FOOD WEB MANIPULATION IN LAKE ZWEMLUST: POSITIVE AND NEGATIVE EFFECTS DURING THE FIRST TWO YEARS

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ABSTRACT

The hypertrophic Lake Zweenlust, a small water body used as a swimming pool, was characterized by algal blooms in summer, reducing the Secchi disk transparency to less than 0.3 m. Since in The Netherlands a Secchi disk transparency of ≥ 1 m is obligatory for swimming waters, corrective measures were called for to improve the light climate of the lake. In March, 1987, as an experiment, the lake was drained by pumping out the water to facilitate fish elimination. Planktivorous and benthivorous fish species, which were predominant, were removed by seine- and electro-fishing. After the lake had refilled by seepage it was restocked by a new simple fish community comprising pike (*Esox lucius*) and rudd (*Scardinius erythrophthalmus*) only. Stacks of willow twigs (*Salix*) and macrophytes (roots of *Nuphar lutea* and 'seedlings' of *Chara globularis*) were introduced into the lake as spawning grounds and refuges for the pike against cannibalism and as shelter for the zooplankton. The effects of this food web manipulation on the light climate, phytoplankton, zooplankton, fish, macrophytes, macrofauna and on the nutrient concentrations were monitored during 1987 and 1988. In summer 1987, despite of high nutrient concentrations, the phytoplankton density was low, due to control by zooplankton, causing a Secchi disk transparency of ≥ 2.5 m, the maximum depth. Chlorophyll-a concentrations were low ($< 5 \mu\text{g Chl. l}^{-1}$), blooms of cyanobacteria did not occur and a shift from rotifers to cladocerans took place. In 1988, however, also some negative effects were noticed. Macrophytes and filamentous green algae reached a much higher biomass (50-60% cover of the lake bottom) than in 1987; some species, growing through the entire water column, interfered with the lake's recreational use. Associated with the macro-vegetation and possibly with the absence of larger cyprinids, the diet of which also comprises snails, a large scale development of the snail population, among them *Lymnaea peregra* var. *ovata* took place. This species is known to act as an intermediate host of the bird-parasitizing trematode *Trichobilharzia ocellata*, the cercariae of which cause an itching sensation at the spot of penetration of the human skin, accompanied by rash (schistosome dermatitis or swimmers' itch); in July, 1988, about 40% of the bathers complained about this itching. A positive effect of the macrophytes and filamentous green algae was the high uptake of nitrogen, resulting in a low nitrogen concentration in the lake and growth limitation of the phytoplankton population by nitrogen in the summer of 1988. In 1988 the cladocerans were abundant in April only; and unlike in 1987, in the summer of 1988 there was a shift from cladocerans to rotifers. Therefore, only in early spring (April) zooplankton grazing controlled phytoplankton growth and in summer nitrogen limitation was the major controlling factor, keeping chlorophyll-a concentrations low.

INTRODUCTION

The two main strategies to control eutrophication of fresh waters are 1. reduction of the external and internal load of nutrients (BJÖRK, 1985), and 2.

control of the internal ecological processes (BENN-DORF, 1988). In recent years, numerous studies have shown that food web manipulation (biomanipulation, strategy 2) can help restoring eutrophied lakes (ANDERSSON *et al.*, 1978; HENRIKSON *et al.*, 1980;

SHAPIRO and WRIGHT, 1984; REINERTSEN and OLSEN, 1984; CARPENTER *et al.*, 1985; EDMONDSON and ABELLA, 1988). These studies, however, were carried out neither in water bodies subjected to very high phosphorus loads nor monitored for a long period. BENNDORF (1987) and BENNDORF *et al.* (1988) stated that eutrophication control of water bodies having a high external phosphorus load seems feasible only, if the two strategies are integrated. There are, however, water bodies to which, at the present, strategy 1 cannot be applied for economic, political or technological reasons. An example of such a water body is the hypertrophic Lake Zwemlust. In this lake restorative techniques, namely sediment dredging

and application of herbicides (LE COSQUINO DE BUSSY, 1968), have been attempted in the past to reduce algal blooms, but without success. Nutrient reduction was not possible, because the lake receives nutrient-rich seepage water directly from the hypertrophic River Vecht, flowing at about 50 m from the lake. Consequently, in Lake Zwemlust strategy 2 only was applied.

In this lake, eutrophication led to a deteriorated light climate, causing a decrease of the submerged macrophytes, which formed spawning grounds and refuges against cannibalism for pike (*Esox lucius*) and shelter for the zooplankton. In shallow waters this process eventually leads to a decrease of pike

Fig. 1. Schematic map of Lake Zwemlust with sampling stations (○), arrangement of *Salix* (willow) twigs, area covered by macrophytes and depths (in cm) at different places.

and a high standing crop of planktivorous and benthivorous fish, mainly bream, *Abramis brama*, (LAMMENS, 1986; GRIMM, 1989). Abundance of planktivorous fish can cause major alterations in the zooplankton structure (DE BERNARDI and GIUSSANI, 1975; ZARET, 1980; EDMONDSON and ABELLA, 1988), which in turn may affect the phytoplankton community (ANDERSSON *et al.*, 1978; LYNCH and SHAPIRO, 1981; DE BERNARDI *et al.*, 1982; LAZZARO, 1987). By elimination of planktivorous fish the biomass of large filter-feeding zooplankton may increase, creating heavy grazing pressure on the phytoplankton (*e.g.* SHAPIRO and WRIGHT, 1984; LAMPERT, 1988). In Lake Zwemlust, as an experiment, a new fish community dominated by predatory fish was introduced in March, 1987, and the effects of this food web manipulation will be monitored for at least five years. In this paper the data collected before manipulation from May, 1986, to March, 1987, and after manipulation from April, 1987, to December, 1988, are discussed.

Lake description

Lake Zwemlust is a small (1.5 ha) and shallow (mean depth 1.5 m; maximum depth 2.5 m) lake, located in the Province of Utrecht, The Netherlands (Fig. 1). The lake is important for the surrounding community because of its intensive recreational use as an outdoor swimming pool (100-3,000 visitors daily in summer). Before the restoration water quality problems during summers were caused by blooms of cyanobacteria, especially *Microcystis aeruginosa*. The lake is replenished mainly by nutrient-rich seepage water from the River Vecht and by precipitation; it has no in- and outflows.

METHODS

Biomanipulation operations

In March, 1987, the lake was drained within four days by pumping out the water. The whole fish community, weighing *ca.* 1,000-1,500 kg and comprising about 75% *Abramis brama* (10-15 cm fork length), was removed by seine- and electro-fishing. It was assumed that fish would penetrate the 'empty lake' eventually, for example transported by birds as adhering eggs. Therefore, it was decided to create and maintain an abundant 0+ pike population. After the lake got refilled by seepage (in *ca.* 3 days), it was restocked with 1,600 artificially propagated 0+ pike (*Esox lucius*), measuring 4 cm, and 140 rudds (*Scardinius erythrophthalmus*), measuring 9-13 cm fork length. The introduced rudd had well developed

gonads. The offspring was meant to serve as food for pike. Also daphnids (*D. magna*, *D. hyalina*; wet weight *ca.* 1 kg), carried along with the fish, were brought into the lake. Furthermore, 'seedlings' of *Chara globularis* and 200 roots of *Nuphar lutea* were introduced, and 170 stacks of willow twigs were fixed to the bottom to provide refuge and spawning grounds for the pike and as shelter for the zooplankton (for details see VAN DONK *et al.*, 1988a; VAN DONK *et al.*, 1989).

Water chemistry and biology

The entire water column was sampled in one stretch with a transparent, perspex tube of 1.5 m length and 5 cm diameter. In 1986, *i.e.* prior to the biomanipulation, the lake was sampled fortnightly between May and September at one station located in the deepest part. In 1987 and 1988 the samples were taken at ten stations (see Fig. 1) and mixed. This composite sample was subsampled for the analyses of nutrients (nitrate, nitrite, ammonium and orthophosphate), total phosphate, chlorophyll-a, phytoplankton, and zooplankton. Temperature, conductivity, pH, oxygen concentration, and Secchi disk transparency were measured *in situ*. Chemical analysis of water was done according to the Dutch Standard Methods (NEN), which comply with the International Standards (ISO). The nutrients were determined by automated colorimetric methods. For chlorophyll-a an ethanol extraction method was used.

To determine zooplankton concentrations, 25 litres of lake water were filtered through 33 µm gauze. The samples were immediately preserved in 4% formaline and subsamples were counted. For counting phytoplankton 1 litre of water was fixed with lugol and the cells were allowed to settle for three days. The top 900 ml were then discarded by removing the supernatant carefully using a pipette; the remaining 100 ml were mixed and subsampled for counting by means of an inverted microscope.

During the growth season fish were caught monthly by electro-fishing, seine-fishing and with fyke nets. After measuring length and weight the fish was set free. In the winter of 1987/1988 and 1988/1989 the fish stock in the lake was estimated using mark-recapture techniques, according to the adjusted Petersen method (RICKER, 1975). The condition of rudd and pike was calculated as the ratio of the average weight of 8-10 individuals per length class of rudd (mm) or pike (cm) and the weight, according to a 'standard' for Dutch waters. This 'standard L-W relation' has been calculated from lengths and weights of 300 small rudds and 2,500 pikes sampled

in different sites and years (BAARDA and KAMPEN, 1988). For some fish the gut-contents were examined.

In 1987 and 1988 the macrofauna was sampled at four locations with a perspex tube and nets. The macrophytes were monitored 4-weekly for growth, composition and degree of bottom cover.

Bioassays

Growth limitation of the phytoplankton was studied in bioassays in June, 1987 and 1988, and August, 1988, in vitro, under the prevalent water temperatures (16–18°C) and light conditions using coolwhite fluorescent tubes (25 Watt.m⁻²; 14 h light/10 h dark). Six one-litre pyrex flasks were filled with lake water filtered through 100 µm gauze to remove most of the crustacean zooplankton. Two flasks were filled with unfiltered lake water to analyse the effect of zooplankton grazing. Four incubations were used in two replicates each, viz. blank; +phosphorus; +nitrogen; +zooplankton. Samples were taken daily and phytoplankton density (using a Coulter Counter 70 µm orifice tube) and chlorophyll-a were measured. Response to nutrient enrichment was evaluated from the exponential phase of the growth curves (VAN DONK *et al.*, 1988b). Mean growth rates ($\bar{\mu}$) with their 95% confidence intervals were

calculated by least squares linear regression analysis of log-transformed data with more than one value of Y per each value of X (SOKAL and ROHLF, 1969).

Zooplankton grazing and phytoplankton primary production

The grazing and assimilation rates of the crustacean zooplankton were measured weekly or fortnightly in the laboratory employing the ¹⁴C-tracer technique (GULATI *et al.*, 1982), and using lake seston (<33 µm) as tracer food. The biomasses of seston food (<33 µm) and of zooplankton (>150 µm) were measured by the COD technique (GOLTERMAN, 1969) with some modifications (GULATI *et al.*, 1982). The oxygen consumed was converted to carbon according to WINBERG *et al.* (1971). The expression of data in carbon units also facilitates comparison with phytoplankton primary production which was measured from 24 June 1987 onwards, using the ¹⁴C-technique (VAN LIERE *et al.*, 1986).

RESULTS

Nutrients and pH

In 1986 the phosphorus and nitrogen concentrations in Lake Zwemlust were very high (Figs. 2 and

Fig. 2. The concentrations of ortho-P (●) and total-P (○) of Lake Zwemlust before and after biomaniipulation.

Fig. 3. The concentrations of $\text{NH}_4\text{-N}$ (●) and $\text{NO}_3\text{-N}$ (○) in Lake Zwemlust before and after biomanipulation.

3) and quite similar to the values for the River Vecht (not shown), from which the lake receives most of its water by seepage. After biomanipulation the phosphate and ammonium concentrations even increased (maximum concentration in July, 1987, of PO_4 was 1.6 mg P.l^{-1} and of NH_4 1.6 mg N.l^{-1}). From the beginning of August, 1987, the concentrations of phosphate and ammonium declined. A nitrate maximum occurred in February, 1988 (0.94 mg N.l^{-1}). In the summer of 1988 phosphorus concentrations were very close to the values measured in 1986 (before biomanipulation). In contrast with the phosphorus concentrations, nitrate and ammonium concentrations declined in the summer of 1988, to near detection levels. The pH declined from its maximum of 9.5 in the summer of 1986 to 7.7 in 1987 but rose to 8.6 in 1988.

Transparency and phytoplankton

The Secchi disk transparency, which had been low (0.1–0.3 m) in the summer of 1986 and was also low after refilling of the lake, increased within four weeks after biomanipulation to 2.5 m (the maximum depth) in June/July, 1987, and remained high until February, 1988 (Fig. 4). Only in March and August, 1988, did the Secchi disk transparency decrease temporarily to lie between 0.6 and 1.0 m. The chlorophyll-a concentration followed an inverse pat-

tern of changes (Fig. 5). The high chlorophyll-a concentration of $250 \text{ } \mu\text{g l}^{-1}$ in the summer of 1986, caused by a bloom of the cyanobacterium *Microcystis aeruginosa*, corresponded to a low Secchi value of 0.2–0.3 m.

Shortly after biomanipulation (April, 1987) there was a bloom of the green alga *Pteridomonas* sp. (ca. $70 \text{ } \mu\text{g Chl.l}^{-1}$) which lasted two weeks and reduced the Secchi value to 0.5 m. The chlorophyll-a concentrations in the summer of 1987 were, however, not higher than $5 \text{ } \mu\text{g.l}^{-1}$ and only green algae (*Chlamydomonas* sp. and *Scenedesmus* sp.) and cryptophyceans were present. In 1987 no cyanobacteria were detected in routine samples. In March, 1988, the chlorophyll-a concentration increased up to $150 \text{ } \mu\text{g.l}^{-1}$ and the Secchi disk transparency decreased to 0.6 m, due to a bloom of the green alga *Ankyra* sp. After the temperature rose above 10°C and the zooplankton *Daphnia pulex* reached ca. 130 ind.l^{-1} (see Fig. 6), the bloom of *Ankyra* sp. disappeared. A second, smaller chlorophyll-a peak in August, 1988, of $35 \text{ } \mu\text{g.l}^{-1}$, accompanied by a Secchi value of 1 m, was caused by the nitrogen-fixing cyanobacteria *Anabaena flos-aquae*. Furthermore, in 1988 algal species, resistant to grazing by zooplankton, appeared. For instance, in April, 1988, *Colacium* sp., a euglenophyte, bloomed, especially adhering firmly onto and completely covering *D. pulex*. In July there

Fig. 4. Secchi disk transparency in Lake Zwemlust before and after biomaniipulation.

Fig. 5. Chlorophyll-a concentrations in Lake Zwemlust before and after biomaniipulation. The phytoplankton species dominant on some of the sampling dates are indicated.

was a small bloom of the green alga *Volvox aureus*, which formed large colonies. Both *Colacium* and *Volvox* did not affect the Secchi disk transparency.

Bioassay experiments

In June, 1987, the lowest mean net growth rates of the phytoplankton ($\bar{\mu} = 0.08 \text{ day}^{-1}$) were found in the bioassays with zooplankton (Table 1). The much higher growth rates in the blanks and in the bio-

assays with nitrogen and phosphorus enrichment did not differ significantly. These results indicate that in June, 1987, zooplankton grazing controlled phytoplankton growth.

In June and August, 1988, the lowest net growth rates were also found in the flasks in which zooplankton was not removed. However, the growth rates in the blanks and in the bioassay with phosphorus enrichment were not significantly higher. Signifi-

Table 1. The mean net growth rates (μ , day⁻¹) of the phytoplankton community in the bioassays for the different combinations of nutrients. Blank (B); added [NO₃] 0.56 mg N.l⁻¹ and [NH₄] 0.30 mg N.l⁻¹ (+N); added [PO₄] 0.32 mg P.l⁻¹ (+P); zooplankton not removed, no nutrient additions (+Zoopl.). The 95% confidence intervals are given in parentheses.

Date	μ , day ⁻¹			
	B	+N	+P	+Zoopl.
1987-06-01	0.30 ($\pm$ 0.05)	0.33 ($\pm$ 0.06)	0.30 ($\pm$ 0.06)	0.08 ($\pm$ 0.05)
1988-06-18	0.12 ($\pm$ 0.05)	0.37 ($\pm$ 0.05)	0.14 ($\pm$ 0.03)	0.04 ($\pm$ 0.06)
1988-08-26	0.21 ($\pm$ 0.10)	0.34 ($\pm$ 0.10)	0.15 ($\pm$ 0.07)	0.09 ($\pm$ 0.03)

cant stimulation of the growth rate was found only with nitrogen addition (μ = 0.37.day⁻¹ in June, 1988, and 0.34.day⁻¹ in August, 1988). Nitrate and ammonium in the lake were at that time close to detection level. This decrease in nitrogen level was probably due to its uptake by macrophytes, causing growth limitation of phytoplankton by nitrogen (pers. comm. Dr. T. Ozimek).

Zooplankton (crustacean grazing and phytoplankton primary production)

A comparison of the data of 1987 and 1988 shows that both the rotifers and crustaceans responded differently in their composition as well as in timing and magnitude of their abundance in the two years (Fig. 6) (see also GULATI, 1989). The rotifers, dominated by *Brachionus* sp., reached their maximum within four weeks after the lake got refilled. Maxima of copepod nauplii and of adult cyclopoids followed in mid May and of calanoid copepods and cladocerans in early June. The seston fraction <33 μ m, which forms the main food for the herbivore zooplankters (GULATI *et al.*, 1982), was dominated by the green alga *Pteromonas* sp., the bloom of which decreased markedly between April and early June. In this period daily grazing rates (G) on the seston food (<33 μ m) of more than 100% (121-195%) were recorded on the three consecutive occasions between 25 May and 10 June (Table 2). This was reflected in sharp decreases initially in seston and chlorophyll-a concentrations and an accompanying increase in Secchi disk transparency (see Figs. 4 and 5; Table 2).

The main grazers in order of their development were: *Bosmina longirostris*, *Daphnia hyalina*, *D. cucullata*, *D. magna* and *D. pulex*. In late summer the last two *Daphnia* species tended to concentrate in the bottom layers and littoral zone during daytime, probably because of high water clarity. An underestimation of the cladoceran abundance during sampling was confirmed in a diurnal study (pers. comm. F.J.

Slim). However, because of the large size, the *Daphnia* spp., especially *D. magna* (length 3.0-3.7 mm), together with *Eudiaptomus gracilis*, contributed chiefly to the second period of high grazing activity during 30 September - 28 October, 1987. At that time both the grazing pressure and the specific clearance rates (SCR) were exceptionally high, with SCR values between 8 and 30 l per mg zooplankton carbon per day (Table 2). These clearance rates are even higher than those recorded by GULATI (1983) in oligo-mesotrophic lakes. Zooplankton appeared to be food-limited, the food concentration dropped to 0.1 mg C.l⁻¹ (Table 2) (GULATI, 1989).

In 1988 the rotifer density maximum was half as high as in 1987, and it occurred in late July, compared with April in 1987 (Fig. 6); the copepod and cladoceran densities were much lower too. *D. pulex*, which became quite dominant already in April was highly beset with *Colacium* sp., a euglenophyte, and with stalked ciliates. Throughout the summer the zooplankton densities were much lower, and thus in sharp contrast with the species succession in 1987 (GULATI, 1989). Like in spring 1987, the grazing pressure of zooplankton in spring 1988 was also high and the peak occurred even earlier (13 April); *D. pulex*, the sole grazer, increased rather rapidly between mid March and mid April, even though the water temperature was still low, having increased from 5 to 10°C in the 4-weeks period (Table 2). Apparently, *Ankya* sp. which developed a major bloom, formed a good food for *D. pulex*, which contributed mainly to the more than two orders of magnitude increase in the community grazing (4 to 441%.d⁻¹). This increase was reflected in equally sharp and concomitant, but inverse, changes in primary production rates and seston concentrations. Subsequently, the filter-feeding zooplankton declined drastically in summer. There is some evidence from the fecundity data as well as from food quality, that the crash in zooplankton was partly related to both low food concentration and poor food quality (e.g. *Volvox aureus*). The relatively low specific

Fig. 6. The abundance of herbivorous zooplankton in Lake Zwemlust before and after biomanipulation; rotifers (A), copepods (B) and cladocerans (C). The species dominant on some of the sampling dates are indicated.

assimilation rates found in this period support this contention. Also selective predation on large zooplankton by 0+ rudd may have caused a decrease in

the crustacean abundance in summer 1988. Summarizing, in 1988 the grazing activities, but especially the zooplankton structure, differed from

those in 1987. In 1987, the crustacean zooplankton contributed mainly to algal mortality and thus to water clarity. The high water transparency in the summer of 1988 was caused, however, mainly by nutrient limitation (N) of phytoplankton, apparently due to competition with the macrovegetation.

Fish

The results of seine- and electro-fishing in March, 1987, are given in detail in VAN DONK *et al.* (1989). The total amount of fish removed, including those eliminated by the pumping, was estimated at 1200-1500 kg wet weight (ca. 70% *Abramis brama* of 10-20 cm).

In 1987 spawning of the stocked rudd was

delayed to mid July, due to low spring temperatures. Therefore, 0+ rudd, which measured only ca. 2.5 cm at the onset of the winter period, and the samples taken in March, 1988, indicated that survival in the winter had been extremely low. Because of low biomass of the young rudd and scarce submerged macrophytes in 1987, the intraspecific predation among the 0+ pike was high. The population of 0+ pike had at the end of 1987 a biomass of ca. 26 kg (ca. 300 ind.), which was far below the expected level of ca. 100 kg. Only 19% of the stocked pike survived the first year.

The abundance of 0+ pike is, however, necessary in maintaining a high predation on planktivorous fish (GRIMM, 1989). In order to obtain a 0+ pike

Table 2. Primary production, grazing and assimilation rates of the phytoplankton and crustacean zooplankton community and other relevant data of Lake Zwemlust in 1987 and 1988. S, seston food (mg C.l⁻¹); Z, zooplankton biomass (mg C.l⁻¹); PP, primary production (mg C.l⁻¹.d⁻¹); SPP, specific primary production (mg C.mg Chl⁻¹.d⁻¹); G, grazing (%.d⁻¹); SCR, specific clearance rate (l.mg C⁻¹.d⁻¹); A, assimilation (mg C.l⁻¹.d⁻¹); C, consumption (mg C.l⁻¹.d⁻¹); A/C, assimilation efficiency (%) and SDA, specific daily assimilation (A/Z in %).

Date	T°C	S	Z	PP	SPP	G	SCR	C	A	A/C	SDA
1987-05-15	13	1.91	0.62	—	—	73	1.17	1.39	0.19	14	31
05-25	18	1.28	1.16	—	—	170	1.47	2.18	0.95	44	82
06-03	18	0.66	0.87	—	—	121	1.39	0.79	0.22	28	26
06-10	17	0.69	0.56	—	—	195	3.48	1.35	0.63	47	112
06-17	17	0.66	0.48	—	—	55	1.14	0.36	0.11	29	22
06-24	17	0.62	0.32	0.35	62.8	80	2.50	0.50	0.21	43	67
07-01	21	0.70	0.66	—	—	112	1.69	0.78	0.32	40	48
07-08	24	0.75	0.34	—	—	65	1.91	0.49	0.15	31	44
07-22	21	0.68	0.32	0.07	142.7	—	—	—	—	—	—
08-05	18	0.71	0.20	0.09	142.2	—	—	—	—	—	—
08-19	21	0.52	0.22	0.07	31.8	14	0.65	0.08	0.04	51	18
09-02	20	0.63	0.30	0.20	49.0	46	1.53	0.29	0.15	53	50
09-16	18	0.45	0.28	0.03	20.0	33	1.18	0.15	0.08	54	29
09-30	14	0.25	0.28	0.04	56.7	226	8.08	0.58	0.19	33	68
10-14	11	0.27	0.15	0.01	28.7	125	8.31	0.34	0.09	25	60
10-28	10	0.10	0.16	0.02	16.0	486	30.37	0.49	—	—	—
11-11	8	0.24	0.18	0.01	4.1	22	1.24	0.05	0.02	44	11
11-25	6	0.25	0.23	—	—	24	1.04	0.06	0.02	29	9
12-22	7	—	—	0.01	12.5	22	—	—	—	—	—
1988-03-16	5	8.11	0.41	1.50	10.3	4	0.10	0.32	0.04	12	10
04-13	10	1.30	2.44	0.43	60.8	441	1.81	5.73	1.14	20	47
04-27	13	0.75	0.53	0.17	27.7	13	0.25	0.10	0.05	50	9
05-11	16	0.26	0.36	0.08	60.3	68	1.90	0.18	0.07	39	19
05-25	19	0.62	0.56	0.19	93.7	103	1.84	0.64	0.10	16	18
05-31	17	0.35	0.54	—	—	176	3.26	0.61	0.10	17	19
06-08	17	0.57	0.53	0.07	30.1	84	1.58	0.47	0.15	32	28
06-22	20	0.49	0.27	0.18	51.8	82	3.07	0.40	0.06	15	22
07-06	18	0.48	0.25	0.10	37.1	48	1.95	0.23	0.11	48	44
07-20	17	0.57	0.13	0.12	89.3	6	0.47	0.03	0.01	33	8
08-03	20	0.43	—	0.91	76.1	22	—	0.32	0.40	12	—
08-17	21	0.69	0.13	0.57	66.1	22	1.70	0.15	0.01	4	8
08-31	18	0.68	0.32	0.17	55.4	80	2.49	0.54	0.19	34	59
09-28	14	0.76	0.23	0.06	25.5	22	0.96	0.17	0.01	9	4
10-19	4	0.88	0.09	—	—	2	0.21	0.02	0.00	29	0
10-26	10	0.67	0.16	—	—	4	0.22	0.02	0.02	71	12

population of a maximum density and biomass, two management measures were taken in the beginning of 1988. (1) In January the resident pike population was reduced from about 300 to 70 individuals (ca. 6.4 kg); this is likely to minimize the chances of a succeeding weak year class of pike because of intraspecific predation (GRIMM, 1981). (2) In April, for the second time, 1600 artificially propagated 0+ pike (4-5 cm), marked by fin amputation, were introduced. This was decided nonetheless the fact that 1+ pike can produce viable offspring (GRIMM, 1984) and the 1+ pike in Lake Zwemlust had well developed gonads. Thus a strong year class was guaranteed.

The first spawning of rudd in 1988 occurred relatively late at the end of May, confronting in the beginning of 1988 the pike population, consisting of yearlings and 0+ pike, with a lack of forage fish. This and the scarce submerged macrophytes in the spring of 1988 led again, as electro-sampling indicates, to a high intraspecific predation among the pike population. In October, 1988, less 0+ pike were present than in October, 1987 (200 *versus* 300 individuals). The 0+ pike in October, 1988, were also smaller and, therefore, consequently their biomass less (16 kg in 1988 *versus* 26 kg in 1987). The length frequencies of the 0+ and 1+ pike in October, 1988, are given in Fig. 7. Fifty per cent of the 0+ pike were originally stocked in April, 1988 (fish with fin amputation), the other fifty per cent was descendant of the 0+ pike stocked in 1987. So 1+ pike were able to produce offspring and only 6% of the 0+ pike stocked in 1988 survived. In one growing season the biomass of the 1987 year class (1+ pike) increased from 6.4 to 42.3 kg, their length ranging from 36 to 49 cm and their average growth being 15 cm. The total pike biomass

Fig. 7. The length-frequency distribution of 0+ (17-31 cm) and 1+ pike (37-50 cm) in October, 1988.

was estimated at 58.7 kg. The condition of the 0+ and 1+ pike in October 1988 was good (Fig. 8).

Fig. 8. The condition factor (C) of 0+ pike and 1+ pike in October, 1988, calculated as the quotient of the average weight of 2-10 individuals per cm-class pike and the weight according to a 'standard length-weight relationship' for Dutch waters. □ = 5 October, 1988; ● = 24 November, 1988.

The rudd spawned the second time in 1988, at the end of July, when the predation pressure on the rudd by pike was low due to intraspecific predation among the latter. Two length cohorts of 0+ rudd were formed (Fig. 9). The abundance of 0+ rudd was very high in August (ca. 200,000 individuals). By October, 1988, however, the 0+ rudd were reduced to low levels. In the beginning of October the ratio small (25-32 mm)/large (32-50 mm) 0+ rudd was 1:1.5, but at the end of November this ratio changed to 1:15. By the end of November there were ca. 60,000 larger 0+ individuals, weighing about 52 kg. Due to vulnerability of the smallest 0+ rudd to handling no mark-recapture estimates are available for this fish. Based upon the data of the larger 0+ rudd and the ratios, the numbers of small rudds and their biomass at the beginning of October and the end of November were estimated at ca. 37,000 ind. (ca. 9 kg) and ca. 3,800 (ca. 0.9 kg), respectively. The condition of the 0+ rudd decreased during autumn of 1988 and was anticipated to surpass a critical point (Fig. 10). For the smallest individuals this probably had been the case already. The 0+ rudd were reduced to low levels, probably due to food shortage induced by a marked decrease in crustacean zooplankton. A shift from cladoceran zooplankton to rotifers was probably the result of both the reduction in phytoplankton as a response to N-limitation and the predation on crustacean zooplankton by 0+ rudd. The data on the gut

contents of 0+ rudd support this hypothesis. Beside 0+ rudd, 1+ rudd (8-12 cm) were incidentally caught, their average growth being 6 cm. The rudd stocked in 1987 (9-13 cm) were in the length range of 16-19 cm at the end of 1987 and 20-25 cm in 1988.

Fig. 9. The length-frequency distribution of 0+ rudd in October, 1988.

Fig. 10. The condition factor (C) of 0+ rudd in October, 1988, calculated as the quotient of the average weight of 2-10 individuals per mm-class rudd and the weight according to a 'standard length-weight relationship' for Dutch waters. □ = 5 October, 1988; ● = 24 November, 1988.

Macrophytes

Submerged macrophytes were nearly absent in 1986 and also remained scarce in 1987. Only 5% of the bottom was covered by them at the end of the season. *Chara globularis*, *Potamogeton crispus*, *P. berchtoldii*, *Elodea nuttallii* and *E. canadensis* formed the main vegetation (Table 3, Fig. 11). Fifty of the

two hundred *Nuphar lutea* roots planted in March, 1987, flowered. In August, 1987, filamentous green algae, dominated by *Hydrodictyon reticulatum* and *Enteromorpha* sp., were present only in the littoral. In summer, 1988, however, the macrophyte abundance was high (average dry weight 89 g.m⁻²), covering 50-60% of the lake bottom (Table 3). Hundred and fifty *Nuphar lutea* plants flowered and some submerged species (*P. berchtoldii*, *E. nuttallii* and filamentous green algae) became emergent, interfering with the recreational use of the lake (VAN DONK and COLLÉ, 1988).

Macrofauna

No data prior to biomanipulation are available, so only the data of some dominant macrofauna species after biomanipulation are presented. In June, 1987, the density of chironomid larvae in the sediment reached ca. 8000 chironomids.m⁻², more than 90% of these being *Chironomus plumosus*. This high chironomid density was probably caused by a decrease in predation by fish. However, in the summer of 1988 the chironomid density in June was reduced to about 500 ind.m⁻².

After biomanipulation the diversity of the macrofauna species in 1988 in Lake Zwemlust was high. In Table 4 the data of the occurrence of species at several sampling sites (habitats) on 7 Sept. 1988 are given. Samples were taken from sandy sediment (without plants), from submerged macrophytes and the bottom underneath, from helophytes and bottom, and from filamentous algae and bottom. No macrofauna was found on *Phragmites* and *Chara* (Table 4). The absence of snail-eating fish like tench and roach and the abundance of macrophytes in 1988 promoted the development of snails (*Gastropoda*) in large numbers (e.g. *Valvata piscinalis*, *Planorbis vortex*, *Bithynia leachi*, *Lymnaea peregra*). Investigation of the snails showed that 2% of the *Lymnaea peregra* var. *ovata* population was infected with larvae of the trematode *Trichobilharzia ocellata*. The adults of this flatworm live as parasites in blood vessels of water birds and snails act as intermediate hosts. Larvae released by the snails (cercariae) cause itching and rash of the human skin (schistosome dermatitis or swimmers' itch). In Lake Zwemlust about 40% of the bathers got the skin irritation in July, 1988. Despite the low percentage of infected snails, the density of *L. peregra*, especially on the macrophytes and bottom, was high enough to cause the swimmers' itch. In September, 1988, about 5x10⁵ and 15x10⁵ *L. peregra* were present on *E. nuttallii* and the bottom under the plants, respectively (pers. comm. Dr. R. Kornijow). The life cycle of *T. ocellata* is well known

Table 3. Lake bottom covered by submerged vegetation in August, 1986, 1987, and 1988. The percentage of the lake bottom covered with plants as well as the relative share of the different species is indicated.

	1986	1987	1988
I. Percentage of total bottom covered with submerged macrophytes	0	5-10	50-60
II. Relative share (%)			
<i>Chara globularis</i>	0	15	37
<i>Elodea canadensis</i>	0	5	3
<i>Elodea nuttallii</i>	0	15	20
<i>Ceratophyllum demersum</i>	0	1	19
<i>Potamogeton berchtoldii</i>	0	5	6
<i>Potamogeton crispus</i>	0	9	2
<i>Cladophora</i> sp.			
<i>Spirogyra</i> sp.			
<i>Enteromorpha</i> sp.			
<i>Hydrodictyon</i> sp.			
<i>Mougeotia</i> sp.			
<i>Oedogonium</i> sp.			
<i>Uronema</i> sp.			
<i>Zygnema</i> sp.			
} filamentous green algae			
	0	50	13

Fig. 11. Area of Lake Zwiemlust covered with submerged vegetation in August, 1987, and August, 1988.
[grid pattern] = Filamentous green algae; x = submerged macrophytes; ★ = clumps of *Elodea nuttallii*.

Table 4. Density of the macrofauna (numbers.m⁻²) at different habitats of Lake Zwemlust in August, 1988. Samples were taken from sandy sediment (without plants), helophytes (*Phragmites*) plus bottom underneath, submerged macrophytes and bottom, and filamentous algae and bottom (data obtained from Dr. Kornijow); on *Phragmites* and *Chara* no animals were encountered.

	Sand	Helophytes	Submerged macrophytes			Filamentous algae	
		bottom	bottom	<i>Elodea</i>	<i>Cerato- phyllum</i>	bottom	algae
TURBELLARIA				21			
OLIGOCHAETA							
Tubificidae	1237	636	601			177	
Naididae							
<i>Dero obtusa</i>		671					
<i>Slavina appendiculata</i>				16		35	
<i>Stylaria lacustris</i>				12	0.2		
HIRUDINEA							
<i>Erpobdella</i> sp.		106		15		35	
Cocoons of <i>Erpobdella</i> sp.							
<i>Helobdella stagnalis</i>	106		35	4		106	
<i>Glossiphonia heteroclita</i>						71	
Hirudinea n.det.							
GASTROPODA							
<i>Acroloxus lacustris</i>							
<i>Armiger crista</i>					0.7		
<i>Anisus vortex</i>		71					17
<i>Bithynia leachi</i>		141		50	1.1	71	
<i>B.tentaculata</i>							
<i>Gyraulus</i> sp.						71	46
<i>Lymnaea</i> sp.		102	33	0.1			
<i>Planorbarius corneus</i>		106		17	3	35	
<i>Planorbis planorbis</i>	18	353	35		1	35	13
<i>Valvata piscinalis</i>	656	530	565	46	1	707	
<i>Potamopyrgus jenkinsi</i>	123						
GASTROPODA n.det.							
CRUSTACEA							
<i>Asellus aquaticus</i>		141					
<i>Gammarus</i> sp.	88						
HYDRACARINA					0.3	35	
DIPTERA							
Chironomidae							
<i>Ablesmyia longistyla</i>				21	0.4		
<i>A. sp.</i>							
<i>Acricotopus lucidus</i>						267	
<i>Chironomus</i> gr. <i>plumosus</i>							
<i>Ch. gr. thummi</i>		35					
<i>Clinotanytus nervosus</i>		35					
<i>Corynoneura scutellata</i>			21				
<i>Cricotopus</i> gr. <i>silvestris</i>			26	2	141		
<i>Cryptochironomus</i> gr. <i>defectus</i>	177						
<i>Endochironomus albipennis</i>		106		350	4		
<i>Eukiefferiella bicolor</i>							
<i>Glyptotendipes pallens</i>		71					
<i>G. sp.</i>							
<i>Holotanytus</i> sp.	106	106	141				
<i>Microtendipes pedellus</i>	35	989					
<i>Parachironomus vitiosus</i>					0.3		
<i>Polypedilum</i> gr. <i>nubeculosum</i>		177					
<i>Psectrocladius</i> gr. <i>psilopterus</i>			5	4	35	9	
<i>Stictochironomus</i> gr. <i>psammophilus</i>	3409						
<i>Tanytarsus</i> gr. <i>gregarius</i>		35					
<i>T. gr. maneus</i>	5203						
Chironomidae pupae							70

(Table 4. Continued)

	Sand	Helophytes	Submerged macrophytes			Filamentous algae	
		bottom	bottom	<i>Elodea</i>	<i>Cerato- phyllum</i>	bottom	algae
Ch. n.det.		35		4			
DIPTERA (REST)							
Heleidae larvae	247		35				128
H.pupae							37
<i>Chaoborus</i> sp.			140			389	
Diptera n.det.		35					37
TRICHOPTERA							27
Hydroptilidae					8		
H.pupae		141		29	1	141	
Polycentropidae							
Trichoptera n.det.	53	35					58
HETEROPTERA		218					
EPHEMEROPTERA		35			0.3		
COLEOPTERA							
<i>Donacia</i> sp.		71					
MEGALOPTERA							
<i>Sialis lutaria</i>		282					
ZYGOPTERA		35					
Total biomass (mg wet weight.m ⁻²)	19930	51986	19553	2304	103	206029	1923

(ERASMUS, 1972; VAN DONK and COLLÉ, 1988). The etiology, epidemiology and clinical aspects of schistosoma dermatitis are described by HOFFLER (1974). More information about schistosoma dermatitis as a draw-back of food web manipulation is given by VAN DONK and COLLÉ (1988).

DISCUSSION

Positive effects

In 1987 the results in Zwemlust were comparable with those found in similar studies in which planktivorous fish were eliminated (HRBÁČEK *et al.*, 1961; ANDERSSON *et al.*, 1978; LEAH *et al.*, 1980; DE BERNARDI *et al.*, 1982; SHAPIRO and WRIGHT, 1984). Large-sized species of herbivore zooplankton (*Daphnia* spp.) became dominant, causing a decline of chlorophyll-a concentrations and algal densities and increase of transparency (VAN DONK *et al.*, 1989). We hypothesized that the decrease in algal abundance and increase in water transparency had resulted mainly from the sharp increase in the herbivore zooplankton populations in the absence of planktivorous fish. The zooplankton grazing studies and the algal bioassays support this hypothesis. The grazing pressure exerted by the crustacean zooplankton community reduced chlorophyll-a concentrations and algal abundance to low levels, despite the high

concentrations of both inorganic N and P (Figs. 2, 3, and Table 2). The net daily grazing losses of seston considerably exceeded the daily primary production of phytoplankton, thus improving water clarity. However, we have no information on the other food sources of zooplankton, *e.g.* bacteria and seston at the lake bottom which should be important. This aspect seems to be crucial in calculations of the carbon balance between phytoplankton and zooplankton (GULATI, 1989). In 1988 only in early spring (April) zooplankton grazing controlled phytoplankton growth. Subsequently, in the summer nitrogen limitation was the major controlling factor for phytoplankton. The concentrations of both nitrate and ammonium in the lake were very low, most likely due to uptake of nitrogen by the macrophytes and filamentous green-algae (pers. comm. Dr. T. Ozimek). The phosphorus concentration, however, remained high after biomanipulation. Also in other lake restoration programmes a decline in nutrient concentrations was observed after removal of planktivorous fishes (STENSON *et al.*, 1978; HENRIKSON *et al.*, 1980; SHAPIRO and WRIGHT, 1984; MEIJER *et al.*, 1989).

Negative effects

In 1988 Lake Zwemlust was still in an unstable stage. Predatory fish, which will control the planktivorous fish, has neither become dominant nor yet

stabilized. By late 1988 young rudd were reduced to low levels probably due to food shortage, induced by a marked decrease in zooplankton densities. The shift from large cladocerans, which graze mainly on phytoplankton, to mainly detritus-eating rotifers, was probably partly caused by a pronounced decrease in phytoplankton, in response to nitrogen limitation and partly by predation on cladocerans by 0+ rudd. Due to the reduced rudd population and particularly to the retarded development of aquatic vegetation the 0+ pike population remained much below the expected level. The high biomass of macrophytes and the epiphytes associated, further promoted a high abundance of snails, probably enhanced by the absence of larger individuals of cyprinids that consume also snails. Coupled with the high abundance of snails was the occurrence of schistosoma dermatitis. To reduce nuisance for swimmers introduction of snail-eating fish like roach (*Rutilus rutilus*) and macrophyte management are being considered. Unlike bream, roach does not increase the turbidity of the water by resuspension of the sediment. In most lakes restored by biomanipulation, the fish population was reduced to low but unknown levels (STENSON *et al.*, 1978; SHAPIRO and WRIGHT, 1984), as is for example the case with rotenone treatments, during which not all the fishes present necessarily have to succumb. Also no measures were taken to improve the fish community by introduction of other species and by construction or creation of new fish habitats. Moreover, these projects were not followed by long-term investigation so that the effect of food web manipulation was not examined conclusively and no data on

the development of fish populations in these waters after biomanipulation are available. LEAH *et al.* (1980) studied the effects of fish elimination by cormorants in Brundall Broad during one year only and SHAPIRO and WRIGHT (1984) followed the effect of fish removal by rotenone in Round Lake for two years. HENRIKSON *et al.* (1980) reported that the beneficial effects of fish removal lasted for at least four years, but their lake was kept without fish. According to an empirical model by McQUEEN *et al.* (1986) fish removal can have a long-term success only in oligotrophic waters. An important question related to the use of biomanipulation as a restoration technique in the hypertrophic Lake Zwemlust is the long-term effectiveness of this measure. We intend to follow the effect of the food web manipulation in Lake Zwemlust for three years more at least.

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REFERENCES

- ANDERSSON, G., H. BERGGREN, G. CRONBERG and C. GELIN, 1978. Effect of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. *Hydrobiologia*, 59: 9-15.
- BAARDA, K. and J. KAMPEN, 1988. Length-weight relationships of the main freshwater fish species in The Netherlands. Intern report OVB, Nieuwegein, The Netherlands (in Dutch).
- BENNDORF, J., 1987. Food web manipulation without nutrient control: A useful strategy in lake restoration? *Schweiz. Z. Hydrol.*, 49: 237-248.
- BENNDORF, J., 1988. Objectives and unsolved problems in ecotechnology and biomanipulation: A preface. *Limnologica* (Berlin), 19: 5-8.
- BENNDORF, J., H. SCHULTZ, A. BENNDORF, R. UNGER, E. PENZ, H. KNESCHKE, K. KOSSATZ, R. DUMKE, U. HORNIG, R. KNISPE and S. REICHEL, 1988. Food web manipulation by enhancement of piscivorous fish stocks: long-term effects in the hypertrophic Bautzen Reservoir. *Limnologica* (Berlin), 19: 97-110.
- BJÖRK, S., 1985. Lake restoration techniques. In: *Proceedings International congress 'Lakes Pollution and Recovery'*, Rome: 281-292.
- CARPENTER, S., J.F. KITCHELL and F.R. HODGSON, 1985. Cascading trophic interactions and lake productivity. *Bioscience*, 35: 634-639.
- DE BERNARDI, R. and G. GIUSSANI, 1975. Population dynamics of three cladocerans of Lago Maggiore related to the predation pressure by a planktiophagous fish. *Verh. Internat. Verein. Limnol.*, 19: 2906-2912.
- DE BERNARDI, R., G. GIUSSANI and E. LASSO PEDRETTI, 1982. Select feeding of zooplankton with special reference to blue-green algae in enclosure experiments. *Mem. Ist. Ital. Idrobiol.*, 40: 113-128.
- EDMONDSON, W.T. and S.E.B. ABELLA, 1988. Unplanned biomanipulation in Lake Washington. *Limnologica* (Berlin), 19: 73-79.
- ERASMUS, D.A., 1972. The biology of trematodes. Edward Arnold, London.
- GOLTERMAN, H.L., 1969. Methods for chemical analysis of freshwater. I.B.P. Handbook, No. 8 Blackwell Sci. Publ., Oxford.

- GRIMM, M.P., 1981. The composition of northern pike (*Esox lucius* L.) populations in four shallow waters in The Netherlands, with special reference to factors influencing O⁺ pike biomass. *Fish. Management*, 12: 61-77.
- GRIMM, M.P., 1983. Regulation of biomasses of small (<41 cm) northern pike (*Esox lucius* L.) with special reference to the contribution of individuals stocked as fingerlings (4-6 cm). *Fish Management*, 14: 115-135.
- GRIMM, M.P., 1984. Pike. In: *Biology, population dynamics and management of pike, pike-perch and bream*. Intern report OVB, Nieuwegein, The Netherlands, 87 pp. (in Dutch).
- GRIMM, M.P., 1989. Northern pike (*Esox lucius* L.) and aquatic vegetation, tools in the management of fisheries and water quality in shallow waters. *Hydrobiol. Bull.*, 23: 59-65.
- GULATI, R.D., 1983. Zooplankton and its grazing as indicators of trophic status in Dutch lakes. *Environm. Monit. Assess.*, 3: 343-354.
- GULATI, R.D., 1989. Structure and feeding activity of zooplankton community in Lake Zwemlust, in the two years after biomanipulation. *Hydrobiol. Bull.* 23: 35-48.
- GULATI, R.D., K. SIEWERTSEN and G. POSTMA, 1982. The zooplankton: its community structure, food and feeding, and role in the ecosystem of Lake Vechten. *Hydrobiologia*, 95: 127-163.
- HENRIKSON, L., H.G. NYMAN, H.G. OSCARSON and J.A. STENSON, 1980. Trophic changes without changes in the external nutrient loading. *Hydrobiologia*, 68: 257-263.
- HOEFFLER, D.F., 1974. Cercarial dermatitis, its etiology, epidemiology and clinical aspects. *Arch. Environ. Health*, 29: 225-229.
- HRBÁČEK, J., M. DVORAKOVA, V. KORINEK and L. PROCHÁZKOVÁ, 1961. Demonstration of the effect of the fish stock on the species composition of zooplankton and the intensity of the metabolism of the whole plankton association. *Verh. Internat. Verein. Limnol.*, 14: 192-195.
- LAMMENS, E.H.R.R., 1986. Interactions between fishes and structure of fish communities in Dutch shallow eutrophic lakes. Thesis of the University of Agriculture, Wageningen, 100 p.
- LAMPERT, W., 1988. The relation between zooplankton biomass and grazing: A review. *Limnologica* (Berlin), 19: 11-20.
- LAZARRO, X., 1987. A review of planktivorous fishes: Their evolution, feeding behaviours, selectivities and impacts. *Hydrobiologia*, 146: 97-167.
- LEAH, R.T., B. MOSS and D.E. FORREST, 1980. The role of predation in causing major changes in the limnology of a hyper-eutrophic lake. *Int. Revue ges. Hydrobiol.*, 65: 223-247.
- LE COSQUINO DE BUSSY, I.J., 1968. Algiciden. Onderzoek over diuron als bestrijdingsmiddel van algen in de zwemvijver 'Zwemlust', Nieuwersluis, IG-TNO report, nr. A48 (in Dutch).
- LYNCH, M. and J. SHAPIRO, 1981. Predation, enrichment and phytoplankton community structure. *Limnol. Oceanogr.*, 26: 86-102.
- MCQUEEN, D.J., J.R. POST and E.L. MILLS, 1986. Trophic relationships in freshwater pelagic ecosystems. *Can. J. Fish. Aquat. Sci.*, 43: 1571-1581.
- MEIJER, M.-L., A.J.P. RAAT and R.W. DOEF, 1989. Restoration by biomanipulation of Lake Bleiswijkse Zoom (The Netherlands): First results. *Hydrobiol. Bull.*, 23: 49-57.
- REINERTSEN, H. and Y. OLSON, 1984. Effects of fish elimination on the phytoplankton community of a eutrophic lake. *Verh. Internat. Verein. Limnol.*, 22: 649-657.
- RICKER, W.E., 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* (191): 382 pp.
- SHAPIRO, J. and D.I. WRIGHT, 1984. Lake restoration by biomanipulation: Round Lake, Minnesota, the first two years. *Freshwat. Biol.*, 14: 371-383.
- SOKAL, R.R. and F.J. ROHLF, 1969. *Biometry. The principles and practice of statistics in biological research*. W.M. Freeman and Comp., San Francisco.
- STENSON, J.A.E., T. BOHLIN, L. HENRIKSON, B.I. NILSSON, H.G. NYMAN, H.G. OSCARSON and P. LARSSON, 1978. Effects of fish removal from a small lake. *Verh. Internat. Verein. Limnol.*, 20: 794-801.
- VAN DONK, E. and C. COLLÉ, 1988. Schistosoma dermatitis, a possible complication of food-web manipulation in swimming waters (in Dutch; English summary). *H₂O*, 24: 696-699.
- VAN DONK, E., R.D. GULATI and M.P. GRIMM, 1989. Restoration by biomanipulation in a small hypertrophic lake: first-year results. *Proceedings 'Trophic relationships in inland waters'*, Tihany, Hungary (Sept. 1987), *Developments in Hydrobiology* (in press).
- VAN DONK, E., F.J. SLIM and M.P. GRIMM, 1988a. Biomanipulation as a restoration method for Lake Zwemlust, first results (in Dutch; English summary). *H₂O*, 13: 338-343.
- VAN DONK, E., A. VEEN and J. RINGELBERG, 1988b. Natural community bioassays to determine the abiotic factors that control phytoplankton growth and succession. *Freshwater Biology*, 20: 199-210.
- VAN LIERE, E., L. VAN BALLEGOOYEN, W.A. DE KLOET, K. SIEWERTSEN, P. KOUWENHOVEN and T. ALDENBERG, 1986. Primary production in the various parts of the Loosdrecht Lakes. *Hydrobiol. Bull.*, 20: 77-85.
- WINBERG, C.G. *et al.*, 1971. *Symbols, units and conversion factors of freshwater productivity*. IBP, London, 23 pp.
- ZARET, T.M., 1980. *Predation and freshwater communities*. Yale University Press, New Haven and London. 187 pp.

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