanipulation was carried out as a stand-alone restoration measure, because reduction of the external nutrient loading was not feasible within a reasonable time-span. The total mass of fish was removed, ca. 1500 kg, including about 75% bream (length 10–15 cm). After the lake was refilled by seepage, in ca. 3 days, it was restocked with juvenile fish: 1600 O^+ pike fingerlings (4 cm), and 140 specimen of rudd (*Scardinius erythrophthalmus*), fork length 9–13 cm. The offsprings of rudd were meant to serve as food for pike. The biomanipulation measures are discussed at some length by Van Donk et al. (1989, 1990).The effects of the experimental biomanipulation on the lake's ecosystem have been studied for more than seven years.

Material and methods

Field observations

Biomass and composition of submerged macrophytes in the lake were estimated according to Ozimek et al. (1990) during six successive years starting August 1987. Fish biomass and composition were determined yearly in October using the mark-recapture method (Ricker, 1975). In the period September–February, when more than 20 coots (*Fulica atra*) are present in and around the lake, the number of coots grazing on the macrophytes in the lake was counted fortnightly. Gut contents of rudd were analysed according to Prejs & Jackowska (1978). The techniques of sampling and monitoring lake's limnology are further outlined in Van Donk et al. (1989).

Estimation herbivory

We estimated consumption of macrophytes by rudd, according to Prejs (1984); Prejs considers 0^+ rudd as planktivorous, whereas 1^+ and $>1^+$ rudd feed mainly on macrophytes. Consumption of macrophytes by rudd is based on the average daily consumption of ca. 8–10 mg DW macrophyte per day per gram fish and multiplied by total biomass of rudd 1^+ and $>1^+$ and number of days of intense grazing on the plants. Besides, only the periods when water temperature is above 16 °C have to be considered as the periods of high feeding. Further, we assumpted that the biomass of rudd was constant over the feeding periods and the same as in October. This assumption may give an overestimation of the grazing by rudd.

Total consumption of macrophytes by coots was assessed from the number of 'birds days' (average number of birds d^{-1} × number of days) and the daily consumption per coot. The mean daily intake of ca. 45 g DW plant per coot, as measured by Hurter (1979), was used for calculation of total consumption.

Exclosures

To evaluate grazing effects by fish and birds on macrophyte composition, six cages made of an iron frame with dimensions of 4 m (length) × 1.5 m (width) × 0.6 m (height) and covered by wire-netting (1 × 1 cm mesh width), were used. The cages were

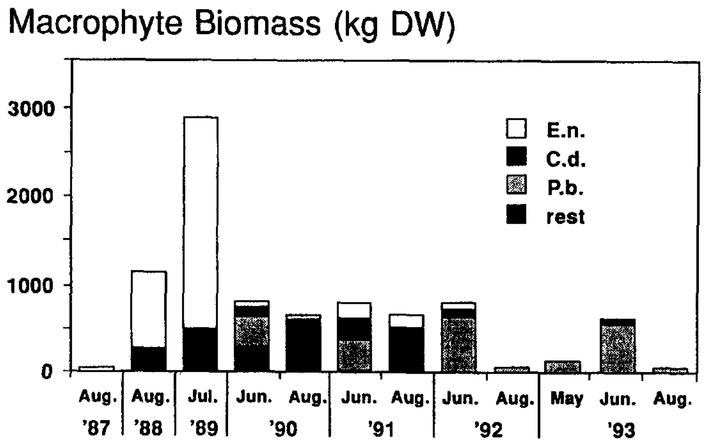

Figure 1. Contribution of the different species of submerged macrophytes (kg Dw) to their total biomass in Lake Zwemlust after biomanipulation.

Table 1. Biomass of rudd > 1^+ (kg/ha) and coverage (%) of submerged macrophytes (E.n. = *Elodea nuttallii*; P.b. = *Potamogeton berchtoldii*; C.d. = *Ceratophyllum demersum*) outside (lake) and inside the exclosures at the start of the experiment in May 1992.

	Rudd (> 1+) kg/ha	Coverage %		
		E.n.	P.b.	C.d.
Lake	297	30	30	5
Exclosures				
1	0	as in the lake		
2	413	" "		
3	363	" "		
4	750	" "		
5	1263	" "		
6	1575	" "		

placed on the lake bottom at a depth of 2.0 m in May 1992, containing an identical macrophyte composition as in the lake. An increasing biomass of rudd was introduced in these cages (0–1575 kg ha^{-1}) (Table 1), while grazing by birds was excluded. During the experiment that lasted up to July 1993 the cages were inspected monthly by divers.

Results

Macrophyte composition and development in the lake (1987–1993)

Total biomass of submerged macrophytes and contribution to it of the different species differed enormously in lake Zwemlust during the years following biomanipulation (Figure 1). In summer 1988 macrophytes occupied ca. 70% of the lake bottom (total biomass ca. 90 g DW m^{-2}) and in summer of 1989 almost 100% (total biomass ca. 200 g DW m^{-2}), with *Elodea nuttallii* dominating. However, in summers of 1990 and 1991 total biomass of the macrophytes decreased (total biomass ca. 60 g DW m^{-2}), *Ceratophyllum demersum* being the dominant species. In 1992 and 1993 *C. demersum* and *E. nuttallii* were nearly absent and *Potamogeton berchtholdii* became the dominant species in spring (biomass ca. 45 g DW m^{-2}), declining to very low abundance during late summer.

Rudd

The development of biomass of rudd $>1^+$ is given in Figure 2. In 1988 and 1989 biomass of rudd $>1^+$ was quite low, but increased in the following years to 297 kg ha^{-1} in 1991, declining to 200 kg ha^{-1} in 1993.

Coots

From 1989 onwards coots invaded Lake Zwemlust extensively during autumn and winter. In 1989/1990, when the lake was dominated by *Elodea*, coots were present in high numbers (ca. 150) from Sept.–Feb. In 1990/1991 and 1991/1992 a maximum was observed at the beginning of December. But the numbers declined in the following months when submerged macrophytes became scarce. In Sept.–Feb. 1992/1993, i.e. after the collapse of *Potamogeton* in August 1992, number of coots was maximally 30 (recorded in October 1992) (Figure 3).

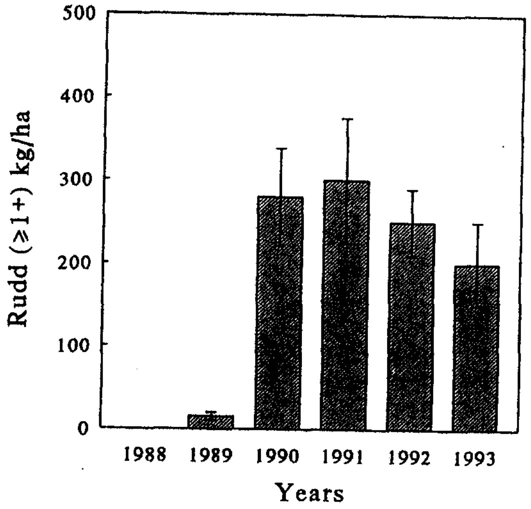

Figure 2. Biomass of rudd ($>1^+$) in Lake Zwemlust after stocking with rudd in March 1987. The 95% confidence intervals are indicated.

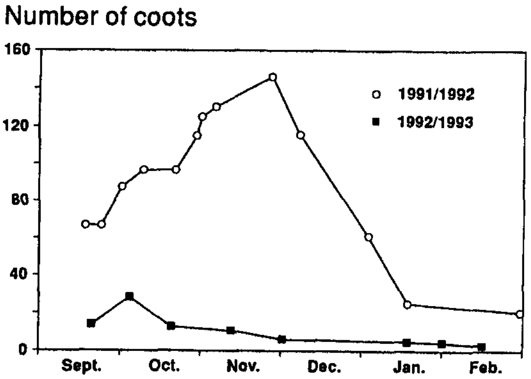

Figure 3. The mean number of coots grazing on submerged macrophytes in Lake Zwemlust during the winter 1991/1992 and 1992/1993.

Herbivory by fish and birds (1989–1993)

In guts of 0^+ rudd, the contribution of macrophytes was low, less than 10% weight of total food. However, in guts of 1^+ and $>1^+$ rudd macrophytes constituted $>85\%$ of food weight. From 1989 onwards the total consumption of macrophytes by 1^+ and $>1^+$ rudd increased to ca. 360 kg DW in 1991 (ca. 40% of maximum macrophyte biomass in 1991) and decreased to 200 kg DW in 1992 and 170 kg DW in 1993 (Table 2).

The highest consumption by coots (1200 kg DW) was found in Sept.–Feb. 1989/1990 (ca. 40% of maximum macrophyte biomass in 1989) (Table 2). In 1990/1991 and 1991/1992 the total consumption by coots decreased but its relative proportion to the maximum macrophyte biomass increased to 70–80% of the preceding years. The consumption by coots in 1992/1993 was the lowest (ca. 7% of the maximum macrophyte biomass of 1992). At the start of autumn 1992 nearly all submerged macrophytes had disappeared and only a low number of coots foraged on the lake during the following winter.

Table 2. Estimates of herbivory (kg DW macrophytes) by rudd (June–Sept.) and coots (Sept.–Feb.) in Lake Zwemlust for the years 1988–1993.

	Consumption (kg DW macrophytes)		
Period (June–Sept.)	By rudd	Period (Sept.–Feb.)	By coots
1989	0	1988/1989	0
1990	330	1989/1990	1200
1991	360	1990/1991	800
1992	200	1991/1992	600
1993	170	1992/1993	40

Exclosures

The percentage vegetated area occupied by the different macrophyte species in and outside the cages, observed at the end of the experiment (July 1993), are given in Figure 4. Outside the cages, *P. berchtholdii* was the dominant species (ca. 90%), while *E. nuttallii* and *C. demersum* were scarce (resp. 1 and 5%). The macrophyte composition of cage 1 differed considerably from the other 5 cages (nos. 2–6) and the lake. In cage 1, excluding herbivory by birds and fish, *E. nuttallii* dominate 100%. The percentages macrophyte cover between cages 2–6 (excluding herbivory by birds, but including fish) did not differ, although total macrophyte biomass varied. In these cages ca. 30% was occupied by *P. berchtholdii* and 10% each by *E. nuttallii* and *C. demersum.* Unlike in Cages 2 and 3, the plants *P. berchtholdii* and *E. nuttallii* did not reach the top of the cages in 4, 5 and 6. Especially young apical leaves of *E. nuttallii* were grazed.

Discussion

Grazing pressure by rudd is unevenly distributed among macrophyte species. Prejs & Jackowska (1978) found for rudd a strong preference for *Elodea* and a low preference for *Ceratophyllum.* In laboratory experiments with macrophytes from Lake Zwemlust rudd fed selectively on *E. nuttallii* followed by *P. berchtholdii,*

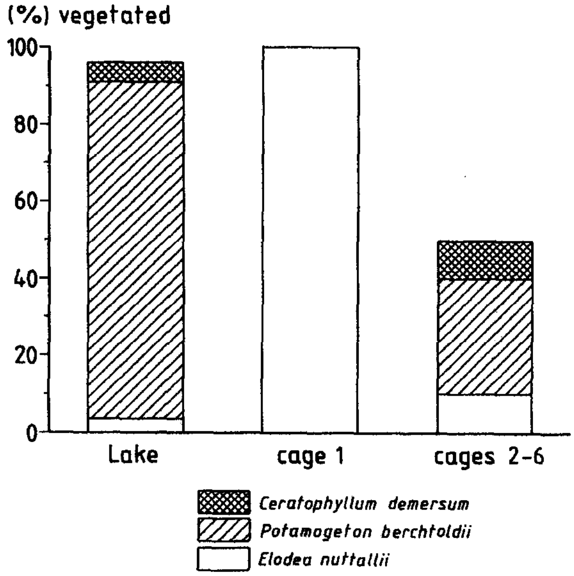

Figure 4. Coverage percentages of the different macrophyte species in the lake and in the exclosures as measured at the end of the experiment in July 1993 (see Table 1).

but did not graze on *C. demersum*, which calcareous structure is apparently much less edible. Rudd, grazing only during the growing season on the macrophytes, prefer young shoots. Prejs (1984) stated that this grazing behaviour may sometimes even stimulate the production of the macrophytes. The difference in macrophyte composition between exclosure 1 (no rudd) and exclosures 2–6 (with rudd) confirmed the results of the laboratory experiments, that grazing by rudd may result in a shift in dominance from *E. nuttallii* (cage 1) to expansion of less edible species (cages 2–6) as *P. berchtholdii* and *C. demersum* (Figure 4).

Kiørboe (1980) stated that grazing by coots has only a minimal effect on macrophyte growth because grazing often takes place outside the growing season of the plants. Coots, however, pull out whole plants and may influence the macrophyte composition and succession by removing especially plants still present during autumn and winter. Contrary to many other submerged macrophytes, *Elodea* is rather unaffected by cold water in late autumn and winter (Wallsten, 1980). It also does not form overwintering structures as in case of *Ceratophyllum* (ca. 10 cm long dormant buds) and *Potamogeton* (turions or tubers). *Potamogeton* starts to form these structures already during the early summer (Sastroutomo, 1981) and decreasing light conditions, e.g. due to epiphyton growth, may even accelerate the formation (Van Vierssen et al., 1994). During winter these tubers or turions lay in or on the sediment, not accessible for coots, while the ca. 10 cm long dormant buds of *Ceratophyllum* are only available when *Elodea* is not dominant. After grazing-induced losses of *Elodea* by coots in Lake Zwemlust during autumn and winter 1989/1990, other macrophyte species like *Ceratophyllum* and *Potamogeton* were able to occupy the whole available area in the subsequent spring period. In winter 1990/1991 and 1991/1992 the coots started to graze on *Ceratophyllum*. Thus, grazing by coots in Lake Zwemlust on *Elodea* and *Ceratophyllum* may eventually result in a dominance of *Potamogeton*. This is confirmed by the exclosure experiments. The macrophyte composition in the lake was dominated by *Potamogeton*, while in cages 2–6, with herbivory by rudd but not by coots, also the other species were relatively abundant (Figure 4). The collapse of *P. berchtholdii* in the lake already in August of 1992 and 1993 may be explained by both grazing of rudd and the formation of turions.

Both fish and bird grazing on macrophytes may affect the internal balance among autotrophic components by reducing the biomass of macrophytes, thereby reducing their competition with algae for nutrients (Lodge, 1991). Furthermore, since some macrophytes species incorporate nutrients from the sediment, these nutrients may be remobilized to the water after the macrophytes eaten by fish and birds are egested, giving phytoplankton access to a supplementary nutrient source (Hansson et al., 1987). Thus, in Lake Zwemlust both fish and bird herbivory reduced the total macrophyte biomass making nutrients more available for phytoplankton growth.

In 1992 and 1993 the amount of filamentous green algae increased and phytoplankton blooms occurred again, chlorophyll-*a* concentrations reaching 60–130 $\mu g\ l^{-1}$. This occurred despite that the external nutrient load to the lake did not differ from previous years and the amount of zooplankton (e.g. cladocerans) even increased (Gulati, 1995). In 1992 and 1993 *P. berchtoldii* was the dominant macrophyte and due to its natural life cycle and herbivory by rudd, nutrients for phytoplankton growth became available already late summer when temperature and light conditions were still suitable for phytoplankton growth.

Fish manipulation in Lake Zwemlust switched the lake from a turbid state (dominating by phytoplankton) to a clear water state (dominated by macrophytes). After five years, however, fish and bird grazing on macrophytes affected the internal balance among autotrophic components by changing composition and lowering the standing crop of the macrophytes, thereby reducing their competition with algae for nutrients. To study in more detail the effects of selective herbivory by waterfowl and fish on longterm recovery of Lake Zwemlust, supplementary experiments in the laboratory and *in situ* exclosures are planned.

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