Verh. Internat. Verein. Limnol.	25	2139–2143	Stuttgart, Oktober 1994

Herbivory by waterfowl and fish on macrophytes in a biomanipulated lake: effects on long-term recovery

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Introduction

In shallow eutrophic lakes submerged macrophytes play a key-role in several mechanisms that tend to keep water transparency high (Carpenter & Lodge 1986). Macrophytes may strongly compete with algae for nutrients (Ozimek et al. 1990, Van Donk 1991), provide a refuge for herbivorous zooplankton (Timms & Moss 1984) and prevent resuspension of the sediment by wind and benthivorous fish (Meijer et al. 1990).

Water transparency of Lake Zwemlust markedly improved after restoration by biomanipulation in 1987 (Van Donk et al. 1989, 1990). Before biomanipulation no submerged vegetation was present in the lake, but from 1987 onwards submerged macrophyte stands developed each year following a clear-water phase caused by high zooplankton grazing in spring (Gulati 1990). 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 (Aquasense 1992).

In cages placed on the lake bottom, serving as exclosures for larger fish and birds, *E. nuttallii* still reached a high abundance in 1990 and 1991 (Van Donk et al. 1993). This observation formed the basis for a hypothesis that herbivory by fish and/or waterfowl may be partly responsible for the decrease in macrophyte biomass and shift in species composition. Fragments of plants were found in Lake Zwemlust in the guts of the cyprinid fish rudd (*Scardinius erythrophthalmus*) (Klein Breteler 1991). Further, the number of herbivorous birds, predominantly coots (*Fulica atra*) increased from 1989 onwards.

As a first step to analyse the effects of herbivory on long-term recovery of Lake Zwemlust, the impact of grazing by fish and waterfowl on the submerged vegetation was estimated.

The lake and biomanipulation measures

Lake Zwemlust is a hypertrophic, small (1.5 ha) and shallow (mean depth 1.5 m; max. depth 2.5 m) water body. It is located in the Province of Utrecht, The Netherlands. Besides precipitation, nutrient-rich seepage water from the polluted River Vecht, running about 50 m from the lake, 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*. In March 1987, the lake was emptied by pumping out the water to facilitate complete fish elimination by seine- and electro-fishing (ca. 1,500 kg, included about 75 % bream). The lake was restocked with juvenile fish: 1,600 O^+ pike, measuring 4 cm, and 140 rudd (*S. erythrophthalmus*) measuring 9 – 13 cm fork length. The offsprings of rudd were meant to serve as food for pike. The biomanipulation measures are discussed at greater detail in Van Donk et al. (1989).

Material and methods

Biomass and composition of submerged macrophytes in the lake were estimated according to Ozimek et al. (1989) during four successive years starting August 1988. In 1991 the total submerged macrophyte biomass was estimated every second month during the growing season. Fish biomass and composition were determined yearly in October using the mark-recapture method (Ricker 1975). In spring and summer 1991 gut contents of rudd were analysed according to Prejs & Jackowska (1978).

The total consumption of macrophytes by rudd in the lake was estimated from the daily consumption per unit biomass of rudd multiplied by total biomass of rudd 1^+ and $>1^+$ and number of days of intense grazing on the plants. According to Prejs (1984) O^+ rudd is planktivorous, whereas 1^+ and $>1^+$ rudd feed mainly on macrophytes, and only the periods when water temperature is above 16 °C have to be considered as the periods of high feeding. We followed the methods of Prejs (1984) for estimation of consumption of macrophytes by rudd. Further we made the assumption that the biomass of 1^+ and $>1^+$ rudd was constant over the feeding periods and equal to the value determined in Oct. 1991. This assumption may give an overestimation of the grazing by rudd.

Total consumption of macrophytes by coots was estimated from the number of "birds days" (average number of birds d^{-1} × number of days) and the daily consumption per coot.

0368-0770/94/0025-2139 $ 1.25

Table 1. Standing stock of the fish populations ($kg \cdot ha^{-1}$) in Lake Zwemlust after biomanipulation.

	Rudd			Pike	
Year (Oct.)	0^+	1^+	$>1^+$	0^+	$>0^+$
1988	50	–	–	16	42
1989	106	–	–	–	18
1990	125	257	16	5	39
1991	24	184	113	3	42

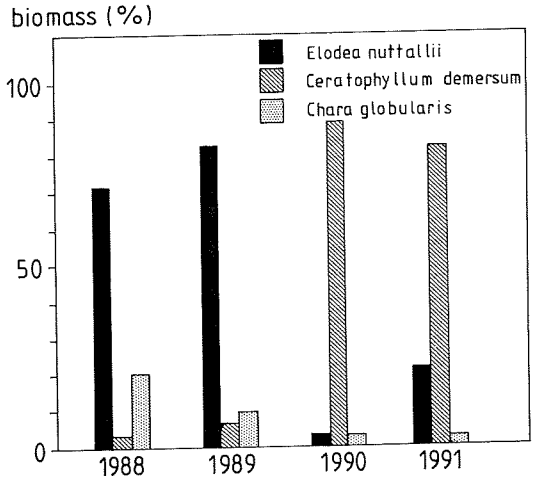

Fig. 1. Contribution of the different species of submerged macrophytes to their total biomass in Lake Zwemlust after biomanipulation determined in August 1988, 1989, 1990 and 1991.

Between September 1991 and February 1992, when more than 20 coots were present in the lake, the number of coots grazing on the macrophytes in the lake was counted fortnightly. The daily consumption per coot was assessed following HURTER (1979).

Results

Development of macrophytes and fish in the lake

The data on development of rudd and pike stocked after the biomanipulation are given in Table 1. Standing stock of rudd increased from 50 kg · ha^{-1} in 1988 to 398 kg · ha^{-1} in 1990, but declined to 321 kg · ha^{-1} in 1991. Pike biomass stabilized in 1990 and 1991 at 45 kg · ha^{-1}.

Contribution of the different macrophyte species to the total biomass of submerged macrophytes in the lake after biomanipulation is given in Fig. 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, total biomass of the macrophytes decrease in summers of 1990 and 1991 (total biomass ca. 60 g DW · m^{-2}), *Ceratophyllum demersum* being the dominant species. In 1991 the highest biomass of submerged macrophytes was found in June (Fig. 2 a).

Herbivory by fish

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 more than 85% of food weight.

Total consumption of macrophytes by 1^+ and $>1^+$ rudd (biomass: 297 kg · ha^{-1} in Oct. 1991) in Lake Zwemlust in 1991 was estimated at ca. 360 kg DW (Fig. 2 b). This estimation is based on the average daily consumption of ca. 8–10 mg DW macrophyte per day per gram fish (PREJS 1984) for the 90 days with temperatures > 16 °C (June–Sept. 1991).

Herbivory by birds

From 1989 onwards coots invaded Lake Zwemlust extensively during autumn and winter. In 1991 a maximum of 180 coots per day was observed in December. HURTER (1979) found for coots grazing on submerged macrophytes a mean daily intake of ca. 45 g DW plant per coot. From this daily ration and the coot numbers the total macrophyte consumption by coots over the period Sept. 1991–Feb. 1992 was estimated at ca. 600 kg DW (Fig. 2 b).

Discussion

WINFIELD (1991) recently remarked that the growing application of biomanipulation has accelerated the need for the full incorporation of aquatic vertebrates within limnology. Especially general understanding of the impact of grazing on macrophyte populations, communities, and material flow is currently poor (LODGE 1991). 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. Furthermore, since some macrophyte species incorporate nutrients from the sediment, these nu-

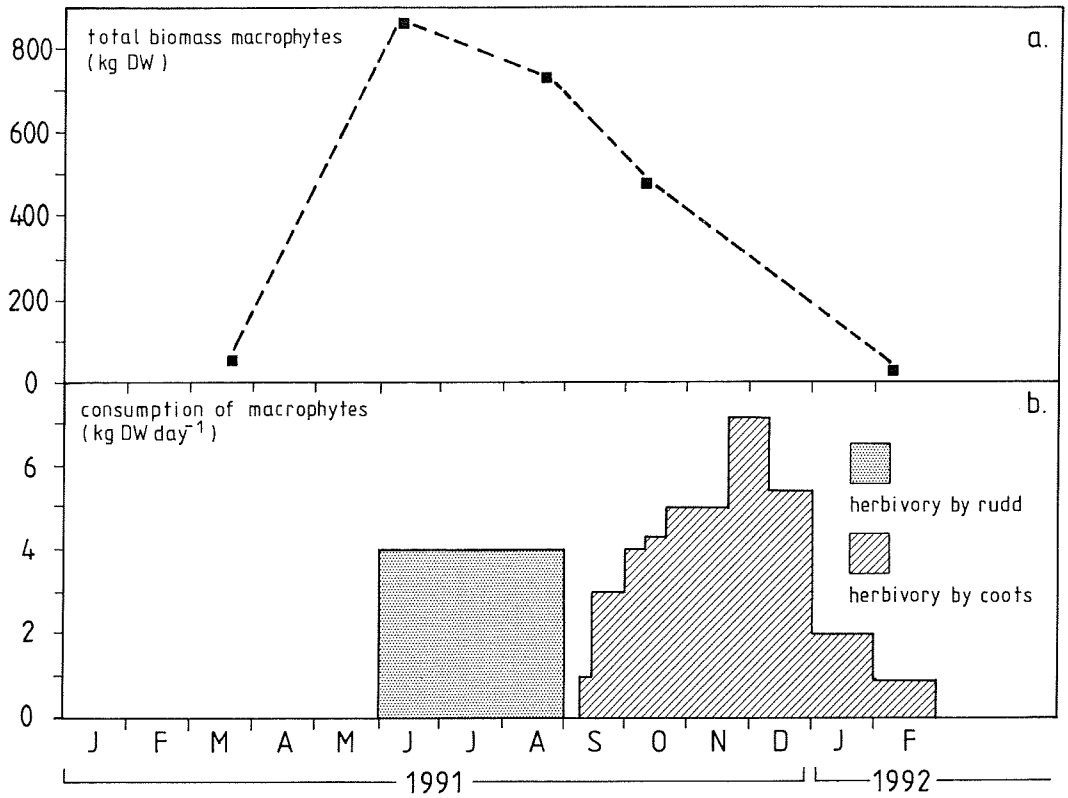

Fig. 2. a) Total biomass of submerged macrophytes (kg DW) in Lake Zwemlust estimated in March, June, August, October 1991 and February 1992; and b) estimates of herbivory (kg DW macrophyte · day^{-1}) by rudd and coots in Lake Zwemlust (March 1991 – Feb. 1992).

trients 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).

Rudd grazing during the growing season on the macrophytes, prefer young shoots. Prejs (1984) stated that this grazing behaviour may even stimulate the production of the macrophytes. In Lake Zwemlust the biomass of submerged macrophytes removed by rudd was ca. 40% of maximum biomass in 1991, compared with ca. 70% by coots. Grazing pressure by rudd is, contrary to grazing by coots, unevenly distributed among macrophyte species. Prejs & Jackowska (1978) found a strong preference for *Elodea* by rudd and a low preference for *Ceratophyllum*. Recently performed grazing experiments with *Elodea* and *Ceratophyllum* taken from Lake Zwemlust confirm these data. *C. demersum*, calcareous in structure, has apparently a much lower edibility. Due to selective grazing on *Elodea* herbivory by rudd may have affected the shift in dominance from *E. nuttallii* to *C. demersum* in Lake Zwemlust.

An increase in herbivorous waterfowl after recovery of submerged macrophyte stands was also observed by Andersson et al. (1990) in Lake Krankesjøn in Sweden. Kiørboe (1980) stated that grazing by coots has only minimal effects on macrophyte growth due to the fact that 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 especially removing 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 and does not form dormant buds (Wallsten 1980). After grazing-induced losses of *Elodea* by coots during autumn and winter, next spring other macrophyte species like *Ceratophyllum*,

which form dormant buds during winter, can occupy the whole available area (BEST 1977).

Up to now, i.e. four years after biomanipulation, macrophyte consumption by the vertebrate grazers in Lake Zwemlust did not negatively affect the lake's recovery. Despite intensive herbivory in 1990 and 1991 the water transparency remained high (bottom visibility). Possibly the shift in dominance from *Elodea* to *Ceratophyllum* may have lowered the internal load of N and P to the lake, because *Elodea* is able to absorb nutrients from the sediment (RØRSLETT 1986, VAN DONK et al. 1993) while *Ceratophyllum* mainly takes up nutrients from the water (BEST 1977). Further *Ceratophyllum* may more strongly compete with algae for nitrogen, due to enhancement of its nitrogen content with increased levels of this nutrient in the water (BEST 1980).

To study in more detail the effects of selective herbivory by waterfowl and fish on long-term recovery of Lake Zwemlust, experiments in the laboratory and in in situ exclosures are planned.

Acknowledgements

We thank Prof. Dr. W. J. WOLFF, Dr. R. D. GULATI, Dr. B. A. FAAFENG and Drs. R. POT for their useful suggestions on the manuscript. The project was partly funded by the Province of Utrecht.

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