Macrophyte-related shifts in the nitrogen and phosphorus contents of the different trophic levels in a biomanipulated shallow lake

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Abstract

Lake Zwemlust, a small highly eutrophic lake, was biomanipulated without reducing the external nutrient loading, and the effects were studied for four years. In this paper we pay special attention to the shifts in relative distribution of nitrogen and phosphorus in the different trophic levels and to the changes in growth limitation of the autotrophs.

Despite of the high external nutrient loads to the lake (ca 2.4 g P m^{-2} y^{-1} and 9.6 g N m^{-2} y^{-1}), the effects of biomanipulation on the lake ecosystem were pronounced. Before biomanipulation no submerged vegetation was present in the lake and P and N were stored in the phytoplankton (44% N, 47% P), fish (33% N, 9% P) and in dissolved forms (23% N, 44% P). P and N contents in sediments were not determined. In the spring and summer following the biomanipulation (1987), zooplankton grazing controlled the phytoplankton biomass and about 90% of N and P were present in dissolved form in the water. From 1988 onwards submerged macrophyte stands continue to thrive, reducing the ammonium and nitrate concentrations in the water below detection levels. In July 1989 storage of N and P in the macrophytes reached 86% and 80%, respectively. *Elodea nuttallii* (Planchon) St.John, the dominant species in 1988 and 1989, acted as sink both for N and P during spring and early summer, withdrawing up to ca 60% of its N and P content from the sediment. At the end of the year only part of the N and P from the decayed macrophytes (ca 30% of N and 60% of P) was recovered in the water phase of the ecosystem (chiefly in dissolved forms). The rest remained in the sediment, although some N may have been released from the lake by denitrification.

In summer 1990 only 30% of the N and P was found in the macrophytes (dominant species *Cerato-phyllum demersum* L.), while ca 30% of N and P was again stored in phytoplankton and fish.

Introduction

Restoration of shallow and turbid eutrophic lakes by means of nutrient reduction is often retarded or even prevented by powerful buffering mechanisms. Biomanipulation may, therefore, be essen-tial to switch shallow lakes from the phytoplank-ton-dominated state to a clear water state with submerged macrophytes, despite of a consider-able nutrient reduction (Moss, 1990; Scheffer, 1990). Submerged macrophytes may act as an ecotone zone by changing the nutrient retention

and cycling in the food-web and by inducing long-term stability (Naiman *et al.*, 1989).

Biomanipulation of eutrophic lakes has mainly focussed on the removal or restructuring of planktivorous fish populations to affect changes in the zooplankton from a community dominated by small-bodied to one dominated by large-bodied cladocerans, particularly of the genus *Daphnia* (Shapiro & Wright, 1984; Gulati, 1990). Intense grazing by the large-bodied zooplankters can then lead to large-scale reductions in phytoplankton biomass and the consequent increases in water clarity and submerged macrophyte population. Benndorf (1990) stated that restoration of eutrophied water bodies, having a high external nutrient load, seems feasible only if two strategies, i.e. nutrient reduction and biomanipulation, are integrated.

To study the effects of biomanipulation separately from nutrient reduction, the fish community in a small highly eutrophic lake was altered without changing the external nutrient loading. The effects of this food-web manipulation were monitored for four years and compared with the situation before restoration. Due to changes in food-web interactions, changes in nutrient dynamics were likely to occur (Boers *et al.*, 1991). Consequently these changes may have their effects on the factors controlling the growth of phytoplankton and macrophytes. In this paper the shifts in relative distribution of nitrogen and phosphorus in the different trophic levels of the lake and the changes in growth limitation of the autotrophs are discussed.

Site description

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 measure), due to nutrient-rich seepage water from the polluted River Vecht located approximately 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* Kütz.. The recurrent and persistent blooms of algae led to deterioration of the light climate and a complete disappearance of submerged macro-vegetation. Only small strips of emerged plants (*Phragmites australis* Cav. and *Nuphar lutea* L.) 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* L.) vanished and the planktivore bream (*Abramis brama* L.) became dominant.

In March 1987, the lake was emptied by pumping out the water to facilitate complete fish elimination. Planktivorous and benthivorous species, which were predominant, were collected by seine- and electro-fishing. The total mass of fish removed, *ca* 1500 kg, included 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, measuring 4 cm, and 140 rudd (*Scardinius erythrophthalmus* L.) measuring 9–13 cm fork length. The offsprings of the latter fish were meant to serve as food for pike. The biomanipulation measures are discussed extensively by Van Donk *et al.* (1989).

Methods

In order to quantify the external P and N loads to the lake, the hydrodynamics of the lake had to be studied. Six piezometers were installed to measure the hydraulic gradient of the water tables. Hydraulic conductance was estimated through pump test, and hydrogeologic boundaries established. Piezometers were also used to analyse the P and N contents of the ground water. Additionally the water levels were read twice a week; simultaneously groundwater and surface water samples were taken for chemical analyses. From these data the net amounts of the incoming P and N in the seepage water were calculated. The nutrient load to the lake due to direct deposition

(wet and dry) was calculated from meteorological data obtained from a station at De Bilt, east of the city of Utrecht. Chemical analyses of the lake sediment were not carried out due to its complexity. Therefore, the sediment is regarded as the closing entry of the balance. The net external nutrient load (L_{net}) was calculated from the total external nutrient load ($\Sigma\,L_{ext}$) minus the sum of all nutrient outputs ($\Sigma\,L_{out}$):

$$\Sigma\,L_{ext} - \Sigma\,L_{out} = L_{net}.$$

The internal nutrient loading (release and uptake of N and P from the sediment) was estimated from nutrient budget data according to Cooke *et al.* (1977). For the period April–September 1989 the net internal P and N loads to the lake ecosystem (L_{int}) were estimated from the change in N and P content of the lake ($\delta E =$ sum of amounts of P and N built up in the different compartments of the ecosystem, excluding the sediment) from April 1989 to September 1989, minus the net external load to the lake (L_{net}) over this period:

$$\delta E - L_{net} = L_{int}.$$

Denitrification loss may produce an underestimation for the internal N load to the lake. For procedures of sampling and analyses of N and P in water, phytoplankton, zooplankton, macrophytes and fish, see Van Donk *et al.* (1989) and Ozimek *et al.* (1990).

To assess the factors limiting the growth of phytoplankton and submerged macrophytes from 1987 to 1990, community enrichment bioassays were performed at the *in situ* temperature and prevailing light-dark cycle. The procedures for these bioassay experiments are described in Van Donk *et al.* (1988, 1990) and Ozimek *et al.* (1990).

Two cages (4 m length, 1 m width and 0.6 m height), clothed with 1.5 cm mesh wire-netting, were stripped of fish and placed at the lake bottom. In these enclosures the growth of the macrophytes was followed without the interference of larger fish (grazing or grubbing up the sediment) and herbivorous waterfowl.

Results

General developments

The mean yearly net inflow of water to the lake of *ca* 20 000 m^3 results in a water residence time of *ca* 9 months. The external loads of N and P were high and did not change discernibly during the study years: *ca* 2.4 g P m^{-2} y^{-1} and 9.6 g N m^{-2} y^{-1} (including a load from wet and dry deposition of *ca* 0.2 g P m^{-2} y^{-1} and 5.3 g N m^{-2} y^{-1}).

After the biomanipulation, despite of the high and unchanged P and N loads to the lake, the effects on the structure of the ecosystem were marked. The Secchi disc depth increased and reached the lake bottom (2.5 m) in the summers following biomanipulation. The mean chlorophyll concentration was reduced from 250 μg l^{-1} in 1986 (before biomanipulation) to 5–13 μg l^{-1} after biomanipulation. The submerged macrophytes responded rapidly to the improved light conditions (Ozimek *et al.*, 1990; Van Donk *et al.*, 1990). In the summer of 1988 macrophytes occupied *ca* 70% of the lake bottom (total biomass *ca* 87 g DW m^{-2}) and almost 100% in summer of 1989 (total biomass *ca* 200 g DW m^{-2}). *Elodea nuttallii* was the dominant species in 1988 and 1989; it contributed 70% and 82%, respectively, to the total macrophyte biomass. In the summer of 1990, however, the total biomass of the macrophytes declined (*ca*. 57 g DW m^{-2}) and *Ceratophyllum demersum* became the dominant species (Fig. 1). The highest biomass of large-bodied zooplankton was found directly after the biomanipulation, *ca* 350 ind. l^{-1} of daphnids in spring 1987.

However in the following years, the contribution of the zooplankton to the total biomass decreased (Gulati, 1989; 1990). Further, a shift in the dominance from daphnids to bosminids was observed from 1987–1989 to 1990.

The rudd population, stocked after the biomanipulation, gradually increased from 50 kg ha^{-1} (all 0$^+$ rudd) in 1988 to 398 kg ha^{-1} (including *ca* 125 kg ha^{-1} 0$^+$ rudd) in 1990. 0$^+$ Rudd is mainly planktivorous, not benthivorous,
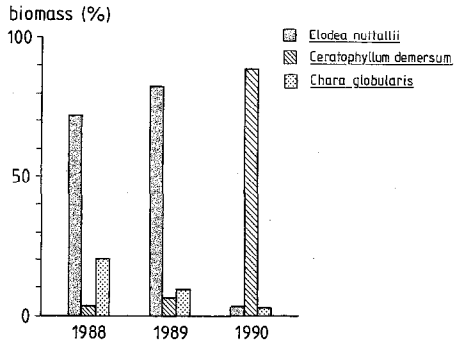
Fig. 1. The contribution of the different species to the total macrophyte biomass after biomanipulation in August 1988, 1989 and 1990 in Lake Zwemlust.

and 1^+ and 2^+ rudd can also feed on macrophytes (Klein-Breteler, 1991). The pike population decreased first, from 58 kg ha^{-1} in 1988 to 18 kg ha^{-1} in 1989, but rose again to 44 kg ha^{-1} in 1990 (Klein-Breteler, 1991).

Nutrient distribution

The distribution of N and P over the different trophic levels of the lake, measured at the end of August in the years before (1986) and after the biomanipulation (1987–1990), are given in Fig. 2. Before the biomanipulation, no submerged vegetation was present and P and N were stored in the phytoplankton (44% N, 47% P), fish (33% N, 9% P) and in dissolved forms (23% N, 44% P). P and N contents of sediments were not determined. In the summer immediately following the biomanipulation (1987), N and P were mainly dissolved in the water as SRP (Soluble Reactive Phosphorus), NH_4-N, NO_3-N and organic-N, which form ca 90% of the total N and P. From 1988 onwards the spring and summer concentrations of both NH_4-N and NO_3-N decreased below detection levels, while the SRP concentration only decreased slightly and was still very high (>0.3 mg l^{-1}). The storage of N and P in the macrophytes above the sediment increased enormously, with the highest percentages in 1989 (ca 86% of total N and 80% of P in *E. nuttallii*). In 1990 only 30% of the N and P was found in the macrophytes (mainly in *C. demersum*), while ca
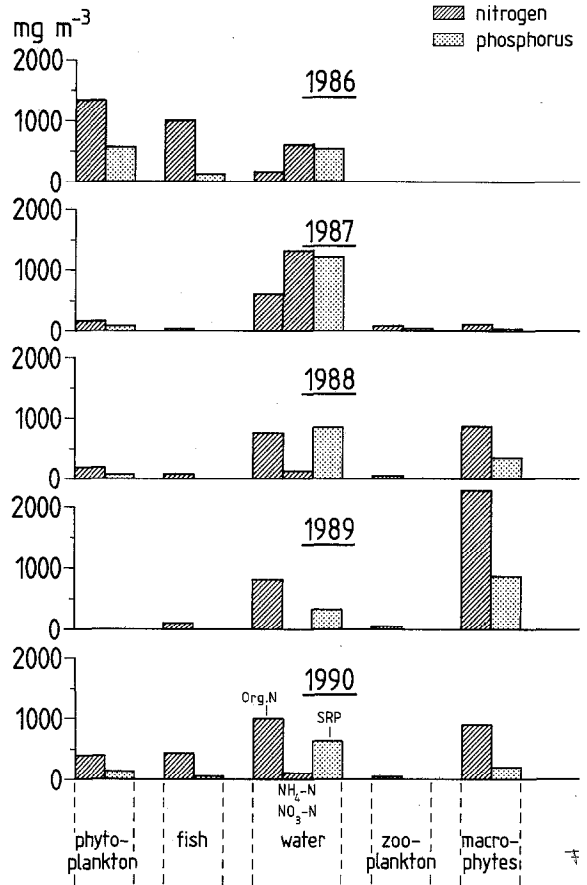

Fig. 2. The concentrations (mg m^{-3}) of phosphorus and nitrogen in the different compartments of the ecosystem of Lake Zwemlust before (Aug. 1986) and after (Aug. 1987, 1988, 1989 and 1990) biomanipulation.

30% of the nutrients was stored in phytoplankton and fish. The amount of dissolved organic N in the water increased from 600 mg m^{-3} in 1987 to 1100 mg m^{-3} in 1990. Although in Lake Zwemlust the biomass of macrofauna and filamentous green algae increased after biomanipulation (Kornijów et al., 1990), their contribution to the total biomass and N and P contents was relatively small, and therefore not included in Fig. 2.

The changes in N and P content of the lake for the period April 1989–September 1989 may be derived from Table 1. The calculated values for the external load of N and P and the estimated values for the internal load are given in Fig. 3. From April to July 1989 the external load of N

Table 1. The amount of nitrogen and phosphorus in mg m^{-3} distributed over the different compartments of the ecosystem of Lake Zwemlust on three dates in 1989.

	12 Apr.		5 Jul.		30 Aug.	
	N (mg m^{-3})	P (mg m^{-3})	N (mg m^{-3})	P (mg m^{-3})	N (mg m^{-3})	P (mg m^{-3})
Phytoplankton	67	17	63	53	123	80
Fish	33	3	67	7	100	10
Org. N	576	0	599	0	856	0
Water NH$_4$-N	107	0	30	0	67	0
NO$_3$-N	76	0	23	0	54	0
SRP	0	323	0	300	0	266
Zooplankton	77	10	27	3	80	14
Macrophytes	120	30	5261	1399	2264	599
Total	1056	383	6070	1762	3544	969

and P to the lake was nearly one-third the amounts of N and P taken up by the macrophytes. *E. nuttallii*, the dominant species at that time, can take up nutrients from the sediment with their root system. However, during July–

Fig. 3. The external and internal loads (mg m^{-3}) of nitrogen and phosphorus to Lake Zwemlust, measured from 12 April to 5 July 1989 and from 5 July to 30 August 1989.

Sept. 1989, a negative internal load was found, probably due to the early decay of macrophytes in August. At that time most of the N and P were still fixed in the dead plants laying on the sediment.

The data obtained from the natural community bioassays have been used to depict changes in growth limitations of phytoplankton and macrophytes (Fig. 4). Before biomanipulation, light was the main growth rate limiting factor for the phytoplankton and the macrophytes. The low light conditions caused by phytoplankton blooms prevented the macrophytes from growing. After the manipulation, zooplankton grazing, and from
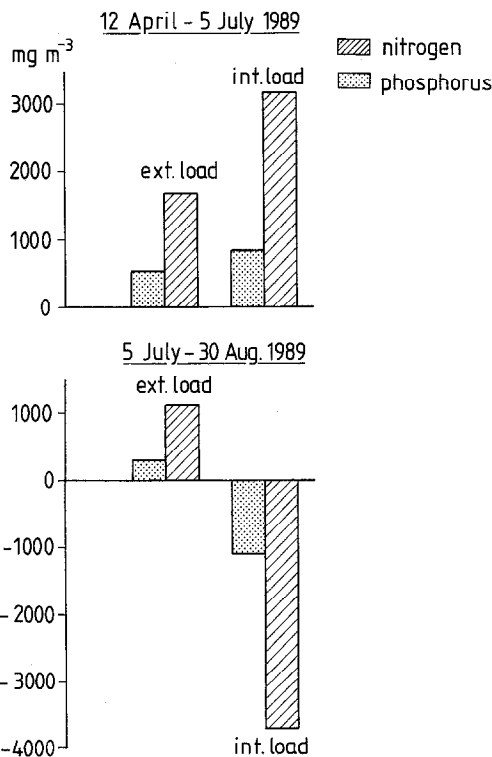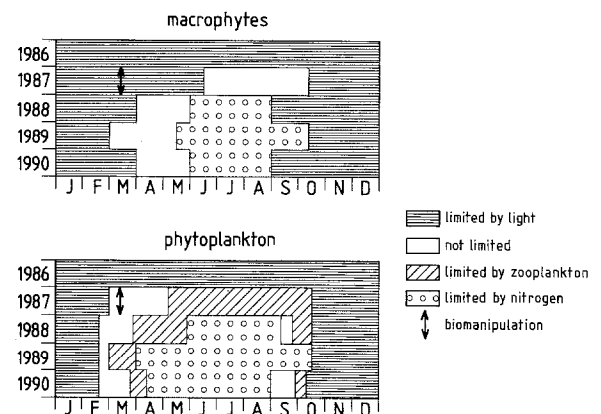

Fig. 4. Annual and seasonal changes in the factors limiting the macrophyte and phytoplankton growth in Lake Zwemlust before (1986) and after (1987, 1988, 1989 and 1990) biomanipulation.

1988 onwards also N limitation, were the controlling factors for the phytoplankton community during the spring and summer. The high uptake of N by the macrophytes apparently caused an N limitation for the phytoplankton. Nitrogen-fixing cyanobacteria did not appear to be important for the nitrogen load to the lake since they were observed only in Aug. 1988 and in relatively small numbers (Van Donk, 1991).

The macrophytes were also mainly limited by nitrogen during the summer months. In 1990, however, fish and/or waterfowl probably influenced the species composition of the macrophytes. In the cages placed on the lake bottom and serving as exclosures for larger fish and birds, *Elodea* reached a high abundance in 1990, but was completely absent outside the cages, where *Ceratophyllum* was the dominant species. Remains of plants were found in the stomachs of the 1^+ rudd (Klein Breteler, 1991). Further, frequently herbivorous coots (*Fulica atra* L.), sometimes more than 100 ind., were observed in Lake Zwemlust.

Discussion

Shifts in abundance and composition of phytoplankton and zooplankton, following a manipulation of the fish population, have been observed in several whole-lake food-web experiments (Shapiro, 1990; Benndorf, 1990). Most of these experiments, however, were followed over relatively short periods only. An enormous increase in macrophytes, as found in Lake Zwemlust, has been described in few other experiments in shallow lakes (Hanson & Butler, 1990; Jeppesen *et al.*, 1990; Meijer *et al.*, 1989; Søndergaard *et al.*, 1990). Nevertheless, little attention has been paid to the role of these macrophytes in changing the nutrient retention and cycling in the food-web, and in inducing long-term stability (Moss, 1990; Van Dijk & Van Donk, 1991). An important question is the extent to which macrophyte stands act as sink or source for nutrients and promote denitrification in the course of the vegetation period. Dense stands of

macrophytes can cause deficiencies of nutrients in the water (Boyd, 1971). In Lake Zwemlust, from April to July 1989, dense stands of *E. nuttallii* acted as a sink for both N and P, withdrawing up to *ca* 60% of its N and P contents directly and/or indirectly from the sediment (internal loading). In the period July–Sept. 1989, however, 60% of the N and P disappeared again from the macrophyte compartment due to leakage, decay and grazing which slightly increase the content of N and P in fish, phytoplankton, water and sediment (Table 1 and Fig. 3). At the end of the year only a part of the N and P from the decayed macrophytes (*ca* 30% of N and 60% of P) was still found in the ecosystem (chiefly in dissolved form). The rest remained in the sediment and some per cent of N probably left the lakes's ecosystem by denitrification. The macrophyte compartment in Lake Zwemlust performed a similar function, i.e. improvement of water quality by changing nutrient retention and recycling in the food-web, as was attributed to land/inland water ecotones by Naiman *et al.* (1989).

The shift in dominance from *E. nuttallii* in 1989 to *C. demersum* in 1990 (Fig. 1) has probably been caused by selective grazing mainly of 1^+ rudd (*ca* 257 kg ha^{-1} in 1990) on *Elodea*. *C. demersum* is apparently not very edible for rudd due to its calcareous structure. This plant has no roots and is, therefore, not able to use nutrients from the sediment directly. Also grazing on macrophytes by herbivorous waterfowl may play a role. Hanson & Butler (1990) found a dramatic increase in waterfowl that fed upon macrophytes in Lake Cristina after biomanipulation. Verhoeven (1978) calculated a consumption of 70 g DW *Ruppia spp.* per 1 coot per day.

It is not clear whether this shift from *Elodea* to *Ceratophyllum* may result in negative or positive effects for the water quality of the lake. One likely positive effect is that *Ceratophyllum* can not take up nutrients from the sediment, so that the internal load of N and P to the lake may decrease. A positive property of *Elodea*, however, is its ability to compete with phytoplankton for nutrients by building up high biomass during summer. The shift in the zooplankton community in 1990, from

daphnids to bosminids, may also be the result of the increased predation, especially of 0^+ rudd (*ca* 125 kg ha^{-1}) on large-bodied daphnids. The relatively higher phytoplankton biomass in summer of 1990, as compared to previous years (Fig. 2), has apparently been one of the consequences of the above changes (mean chlorophyll-a conc. of 14 μg l^{-1} with a maximum on 8–29 of 35 μg l^{-1}). Hence, the increased rudd population, consuming not only zooplankton but also *Elodea*, may lead to the return of the lake to its former state, dominated by phytoplankton blooms. Obviously the stocked pike population is not able to control the rudd population. Continuation of the monitoring programme will probably give more information on the question if regular fish stock management will be a necessary tool to keep this lake with a high nutrient load in its clear water state.

Conclusions

We may conclude from this study that fish manipulation in a eutrophic shallow lake can switch the lake from a turbid state (dominating by phytoplankton) to a clear water state (dominated by macrophytes). The macrophytes had a stabilizing function, acting as a sink for N and P and therefore changed the nutrient retention and cycling in the food web. However, it is unclear whether in the long-term the manipulated system will return to its initial turbid condition, or will stay in the clear water state.

Acknowledgements

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