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First attempt to apply whole-lake food-web manipulation on a large scale in The Netherlands

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Key words: Biomanipulation, whole-lake experiment, lake restoration, Lake Breukeleveen, planktivore fish, *Daphnia*, predation

Abstract

Lake Breukeleveen (180 ha, mean depth 1.45 m), a compartment of the eutrophic Loosdrecht lakes system, was selected to study the effects of whole-lake foodweb manipulation on a large scale. In Lake Loosdrecht (dominated by filamentous cyanobacteria), due to water management measures taken from 1970–1984 (sewerage systems, dephosphorization) the external P load has been reduced from 1.2 g m^{-2} y^{-1} to 0.35 g m^{-2} y^{-1}. The water transparency (Secchi-depth *ca.* 30 cm), however, has not improved. The aim of the food-web manipulation in Lake Breukeleveen was not only to improve the light climate of the lake, but also to study if the successfull effects observed in small lakes (a few ha) can be upscaled. In March 1989 the standing crop of planktivorous and bentivorous fish populations was reduced by intensive fishery, from *ca.* 150 kg ha^{-1} to *ca.* 57 kg ha^{-1}. The lake was made unaccessible to fish migrating from the other lakes and it was stocked with large-sized daphnids and 0^{+} pike. However, water transparency did not increase in the following summer and autumn 1989, which is in contrast with great improvement in the light conditions previously observed in smaller lakes. The main explanations for the negative outcome in Lake Breukeleveen are: 1) the rapid increase of the planktivorous fish biomass and carnivorous cladocerans, predating on the zooplankton community; 2) suppression of the large daphnids by the high concentrations of filamentous cyanobacteria; 3) high turbidity of the lake due to resuspension of bottom material induced by wind, unlike in smaller lakes, and thus inability of submerged macrophytes to develop and to stabilize the ecosystem.

Introduction

After the successful restoration of the small, eutrophic Lake Zwemlust by food-web manipulation (Van Donk *et al.*, 1989, 1990), the Provincial Waterboard of Utrecht (The Netherlands) decided to attempt analogous restoration measures in lake Breukeleveen, a hundred times larger lake. Lake Breukeleveen, a compartment of the Loosdrecht lakes system, became highly eutrophic by external loadings of phosphorus and nitrogen. This led to serious water quality problems, especially the high densities of cyanobacteria (De Kloet *et al.*, 1984). These changes were accompanied by a decline in submerged vegetation (Best *et al.*, 1984). Water management measures were taken from 1970–1984 (sewerage systems, dephosphorization) to reduce the external total-P load to these lakes from 1.2 g P m^{-2} y^{-1} to 0.35 g P m^{-2} y^{-1} (Van Liere *et al.*, in press). Although summer averages of both total-P and chlorophyll-*a* of the Loodrechts lakes system markedly decreased from 1980–1984 (Van Liere *et al.*, 1990), this decrease did not proceed with the same rate in the years after 1984.

The aim of applying food-web manipulation measures to Lake Breukeleveen was not only to accelerate the restoration of the lake but also to study in how far effects found in a small-scale experiment, like Lake Zwemlust (Van Donk *et al.*, 1989, 1990), can be observed in larger lakes. The other compartments of Lake Loosdrecht may serve first as references and are planned to be treated later, if the results of measures on Lake Breukeleveen project are promising. The power of this approach lies in its ability to confirm that results observed in response to the initial treatment are reproducible in a second compartment. If successfull in the different lake parts, despite the prevailing limnological differences between these parts, it can add to our confidence in the manipulation approach (Frost *et al.*, 1988).

Lake description and background limnology

Lake Breukeleveen is one of the compartments of the eutrophic Loosdrecht lakes system (Fig. 1), which has been formed by excavation of peat during the 17th and 18th century (Kal *et al.*, 1984). Lake Breukeleveen is shallow (mean depth 1.45 m) with a surface area of 1.8 km^2. The seepage losses of water from the lake to a low-lying polder are replenished by inflow of water from Lake Loosdrecht, through two small waterways (Fig. 1). The water from Lake Loosdrecht is rich in P (summer average of total-P was *ca.* 100 $\mu g\,l^{-1}$; Table 1); also summer average chlorophyll-*a* exceeds 100 $\mu g\,l^{-1}$. Eutrophication led to increase in turbidity which in turn led to the disappearance of submerged macrophytes and accumulation of debris at the lake bottom. Lake Breukeleveen has the form of a square, the SW-diagonal representing also the prevailing wind direction in this area; absence of islands accentuates the windfetch effect, this contributing to resuspension of bottom-material and high degree of turbidity (Gons, 1987).

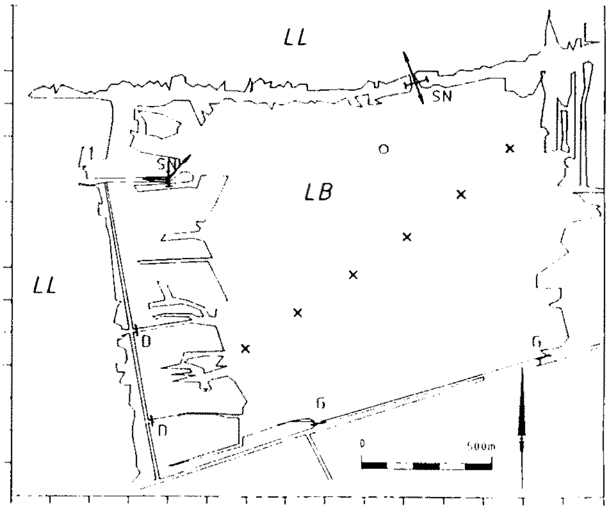

Fig. 1. Schematic map of Lake Breukeleveen (LB) with sampling stations (o = WQL (= Water Quality Loosdrecht) station; × = PWB (= Provincial Water Board station) and fish barriers (SN = sinknet; G = gate; D = dam) LL = Lake Loosdrecht.

The phytoplankton was dominated by filamentous cyanobacteria, namely *Oscillatoria redekei* and *O. limnetica* (De Kloet *et al.*, 1984) and the prochlorophyte *Prochlorothrix hollandica* (Burger-Wiersma *et al.*, 1986). The zooplankton comprised predominantly small-sized cladocerans (*Bosmina* spp., *Chydorus sphaericus*, *Daphnia cucullata*), while large-sized crustacean zooplankton was conspicuous by its absence (Gulati, 1990). Bream (*Abramis brama*) comprised 90% of lake's total fish biomass. The average growth of the fish, however, and its condition, especially the fish > 30 cm, were low (Van Densen *et al.*, 1986). Pike (*Esox lucius*) and pikeperch (*Stizostedion lucioperca*) were the main piscivore fish species. The total fish biomass was estimated at *ca.* 150 kg ha^{-1}.

Methods

Foodweb manipulation measures

The planktivorous and benthivorous fish populations were reduced in March 1989. Target standing crop levels after the reduction were set arbitrarily at 20–50 kg ha^{-1} for 1$^+$ and older fish, and 10–15 kg ha^{-1} for 0$^+$ fish. The main gear used was a beach seine (length 550 m; height 8 m; stretched mesh in wings 40 mm and in pouch 32 mm; length of hauling ropes 600 m). The pouch of the seine with two adjacent wing sections of 25 m could be replaced by a fine-meshed one (10 mm). The section of the lake fished was blocked off from the remaining lake part by blocknets (stretched mesh 14 mm; total length 3 km). Thus, section by section fishing and blocking, led the fish to concentrate in the unfished part, such that the whole lake could be seined in 5 days. This operation was repeated twice, thereafter, the fish caught were stored first and later transported in bins. The average weight per transport was recorded. The length of all fish in one out of every ten bins was measured to the nearest 0.5 mm and fish were weighed to the nearest two grams. During the second thinning fishery fish were marked at random by partial removal of the pectoral fin. The mark-recapture ratio was calculated using the data from the third seine fishery and of a last sampling by trawl, since the mark-recapture data of the seine fishery may be biased by gear avoidance (Beukema & de Vos, 1974; Buck & Thoits, 1965). About 93 kg ha^{-1} of the original standing crop of *ca.* 150 kg ha^{-1}, were removed; bream comprised the bulk (*ca.* 89 kg ha^{-1}) of the total fish removed.

Sink nets were installed in the two waterways which connect Lake Breukeleveen with Lake Loosdrecht, to prevent fish immigration (Fig. 1). Infra-red sensors automatically lowered the nets to let boats pass. In the three remaining small connections with other waterways, dams and gates were built. The lake was restocked with 0$^+$ pike (400 ind. ha^{-1}; *ca.* 2–3 cm) and large-sized daphnids (*ca.* 12 ind. m^{-3}; *D. hyalina* and *D. pulex*).

Water chemistry and biology

Before and after the manipulation, the lake was sampled 4-weekly at one station (WQL station in Fig. 1). The techniques of sampling and monitoring lake's limnology are outlined in different publications in Loogman & Van Liere (1986). In 1989, besides the 4-weekly monitoring, the lake was also sampled fortnightly at six stations (PWB stations in Fig. 1) to study spatial heterogeneity; for procedures used see Van Donk *et al.* (1989). The spatial samples are pooled for description of results in this paper.

The development of the fish stock was monitored during the growing season. In June and July 0$^+$ fish were sampled by a small trawl with a fixed frame (0.8 × 2.2 m; stretched mesh size 4 mm). Per sampling 20 hauls of *ca.* 3 min each were made. In mid July and September the fish population was sampled using the large trawl mentioned earlier. The efficiency of the small trawl was calibrated using the data of a simultaneous sampling effort with the large trawl (5 hauls of 10 min). The gear efficiency of the large trawl was calculated using the data from the sampling in January and the population estimates based on the results of the reduction fishery in March was about 90% for fish up to 26 cm, and about 70% for larger individuals. The efficiency of the small trawl for fry was 45%.

Nutrient enrichment experiments (bioassays), zooplankton grazing (^{14}C-tracer technique) and primary production rates were measured to assess the factors limiting the growth of the phytoplankton and to quantify the role of zooplankton grazing. These methods are outlined in Van Donk *et al.* (1990).

Results

Nutrients, phytoplankton and bioassays

The mean concentrations of parameters during the growth season (April–September), indicating the trophic state of Lake Loosdrecht and Lake Breukeleveen (Table 1), do not indicate any sig-

Table 1. Mean concentrations of parameters during the growth season (April–September), indicating the trophic state of Lake Breukeleveen and Lake Loosdrecht.

Year	Lake Breukeleveen			Lake Loosdrecht		
	Total-P ($\mu g\ l^{-1}$)	Chlorophyll-*a* ($\mu g\ l^{-1}$)	Suspended matter (mg DW l^{-1})	Total-P (mg l^{-1})	Chlorophyll-*a* ($\mu g\ l^{-1}$)	Suspended matter (mg DW l^{-1})
1985	110	112	37	113	125	31
1986	105	126	44	111	155	42
1987	93	127	37	85	120	30
1988	107	113	37	96	116	33
1989	106	91	35	102	119	35

nificant changes in Lake Breukeleveen in 1989; this holds true also for Lake Loosdrecht in general. However in Lake Breukeleveen the chlorophyll-*a* concentration in 1989 was lower than in Lake Loosdrecht. Nevertheless, it is premature to say that this difference is due to the biomanipulation measure, since such differences have been also observed earlier in the Loosdrecht lakes system (Van Liere *et al.*, in press). Secchi disc transparency ranged between 30 and 40 cm, indicating no change. Also phytoplankton composition and abundance in 1989 did not change significantly, compared with preceding years in the lake itself as well as in Lake Loosdrecht. In the summer of 1989 *Oscillatoria* species (*O. redekei* and *O. limnetica*) and *P. hollandica* were still predominant with a mean concentration of $2.3\ 10^5$ filaments ml^{-1} in Lake Breukeleveen and $2.4\ 10^5$ fil. ml^{-1} in Lake Loosdrecht (Boesewinkel-de Bruijn, pers. comm.); this is 2–3 fold higher than at the start of the experiment in March 1989.

The outcome of the bioassays before manipulation (July 1988) and after manipulation (July 1989) did not significantly differ (Table 2). The net growth rate of the phytoplankton community was very low in all combinations ($\mu < 0.05\ d^{-1}$) and there were no significant differences between the bioassays performed on one date. According to the assays the phytoplankton in Lake Breukeleveen was not limited by nutrients before or after the food-web manipulation. Mortality induced by zooplankton grazing did not seem to be of any importance. Light was the most probable growth controlling factor of the phytoplankton during the summer, self-shading being high.

Zooplankton and crustacean grazing

The crustacean zooplankton in 1989, like in the preceding years (Gulati, 1990), i.e. period before

Table 2. The mean net growth rates ($\bar{\mu}$ day^{-1}) of the phytoplankton community of Lake Breukeleveen in the bioassays for the different combinations. Blank, zooplankton removed [B]; zooplankton not removed, no nutrient additions [+Zoopl]; (NO_3) added, 0.56 mg N l^{-1} and (NH_4), 0.30 mg N l^{-1} [+N]; (PO_4) added, 0.32 mg P l^{-1} [+P]; addition of complete freshwater medium [Total]. The 95% confidence intervals are given in parentheses.

Date		$\bar{\mu}$ day^{-1}				
	Watertemp. (°C)	B	+N	+P	+Zoopl.	Total
1988–07–12	18	0.01 (0.02)	0.02 (0.01)	0.03 (0.02)	0.02 (0.02)	0.04 (0.03)
1989–07–28	22	0.02 (0.03)	0.03 (0.02)	0.02 (0.03)	0.05 (0.03)	0.05 (0.01)

biomanipulation, was characterized by the presence of: 1) cyclopoid copepods and their nauplii, which fluctuated around 500 ind. l^{-1} during spring and summer, and 2) cladocerans (mainly *Bosmina longirostris* and *B. coregoni* and *Chydorus sphaericus*), which dominated in May with a peak of 1500 ind. l^{-1} (Fig. 2). *Daphnia cucullata*, which fluctuated between 10 and 20 ind. l^{-1} in the initial few weeks after biomanipulation, increased markedly up to mid June (Fig. 3), declined subsequently and remained sparse during rest of the year. The *Daphnia* maximum of 270 ind. l^{-1} this year is the highest recorded for daphnids since 1981, from which year onwards the lake has been regularly monitored (unpublished data of R. D. Gulati, see also Gulati, 1990). The stocked, large-sized daphnids were only occasionally encountered in the samples (< 5 ind. l^{-1}). After fish removal, *Leptodora kindtii* a carnivorous cladoceran increased, with *ca.* 10 ind. l^{-1} at the end of May. Rotifers, like in the years 1981–88, formed the dominant micro-zooplankton in the open water. *Anuraeopsis fissa*, the smallest of all rotifers in Lake Loosdrecht, including Lake Breukeleveen, contributed *ca.* 90% of total rotifer density on 28 June and about two-thirds of the annual average total rotifer density (5383 ± 6334 ind. l^{-1}).

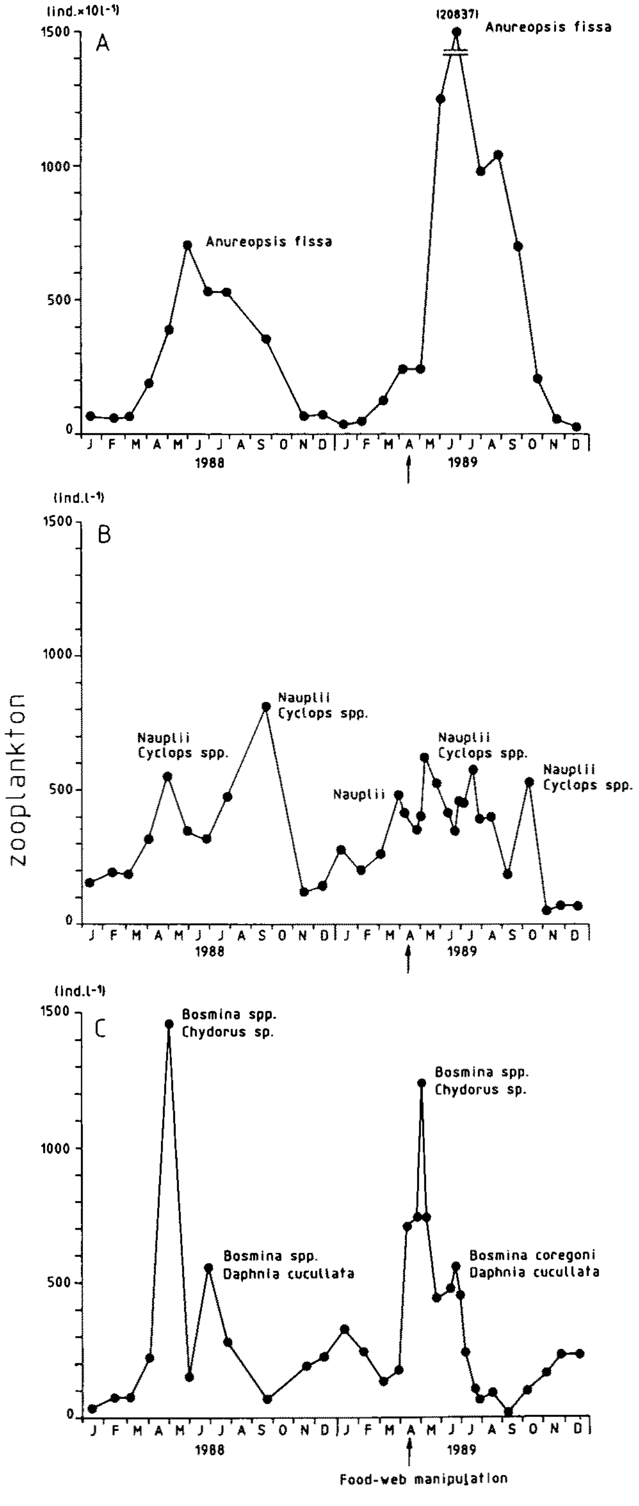

Fig. 2. The abundance of herbivorous zooplankton in Lake Breukeleveen before and after food-web manipulation; rotifers (A); copepods (B) and cladocerans (C). The species dominant on some of the sampling dates are indicated.

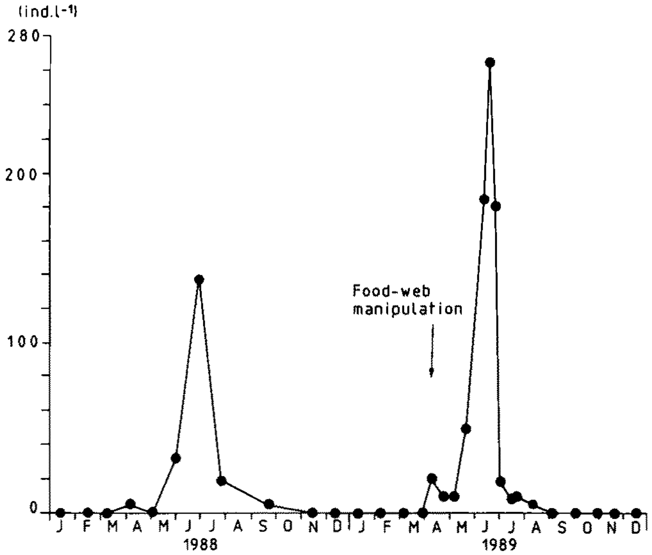

Fig. 3. The abundance of the cladoceran *Daphnia cucullata* in Lake Breukeleveen in the year before (1988) and after (1989) the food-web manipulation.

B. coregoni, the only cladoceran which was encountered in all samples from 5 April to 13 December 1989, had the highest fecundity in spring. The percentage of adult females decreased from >90% in April–May to zero% in August. A similar pattern was observed for the egg-bearing population, i.e. a fecundity minimum in mid summer when *Bosmina* population of 50 ind. l^{-1} was comprised virtually of juveniles only, which had mean annual size minimum of 0.29 mm; the mean population length in summer was only one-half of the mean length in April. Subsequently in late summer/autumn, even though the mean clutch size of 1.3 eggs per egg-bearing female was similar to the size in spring, the minimum, maximum and mean lengths were all relatively lower, i.e. the animals appeared to mature at a shorter length than in spring. For *D. cucullata* the percentage of adult females in the total population was much lower than for *Bosmina* sp., decreasing from 60% at the end of May to 42% at the end of June. Also the daphnid clutch size decreased in mid summer, like in *Bosmina* sp. The decrease, however, coincided with a three-fold increase in population density (Fig. 2). In the end of July the daphnid population decreased to 10 ind. l^{-1} and the clutch size decreased further, despite no observable changes in mean population length or adult length compared with May.

The mean daily grazing rate by curstacean zooplankton in Lake Breukeleveen of 13.6 ± 16.2% d^{-1} in 1989 (Table 3) was somewhat higher than rates measured in this lake, as well as Lake Loosdrecht, in the years 1982–1984 for which years grazing data are available (Gulati, 1984). However, zooplankton grazing was important only in spring and early summer (5 April–28 June) when the grazing rates based on seston food fraction <33 μm (see Table 3) varied between 10 and 48% d^{-1}. Especially in May the food daily ingested by zooplankton was high; it equalled between one-quarter and one-half of the seston (<33 μm) standing crop. In this period of relatively high grazing rates the densities of filter-feeding crustaceans, particularly *B. coregoni*, *Chydorus sphaericus* and *D. cucullata*, were also high. In late May all these species, but especially the *Daphnia* sp., mainly contributed to the annual grazing maximum of 48% d^{-1}. By the end of June, the zooplankton grazing pressure had decreased to about one-fourth the level in late May i.e. to about 13% d^{-1}, even though the filter-feeders densities had only halved between late May and late June. This apparent discrepancy between the decrease in grazing rates and the grazers' density is related to a decrease in average size per individual of the main grazer species, viz. *D. cucullata* and *B. coregoni*, as well as a decrease of *ca.* 25% in zooplankton community biomass in June compared with its biomass early in May.

Table 3. Primary production, grazing and assimilation rates of the phytoplankton and crustacean zooplankton community and other relevant data of Lake Breukeleveen in 1989. 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}) and SDA, specific daily assimilation (A/Z in %). (– experiment failed).

Date	T °C	S(<30 μ/30–150 μ)		Z(>150 μ)	PP	SPP	G	SCR	C	A	SDA
89–05–04	5.8	11.5	0.6	0.68	0.32	3.9	9.9	0.15	1.14	0.48	71
03–05	15.2	8.1	1.8	0.59	0.48	8.1	26.7	0.45	2.16	0.31	52
30–05	16.4	8.1	2.7	1.32	0.95	8.8	47.9	0.36	3.87	1.24	94
28–06	19.3	9.0	1.0	0.41	1.01	11.9	12.8	0.31	1.16	0.42	102
26–07	21.6	11.7	2.0	0.33	0.55	6.2	2.1	0.06	0.25	0.20	61
23–08	21.0	9.7	3.1	0.15	0.59	6.2	–	–	–	–	–
20–09	17.8	10.3	–	0.14	0.54	4.5	–	–	–	–	–
18–10	11.5	8.0	0.9	0.14	0.30	4.1	3.0	0.21	0.24	0.07	52
15–11	6.5	7.9	1.3	0.23	0.26	3.0	4.7	0.20	0.37	0.18	77
13–12	2.4	5.1	0.8	0.16	0.07	1.5	1.1	0.07	0.06	0.02	11

Mean specific clearance rate of 0.23 ± 0.14 l d^{-1} mg^{-1} zooplankton carbon during 1989 is also comparable with the mean rates in the years 1982–1984 (Gulati, 1984) in Lake Loosdrecht in general. Similarly assimilation efficiencies of the food ingested corresponded to the earlier data on this lake. In mid summer (July–August) an increase in seston, especially of the size fraction 33–150 μm, was accompanied by a decrease in zooplankton biomass, filter-feeders densities and grazing pressure to low levels (Table 3).

Fish

The total fish biomass was reduced in March 1989 to about one-third after the thinning operation, i.e. from 150 to 57 kg ha^{-1}. The biomass estimates of the fish removed per species and per length class, and of the fish remaining in the lake, as well as total fish before the thinning operations, are presented in Table 4. The results of the monitoring fishery with the large trawl after the manipulation are presented in Table 5; for estimates of 0^+ fish see Table 6. Within six months after manipulation the fish biomass increased again to values as high as before the measures (Table 5). Assuming that no mortality occurred individual growth rate explained an increase of 23 kg in bream biomass and of 3 kg roach biomass per ha. The observed increases, however, are about 4 and 5 times higher (*ca.* 86 and *ca.* 17 kg ha^{-1}) respectively, indicating immigration, especially bream of 15–25 cm from the other compartments of the lake. The numbers of 0^+ cyprinids remained fairly stable from June to September, those of the pikeperch (*Stizostedion lucioperca*), perch (*Perca fluviatilis*), ruffe (*Gymno-*

Table 4. Estimates of fish biomass (kg ha^{-1}) in Lake Breukeleveen; I original population; II fish removed; and III fish population remaining (dash represents no estimates). Others include Perch, Smelt, Ruffe and Carp.

		I		II	III	
	Size	Min	Max	Mean	Min	Max
Bream	< 10 cm	3.0	3.6	0.7	2.3	2.9
	10–14	15.6	17.1	12.3	3.3	4.8
	15–25	47.6	52.7	38.1	9.5	14.6
	> 25 cm	52.7	54.9	37.5	15.2	17.4
	total	118.9	128.3	88.6	30.3	39.7
					Mean	
Roach	< 10 cm	0.4	0.5	0.1	0.4	
	10–20	5.1	6.2	0.8	4.8	
	> 20 cm	0.3	0.3	0.1	0.2	
	total	5.8	7.0	1.0	5.4	
Pikeperch	0–45 cm	2.3	2.3	0.0	2.3	
	> 45 cm	6.9	6.9	0.3	6.6	
	total	9.2	9.2	0.3	8.9	
White bream	< 20 cm	2.2	2.6	0.7	1.7	
	≥ 20 cm	–	–	–	–	
	total	2.2	2.6	0.7	1.7	
Pike	< 20 cm	–	–	–	–	
	20–65 cm	2.4	2.4	1.1	1.3	
	> 65 cm	4.4	4.4	0.2	4.2	
	total	6.8	6.8	1.3	5.5	
Others	total	1.5	1.7	1.5	0.0	
General total		144.5	155.7	93.4	57.4	

Table 5. Estimates of the fish population (kg ha^{-1}) in 1989 in Lake Breukeleveen after food-web manipulation, based on the trawl fishery. (dash represents no estimates). Others include Perch, Smelt and Carp.

		July		September	
		Min	Max	Min	Max
Bream	0^+	7.0	8.7	17.4	21.8
	< 10 cm	3.5	4.4	2.1	2.7
	10–14	6.3	7.9	9.1	11.3
	15–25	23.7	29.6	46.4	58.0
	> 25 cm	8.5	11.3	31.9	42.5
	total	49.0	61.9	106.9	136.3
Roach	0^+	4.5	5.6	9,0	11.3
	< 10 cm	0.8	1.1	1.1	1.3
	10–20	3.0	3.7	9.8	12.2
	> 20 cm	–	–	–	–
	total	8.3	10.4	19.9	24.8
Pikeperch	0^+	0.8	1.0	0.1	0.1
	0 ± 45 cm	0.7	0.9	2.1	2.6
	> 45 cm	–	–	14.3	19.1
	total	1.5	1.9	16.5	21.8
White bream	0^+	–	–	–	–
	< 20 cm	1.0	1.2	3.6	4.5
	≥ 20 cm	–	–	0.3	0.4
	total	1.0	1.2	3.9	4.9
Pike	0^+	–	–	–	–
	< 20 cm	–	–	0.0	0.0
	20–65 cm	0.3	0.4	1.8	2.4
	> 65 cm	–	–	–	–
	total	0.3	0.4	1.8	2.4
Others	total	7.7	9.9	7.7	9.5
General Total		67.9	85.6	156.7	199.7

cephalus cernua) and smelt (*Osmerus eperlanus*) declined markedly between June and July (Table 6). The total biomass of the 0^+ fish (25–41 kg ha^{-1}) remained rather constant.

Macrophytes

In 1989 only a few submerged species were recorded, most possessed floating leaves. *Nuphar lutea* and *Nymphaea alba* were quite common in the eastern and western parts of the lake. *Nymphoides peltata* was found in the southwest and in the northwest corners of the lake and the nymphoid-water-form of *Polygonum amphibium* on the eastern coast. Also very small patches of *Potamogeton lucens* and *Stratiotes aloides* were encountered. Earlier investigations (Leentvaar & Mörzer Bruijns, 1962) indicate that macrophytic vegetation changed markedly since 1942, when almost the entire bottom of the lake was covered with characeans. By 1961 the characeans had disappeared and there was an abundant vegetation of *Potamogeton lucens, P. perfoliates, Nymphaea alba, Ceratophyllum demersum* and *Hottonia palustris*.

Table 6. The estimated numbers (I) (ind. ha^{-1}) and biomasses (II) (g ha^{-1}) of 0^+ fish in Lake Breukeleveen in 1989 after the food-web manipulation. A = roach, B = bream, C = pikeperch, D = perch, E = smelt, F = ruffe.

		A	B	C	D	E	F	Total
June	I	4509	10975	22789	20628	10808	589	70719
	II	1242	3184	8253	14727	5424	157	32988
July	I	6383	10608	2092	2110	6326	2581	30109
	II	6288	8561	1491	2400	5647	3174	27561
Sept.	I	6672	9934	120	774	3838	338	21678
	II	10178	19612	108	1182	5320	548	36949

Discussion

The application of food-web manipulation in Lake Breukeleveen in March 1989 did not improve the underwater light climate in the ensuing summer and autumn periods. This in contrast with the results found for the small lake Zwemlust, in which lake despite the four times higher N and P loads, zooplankton grazing increased and controlled the phytoplankton abundance already within two months after fish removal (Van Donk *et al.*, 1989, 1990). In Lake Breukeleveen there was also no change in the mean summer chlorophyll-*a* concentration (*ca.* 90 μg l^{-1}), whereas in Lake Zwemlust chlorophyll-*a* concentrations decreased from 250 μg l^{-1} < 5 μg l^{-1}. After the fish removal both lakes were stocked with large-bodied daphnids in such numbers that the starting concentration in the two lakes were comparable (*ca.* 0.012 ind. l^{-1}). In Lake Zwemlust these stocked daphnids increased to relatively high concentrations within 10 weeks (*D. hyalina ca.* 90 ind. l^{-1}, *D. magna ca.* 30 ind. l^{-1}: Gulati, 1989). In Lake Breukeleveen, however, large-bodied daphnids were extremely sparse (< 1 or 2 ind. l^{-1}) only occasionally found in the sampels during the whole summer and autumn.

Several possible explanations can be given for this striking difference in the outcome in the two lakes. Low population density of large-bodied zooplankton are frequently attributed to predation by 0^+ fish (Gliwicz & Pijanowska, 1989). In contrast to Lake Zwemlust, in Lake Breukeleveen the standing crop of planktivorous fish was only partially removed. Moreover, the remaining biomass (*ca.* 57 kg ha^{-1} of planktivorous fish, Table 4) increased rapidly after the manipulation and reached values as high as before within 6 months (*ca.* 150 kg ha^{-1}, Table 5). In June, i.e. 3 months after the manipulation, the biomass of 0^+ fish was estimated at *ca.* 33 kg ha^{-1} (Table 6). So, the continuous absence of larger zooplankton may well have been due to fish predation. The increase of the fish biomass due to immigration of fish from adjacent waters, probably occurred after mid July, when one of the gates stopped functioning, due to vandalism. Hence this immigration is considered to be unimportant in the failure to create a cascading top-down-effect.

The densities of the invertebrate predator *Leptodora kindtii* of 10 ind. l^{-1} are the higehst so far known for Lake Loosdrecht (see e.g. Gulati, 1990) and were perhaps caused by initial fish reduction followed by mild spring temperatures. So also predation by this carnivorous crustacean may have had impact on the *Daphnia* population dynamics (Karabin, 1974). *Leptodora* of 4–5 mm length consume about 10 prey ind.$^{-1}$ day^{-1} at 10 °C (Mordukhai-Bottovskaya, 1958).

Besides, filtering rates of large-sized cladocerans especially *Daphnia* spp. may be depressed due to abundance of filamentous cyanobacteria (e.g. Gliwicz, 1977; Edmondson & Litt, 1982; Richman & Dodson, 1983). Filaments cause serious disturbance of the filtering process in *Daphnia*, which is forced to clean its food groove

(Burns, 1969; Gliwicz, 1980). This vulnerability to interference appears to be size-specific, with cladocerans of greater body size more severely affected (Gliwicz, 1977, 1990; Richman & Dodson, 1983; Threlkeld, 1985). In Lake Breukeleveen only the small-sized *D. cucullata* increased in numbers after the manipulation (end of May 270 ind.l^{-1}, Fig. 3), but it declined again in mid June; its small clutch size indicate a bad food condition in the summer. The zooplankton grazing pressure in 1989 did not differ from the rates already known for this lake (Table 3, Gulati, 1984) except in end May when the rates were invariably high. Also the specific clearance rates (SCR: Table 3) support the idea that the lake has not changed since 1984. The concentration of filamentous cyanobacteria was already high (100000 fil ml^{-1}) at the start of the manipulation in March 1989, probably due to the relative high temperatures in the proceding winter. These concentrations are higher than those (80000 fil ml^{-1}) shown by Dawidowcz *et al.* (1988) to be critical for *D. magna*. Most probably the large-bodied *Daphnia* spp. were not able to establish due to the high concentration of filamentous cyanobacteria from the beginning of the manipulation onwards, while *D. cucullata* did not have such a disadvantage during the spring (Gliwicz, 1990). On the other hand, in Lake Zwemlust, the phytoplankton population consisted at the start of the food-web experiment of small colonies of *Microcystis aeruginosa*, which are readily ingested by large-bodied daphnids (Thompson *et al.*, 1982). The difference in phytoplankton composition of both lakes perhaps influenced the outcome of the manipulation.

A third possible factor contributing to the ineffectiveness of the manipulation measures in Lake Breukeleveen is the inability of macrophytes to establish because of the low transparency of the lake due to resuspension of bottom material induced by wind. Thus, submerged macrophytes could not grow, spread and stabilize the ecosystem, like they did in Lake Zwemlust. Only near the shore and in the bays, where turbulence was less, the macrophytes were able to develop.

Concluding, in Lake Breukeleveen food-web manipulation by reducing the planktivorous fish population from 150 kg ha^{-1} to 57 kg ha^{-1} did not cause an increase in water transparency nor a change in the lake's ecosystem from one dominated by cyanobacteria, rotifers and planktivorous fish to one characterized by submerged macrophytes and piscivorous fish. Application of additional measures is necessary to restore this lake, especially aimed at lowering the concentrations of cyanobacteria filaments to levels not inhibiting filtering mechanisms of large-bodied zooplankton. One may think of a further reduction of the P load to the lake and of applying coagulants to reduce suspended particles. Also the application of species specific-phytoplankton parasites, so as to increase phytoplankton mortality as demonstrated for diatoms (Van Donk & Ringelberg, 1983) and cyanobacteria (Canter, 1972), may be useful in future. Resuspension of bottom material by wind can be reduced by dredging or building islands and dams. In 1990 *in situ* experiments will be carried out to study the effect of different combinations of measures.

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