

Cascading Trophic Interactions from Fish to Bacteria and Nutrients after Reduced Sewage Loading: An 18-Year Study of a Shallow Hypertrophic Lake

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ABSTRACT

The effects of major reductions in organic matter, total phosphorus (TP), and total nitrogen (TN) loading on the chemical environment, trophic structure, and dynamics of the hypertrophic, shallow Lake Søbygård were followed for 18 years. After the reduction in organic matter loading in 1976, the lake initially shifted from a summer clear-water state, most likely reflecting high grazing pressure by large *Daphnia* species, to a turbid state with extremely high summer mean chlorophyll *a* (up to 1400 µg L⁻¹), high pH (up to 10.2), and low zooplankton grazing. Subsequently, a more variable state with periodically high grazing rates on phytoplankton and bacteria was established. Changes in zooplankton abundance and grazing could be attributed to variations in cyprinid abundance due to a fish kill (probably as a consequence of oxygen depletion) and pH-induced variations in fish recruitment and fry survival. The results suggest strong cascading effects of fish on the abundance and size

of zooplankton and phytoplankton and on phytoplankton production. A comparatively weak cascading effect on ciliates and bacterioplankton is suggested. Due to high internal loading, only minor changes were observed in lake-water TP after a reduction in external TP loading of approximately 80% in 1982; net retention of TP was still negative 13 years after the loading reduction, despite a short hydraulic retention time of a few weeks. TN, however, decreased proportionally to the TN-loading reduction in 1987, suggesting a fast N equilibration. Only minor improvement in the environmental state of the lake has been observed. We suggest that another decade will be required before the lake is in equilibrium with present external P loading.

Key words: recovery; top-down control; bottom-up control; loading reduction; internal loading; fish; zooplankton; phytoplankton; ciliates; bacteria; size distribution; production.

INTRODUCTION

Eutrophication has resulted in a deterioration of lake ecosystems worldwide (OECD 1982; Sas 1989; Kristensen and Hansen 1994). In many countries,

attempts to restore lakes by reducing external nutrient loading (Sas 1989) have in some cases resulted in a new equilibrium within a few years (Kristensen and others 1990). Many lakes, however, are resistant to recovery (Ryding 1981; Cullen and Forsberg 1988; Marsden 1989; Sas 1989; Jeppesen and others 1991; Cooke and others 1993; Van der Molen and Boers 1994). Delayed response to restoration measures is not restricted to lakes with a long hydraulic

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retention time. Some shallow lakes with a water renewal time of only a few weeks may respond in 10–15 years (Jeppesen and others 1991). Apart from dilution (renewal of the water mass), delayed recovery may be attributed to phosphorus (P) release from the accumulated sediment pool (internal loading). Internal P loading seems to be an important factor in the long term (Ryding 1981), while internal nitrogen (N) loading following N-loading reduction appears important only in the short term (Jensen and others 1992).

Resistance may also be related to a delay in biological changes, for example, in the fish community or in the appearance of submerged macrophytes (Gulati and others 1990; Moss 1990; Lauridsen and others 1993). Biomanipulation experiments show that active combating of biological resistance will often reduce internal nutrient loading (Shapiro and Wright 1984; Jeppesen and others 1998), suggesting that chemical and biological resilience are highly interlinked (Boers and others 1991; Carpenter and others 1992). Recent studies suggest that the structuring role of fish in the entire pelagic ecosystem is most significant in eutrophic lakes (Leibold 1989; Sarnelle 1992) and generally more so in shallow lakes (Jeppesen and others 1997b). The duration, course, and outcome of the transient phase in shallow, eutrophic lakes after an external nutrient-loading reduction are particularly affected. The majority of detailed lake-recovery studies following nutrient-loading reduction describe the early, short-term effects; only a few cover more than a decade [for example, see Sas (1989), Edmonson (1985), Cullen and Forsberg (1988), Welch and Cooke (1995), Lathrop and others (1996) and Hosper (1997)]. To our knowledge, no long-term recovery studies have investigated the entire pelagic, biological community from bacteria to fish in combination with nutrient dynamics.

We followed the recovery phase of shallow hypertrophic Lake Søbygård for 18 years and more intensively for the past 12 years. The study consisted of N and P mass balances (Jensen and others 1992; Søndergaard and others 1993), internal P loading (Søndergaard and others 1990, 1993), and changes in pelagic trophic structure from bacteria to fish (Jeppesen and others 1990b, 1990c, 1992, 1996, 1997a; Hansen and Jeppesen 1992; Mortensen and others unpublished data). Phytoplankton and bacterioplankton production and zooplankton grazing were also measured (Jeppesen and others 1996, 1997a). In this report, we present an analysis of data from the entire study period, with special emphasis on biotic changes in the pelagial. We demonstrate how profoundly the recovery process in shallow

hypertrophic lakes may be affected by perturbations in the fish community, mediated by both external factors and internal feedback mechanisms.

STUDY AREA

The study was conducted in Lake Søbygård, a small (0.39 km²) shallow (mean depth, 1.0 m; and maximum depth, 1.9 m) lake in Jutland, Denmark. The hydraulic retention time is short, with an annual mean of 18–27 days and a summer mean of 23–34 days. The lake catchment area is 12 km², consisting of grassland, areas under intense agricultural cultivation, and forest. The lake shoreline is forested, except to the west, where it is exposed to the prevailing westerly wind. Emergent and floating-leaved macrophytes are sparsely developed, and submerged vegetation is absent.

The lake receives from 80% to 90% of its water from an inlet that also receives sewage effluent from a small town, while iron-rich groundwater represents approximately 10% of the water input. The lake received large amounts of primary treated sewage water during the 1960s and early 1970s. In 1976, biological treatment was initiated at the sewage plant, and this led to a threefold to tenfold reduction in organic matter loading to the lake. In 1982, P stripping was introduced at the plant and, in 1987, external N-loading was reduced by closing down a local slaughterhouse.

MATERIALS AND METHODS

Chemical Variables

Water samples were collected fortnightly or more often (between 1000 and 1200 h) with a Patalas sampler at a midlake station at 0.5-m and 1.5-m depth. Mixed total P (TP) was determined as molybdate-reactive P (Murphy and Riley 1962) after persulfate digestion (Koroleff 1970). Total N (TN) was determined as nitrites + nitrate after potassium persulfate digestion (Solórzano and Sharp 1980). Nitrites and nitrate were determined as nitrite on a Tecator 5012 flow-injection analyzer supplied with a copper-cadmium reductor column. Chlorophyll *a* was determined spectrophotometrically after ethanol extraction [according to the method described by Jespersen and Christoffersen (1987)], except for 1978–81, when acetone extraction was used. Because acetone extraction of chlorophyll *a* in green algae is inefficient, chlorophyll *a* before 1982 was most likely underestimated.

Mass Balances

The study of Lake Søbygård was initiated in 1978 and a more intensive program began in 1984. To

estimate N and P loading and retention, water was sampled manually in the main inlet and in the outlet in 1978 and in 1981 and with an automatic sampler from 1984 to 1995. In 1978 and in 1981, discrete samples were taken monthly in the inlet and outlet. Beginning in 1984, 3–4 samples were taken during each 24-h period. Before analysis, samples were pooled to represent either a 1-day or 7-day average. Additional water samples were taken 2–8 times in 1985 from other small streams entering the lake. Discharge (Q) of the lake inlet was measured 46 times during the study period. In the lake outlet, discharge was calculated from automatically recorded data of water level (H) by using a derived relationship between H and Q. In the small spring-fed streams along the lake shore, discharges were also measured 2–8 times during 1985. These sources accounted for approximately 10% of the total water input to the lake throughout the season. Daily values of Q inlet could therefore be calculated as Q-outlet minus Q-springs. Daily total N and P concentrations were calculated by linear interpolation of observed values. N and P transport in the main inlet, in the outlet, and in the springs entering the lake was calculated by multiplying daily water discharge values with interpolated daily N and P concentrations. N and P precipitation on the lake surface was considered to be constant during the investigation period ($5 \text{ mg N m}^{-2} \text{ d}^{-1}$ and $0.04 \text{ mg P m}^{-2} \text{ d}^{-1}$) (Hovmand and others 1993). Monthly retention of P and N was then calculated by using the mass balance model of Messer and Brezonik (1978): retention = total input + storage – total output. N fixation was not included, but is considered of minor importance because cyanobacteria biomass was low during 1984–95.

Biological Variables

The abundance and biomass of phytoplankton and zooplankton were determined on composite samples from a midlake station and, in the case of zooplankton, also at an eastern station and a western station on occasion. For enumeration of zooplankton, 6.6–7.2 L of water from each station was filtered through a $50 \mu\text{m}$ (1984) or $20 \mu\text{m}$ (1985–95) mesh sieve and then fixed with 1 mL Lugol's solution in 100 mL tap water. Subsamples were counted at 40- to 100-fold magnification, depending on zooplankton size. Between 2% and 100% of the sample volume was counted on each sampling date, depending on zooplankton abundance. During periods with peak zooplankton densities, all samples were counted; otherwise, only one sample (midlake station) was analyzed. Phytoplankton were counted in an inverse microscope, and biovolume was determined

for each species or subspecies by using geometric formulae (Olrik 1991). We used $0.24 \text{ pg C } \mu\text{m}^{-3}$ (Reynolds 1984) to convert biovolume to carbon.

Ciliates were counted from the phytoplankton samples. At least 100 individuals per sample were counted, if possible, and maximum length measured on a minimum of 50 cells. Species determination was not performed.

Bacterioplankton production was estimated according to the method described by Fuhrmann and Azam (1982), with only minor changes (Jeppesen and others 1992). Triplicate 25-mL samples and controls (formalin killed) were incubated in situ with $12.5 \text{ nM } ^3\text{H-methylthymidine}$ for 15–60 min, depending on lake-water temperature. Production was calculated from $^3\text{H-methylthymidine}$ by using the following conversion factors: $2 \times 10^9 \text{ cells nmol thymidine}^{-1}$ (Riemann and others 1982) and $25 \text{ tg C cell}^{-1}$ (R. Bell personal communication). Bacteria were enumerated according to the method described by Hobbie and colleagues (1977), with minor modifications (Jeppesen and others 1992) at $1560\times$ magnification by using a Leitz epifluorescence microscope equipped with a 75-W mercury lamp. At least 500 cells were counted on 2–3 different fields, and cell dimensions recorded. Cells were divided into rods (8 size classes) and cocci (8 classes), and cell volume was calculated by using standard geometric formulae.

Phytoplankton production corrected for dark fixation was estimated from the photosynthesis-versus-irradiance relationship determined from laboratory incubation with $\text{H}_2^{14}\text{CO}_3$ at six different light intensities. From this relationship, a 24-h integrated value of areal production was then calculated by using observations of lake Secchi depth (converted to a light-extinction coefficient) and hourly data of surface irradiance at a station situated 30–40 km from the lake. Zooplankton community grazing on phytoplankton and bacteria was estimated according to the method described by Jeppesen and colleagues (1996). In total, 32 grazing experiments were carried out during 1984–86 and 1992 by using $^3\text{H-thymidine}$ -labeled bacterioplankton and ^{14}C -labeled phytoplankton. Specific clearance rate and daily ingestion of the different zooplankton species, which were temperature corrected to 15°C according to the method described by Gulati and colleagues (1982) and corrected for isotope loss (Jeppesen and others 1996), were estimated by multiple regression. Total daily ingestion for the entire study period was then calculated by multiplying the calculated biomass-specific daily ingestion, adjusted to actual water temperature, with the biomass of the different zooplankton.

Density, biomass, and age structure of fish populations were estimated by mark-recapture and scale analysis in midsummer 1986 (Mortensen and others unpublished manuscript). Beginning in 1987, an annual gill-net survey was conducted (Mortensen and others unpublished manuscript) between 15 August and 15 September (November in 1988) at a time when fish fry could be included in the catches. The lake was divided into six sections, and in each section three multi-mesh-size gill nets (14 different mesh sizes ranging from 6.25 to 75 mm) were set overnight (from about 1600 to 0900 h). One gill net was set perpendicular to the shoreline, another was set parallel with and about 25 m from the shoreline, and the third was set at about half the distance from the center of the lake.

All chemical and biological variables, except fish, are interpolated summer (1 May–1 October) or annual means of 10–91 samples based on fortnightly or more frequent samplings.

RESULTS

Nutrient Loading, Water Chemistry, and Secchi Depth

Since 1982, P removal measures at the treatment plant have resulted in a loading reduction from 28–33 g P m⁻² y⁻¹ in 1978–81 to 2–7 g P m⁻² y⁻¹ (Figure 1). Annual mean TP concentrations in the main inlet decreased from 1–3 mg P L⁻¹ to 0.15–0.25 mg P L⁻¹ (Søndergaard and others 1993). Comparatively minor changes were observed in inlake mean summer TP ranging from 0.9–1.6 mg P L⁻¹ before the P-loading reduction to 0.4–1.0 mg P L⁻¹ after the reduction (Figure 2). However, linear regression with time as the independent variable revealed a significant decline in summer mean TP from 1978 to 1995 ($P < 0.04$, $r^2 = 0.25$, $n = 15$). The minor response to the P-loading reduction reflects high internal loading. Accordingly, lake retention of TP shifted from positive values before 1982 to negative values after. Net release ranged between 1.9 and 5.4 g P m⁻² y⁻¹ during 1983–95 without showing any declining trend over time. Net release was, however, positively related to annual mean lake-water chlorophyll *a* (log-transformed data, $r^2 = 0.54$, $P < 0.02$, $n = 12$) after the P-loading reduction. The observed annual mean inlake TP (TP_{lake}) was lower than predicted from the Vollenweider (1976) equation (TP_{lake} = [TP_{in} / (1 + √(tw))], TP_{lake}, where *tw* is the hydraulic retention time (years) and TP_{in} is the annual mean inlet TP concentration). Following the reduction, the observed TP_{lake} was substantially higher than the predicted values (Figure 3). Closing the slaughter-

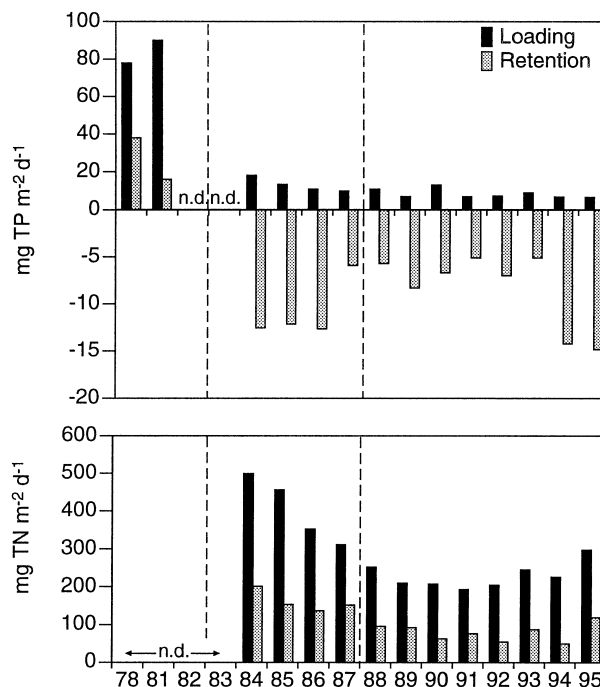


Figure 1. Estimated annual mean external loading of total phosphorus, total nitrogen and net retention from 1978–1995. External sewage loading of phosphorus and nitrogen was reduced in 1982 and in 1987, respectively (shown by broken lines). n.d. = no data.

house in July 1987 resulted in a reduction in N loading from 350–498 mg N m⁻² d⁻¹ during 1984–86 to 195–299 mg N m⁻² d⁻¹ during 1988–95 (Figure 1). N retention ranged from 137–200 mg N m⁻² d⁻¹ before 1987 to 55–118 mg N m⁻² d⁻¹ after the N-loading reduction. Between 22% and 40% of the loading was retained (including loss by denitrification) in the lake, and there was no tendency toward a temporary reduction in the retention percentage after the TN-loading reduction. The lake summer mean TN averaged 4.0 mg N L⁻¹ before and 2.2 mg N L⁻¹ after the N-loading reduction in 1987 (Figure 2).

The changes observed in annual mean inlake TN (TN_{lake}) closely followed those predicted by Windolf and colleagues (1996) for 16 shallow Danish lakes [TN_{lake} = 0.27 TN_{in} tw^{-0.22} z^{0.12}, where TN_{in} is annual mean inlet concentration and *z* is mean lake depth (in meters)] (Figure 3). The TN-TP ratio was low, ranging from 3.5–7.8 (mean, 5.4) before 1987 to 3.0–6.0 after 1987 (mean, 4.2) (Figure 2).

Despite the relatively small changes in TP and TN in the lake, chlorophyll *a*, water transparency, and pH changed markedly (Figure 2). Mean summer chlorophyll *a* was relatively low (50 µg L⁻¹) in 1978, two years after biological treatment was implemented at the upstream sewage plant, and in 1981 chlorophyll *a* then increased, peaking in 1984 (840

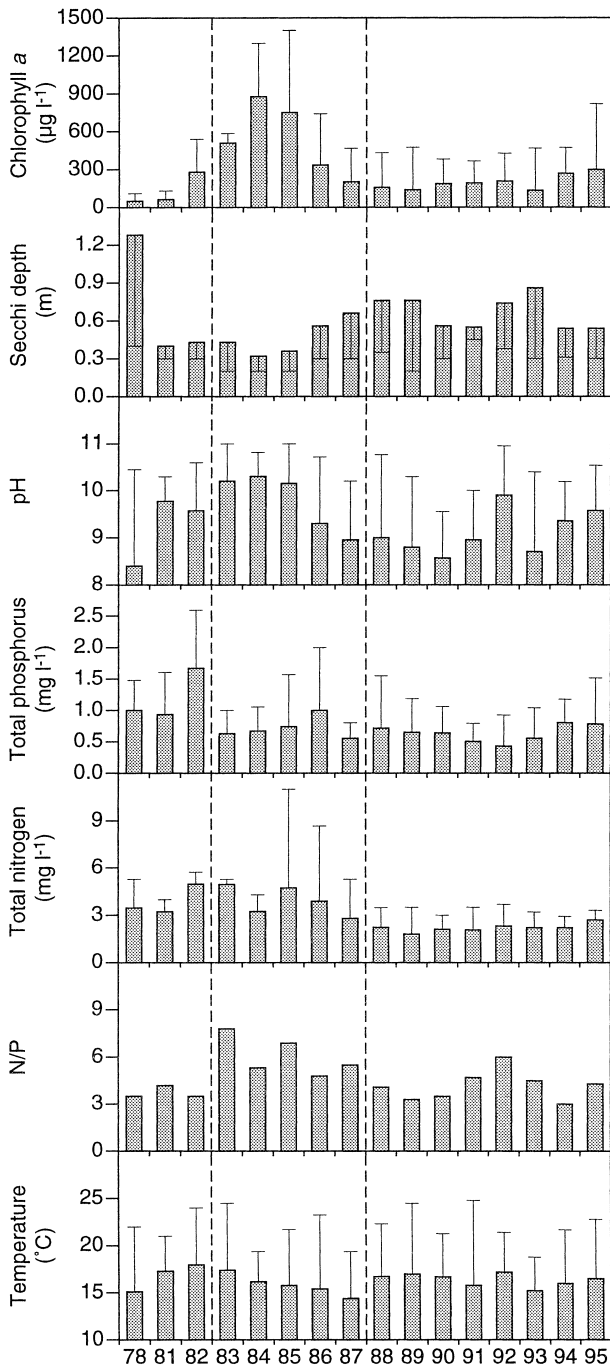


Figure 2. Interpolated summer (1 May–1 October) mean chlorophyll *a*, Secchi depth, pH, total phosphorus (P), total nitrogen (N), N-P ratio, and lake-water temperature during 1978–95. Minimum Secchi depth and maximum values of the other variables, except for the N-P ratio, are also shown.

$\mu\text{g L}^{-1}$), two years after the external P-loading reduction caused by P stripping at the plant. Thereafter, chlorophyll *a* decreased to $139 \mu\text{g L}^{-1}$ in 1989 and has since fluctuated between 133 and $299 \mu\text{g L}^{-1}$ without any distinct pattern. Maximum chloro-

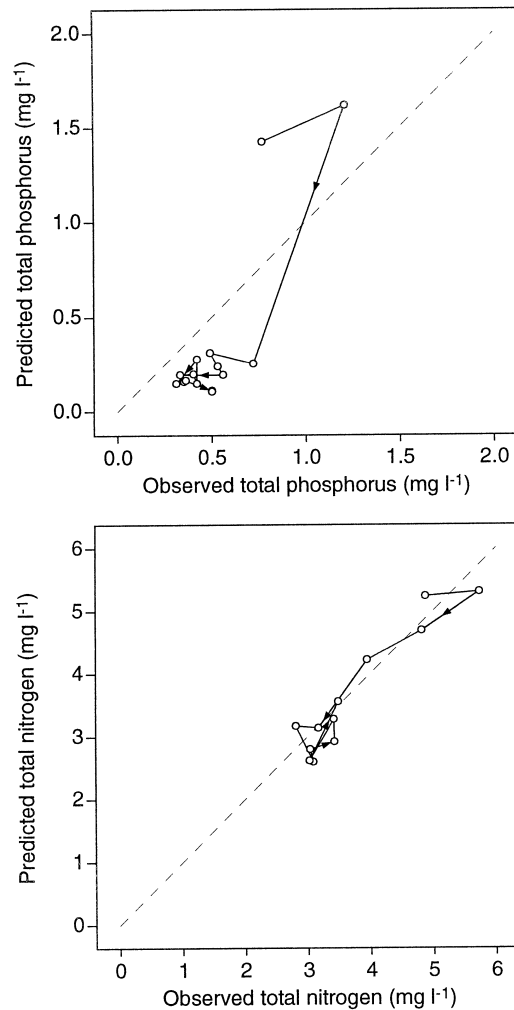


Figure 3. Observed annual mean total phosphorus and total nitrogen concentrations compared with predicted values based on equations developed by Vollenweider (1976) and Windolf and colleagues (1996), respectively.

phyll *a* varied from $110 \mu\text{g L}^{-1}$ in 1978 to as much as $1400 \mu\text{g L}^{-1}$ in 1985. Concurrent with the changes in chlorophyll *a*, summer mean Secchi depth decreased from more than 1.20 m in 1978 to 0.31 m in 1984 and has since fluctuated between 0.55 and 0.84 m. Mean pH increased from 8.3 in 1978 to 10.2 in 1984–85, after which it ranged between 8.6 and 9.9. Maximum recorded pH was as high as 11 in 1985. The diel variation in pH was typically less than 0.3 (Søndergaard and others 1990).

Phytoplankton and Zooplankton

The major changes in chlorophyll *a* were accompanied by changes in the phytoplankton community structure (Figure 4). In 1978, when chlorophyll *a* was low, cyanobacteria (primarily *Aphanizomenon flos-aqua*) and small spherical green algae (mainly

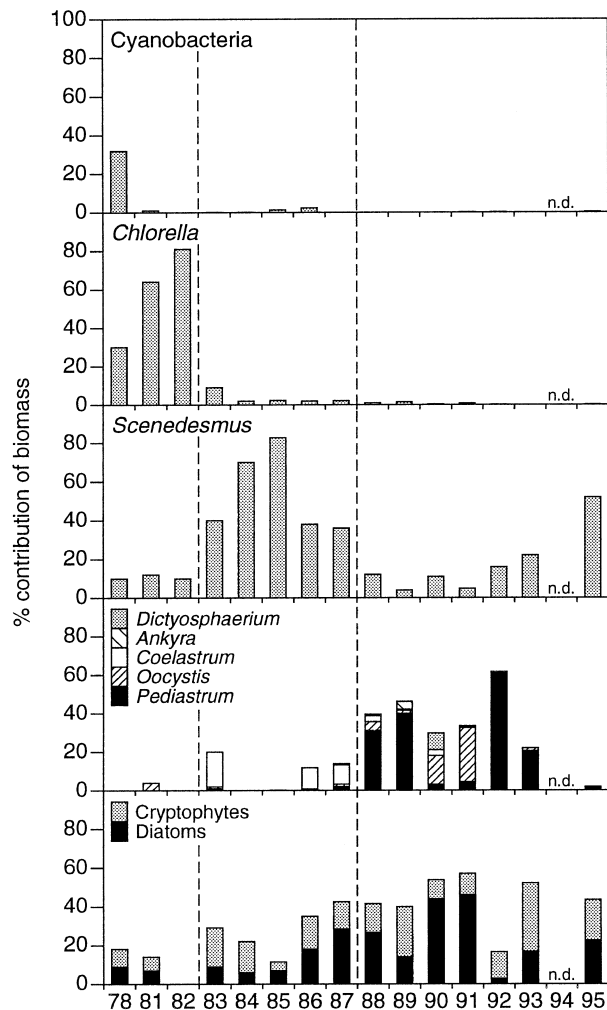


Figure 4. Percentage contribution to the biovolume of various lake-water phytoplankton groups during 1978–95. The percentages are estimated from interpolated summer mean values (n.d., no data).

Chlorella) were most abundant, each constituting about 30% of the total volume. Following the major increase in chlorophyll *a* during 1981–85, cyanobacteria almost disappeared, while first *Chlorella* in 1981–82 and subsequently *Scenedesmus* spp. in 1984–85 became exclusively dominant, constituting 64%–82% and 70%–83% of the total volume, respectively. The decline in chlorophyll *a* during 1986–92 corresponded with an increase in the abundance of large or gelatinous green algae. Subsequently, *Scenedesmus* increased again to 52% in 1995. In addition, the contribution of diatoms and cryptophytes to the total biovolume (summer means) increased significantly with time (linear regression, $P < 0.01$, $r^2 = 0.43$, $n = 14$).

Changes in phytoplankton mean volume were accompanied by significant changes in light-satu-

rated phytoplankton production (P_{\max}). P_{\max} had a significant positive relationship to phytoplankton volume and temperature, but declined with increasing phytoplankton mean volume (Table 1). Accordingly, volume-specific chlorophyll *a* declined significantly with increasing mean volume. However, P_{\max} per unit of chlorophyll *a* increased slightly with phytoplankton mean volume, indicating a “chlorophyll *a* package effect” (Elser and others 1986) that partly compensated for the reduction in volume-specific P_{\max} . Nevertheless, total biomass and total primary production decreased with increasing phytoplankton mean volume (Figure 5).

From the foregoing data, it is obvious that the major changes in chlorophyll *a* and the phytoplankton community and its size distribution cannot be explained by changes in nutrient concentrations. On the other hand, these changes suggest major top-down control variations mediated by changes in zooplankton abundance, size distribution, and grazing. The macrozooplankton community consisted of only a few species. *Daphnia longispina* and *Bosmina longirostris* completely dominated the cladoceran community, contributing 95%–100% of the cladoceran biomass. No calanoid copepods were found, and the cyclopoids were exclusively dominated by *Cyclops vicinus*, whose mean summer density ranged between 200 and 492 individuals L^{-1} (Figure 6), except for 1990, when low densities were recorded. Maximum densities of *C. vicinus* exceeded 2000 individuals L^{-1} (Hansen and Jeppesen 1992). During the study period, the number of rotifer taxa identified in a given year ranged between 6 and 31. Species of *Brachionus* were exclusively dominant in 1984–86 and again in 1995. In other years, the rotifer community was diverse, with species of *Keratella*, *Synchaeta*, *Filinia*, *Polyathra*, and *Asplanchna* dominating the rotifer biomass (unpublished data).

The structure and abundance of filter-feeding zooplankton changed markedly (Figure 6). In the early 1980s, densities of *B. longirostris* were high: in 1981, the mean abundance was 200 indiv L^{-1} . In 1983, it was 850 indiv L^{-1} , and maximum densities as high as 10,000 were recorded, while chlorophyll *a* was relatively low (data now shown). However, *Bosmina* almost disappeared in June 1983, and phytoplankton became abundant. Low cladoceran density and biomass were also recorded in 1984 and 1985 (Figures 5 and 6), when summer mean chlorophyll *a* was at its highest. Concurrently with the subsequent decline in chlorophyll *a* and algal biomass during 1986–89, cladoceran biomass increased with *Daphnia longispina* dominating (Figures 2 and 6). At the same time, *Scenedesmus* spp. were replaced by less-grazing-sensitive species (Figure 4). Among

Table 1. Multiple-Regression Analysis Relating Light-Saturated Phytoplankton ^{14}C Production (P_{\max} , $\text{mg C L}^{-1} \text{d}^{-1}$) During Summer (1 May–1 October) to Chlorophyll *a* (Chl*a*, $\mu\text{g l}^{-1}$), Mean Phytoplankton Volume (M_{vol} , $\mu\text{m}^3 \text{Cell}^{-1}$), Phytoplankton Volume (T_{vol} , $\text{mm}^3 \text{l}^{-1}$), and Water Temperature (Temp, $^{\circ}\text{C}$) for the Entire Study Period. All, Except Temperature, Are Log_e Transformed, SE in Parenthesis

	Intercept	Log_e (Chl <i>a</i>)	Log_e (T_{vol})	Log_e (M_{vol})	Temp	$P <$	r^2	n
Log_e (P_{\max})	−5.3**** (0.2)	0.93*** (0.03)	—	0.15*** (0.04)	—	0.0001	0.87	137
Log_e (P_{\max})	−5.9**** (0.2)	0.91**** (0.03)	—	0.09* (0.04)	0.04*** (0.01)	0.0001	0.88	134
Log_e (P_{\max})	−3.5**** (0.1)	—	0.82**** (0.04)	−0.21**** (0.05)	—	0.0001	0.79	137
Log_e (P_{\max})	−4.4**** (0.3)	—	0.81**** (0.04)	−0.27**** (0.05)	0.05*** (0.01)	0.0001	0.80	134

*, **, ***, **** are $P < 0.05, 0.01, 0.001, 0.0001$, respectively.

these, *Coelastrum* spp. dominated in 1986–87, and *Pediastrum boryanum* and *Ankyra judayi* dominated in 1988–89 (Figure 4). Thereafter, the zooplankton community shifted to a dominance by *B. longirostris* and rotifers in 1990–91, with an accompanying increase in intermediate-sized green algae, such as *Oocystis* and *Dictyosphaerium* sp. In 1992, *D. longispina* was again the most abundant filter feeder, and the large *P. boryanum* returned as the dominant green algae.

Accordingly, mean sizes of phytoplankton and zooplankton changed markedly. Cladoceran mean size increased threefold from approximately 0.4 mm in 1984–85 to 1.1–1.2 mm in 1988–89, and the phytoplankton mean volume simultaneously increased five- to eightfold to 1140–1230 μm^3 (Figure 5). Intermediately low phytoplankton mean volumes were found in 1990–91. Linear regression revealed a significant positive relationship between the mean size of phytoplankton compared with total cladoceran biomass, total zooplankton biomass, and the estimated zooplankton-grazing pressure on phytoplankton (Table 2), and between mean phytoplankton volume (M_{vol}) compared with mean size of cladocerans (C_{size}) [$M_{\text{vol}} (\mu\text{m}^3) = -0.1 + 1.0 * C_{\text{size}} (\mu\text{m})$ ($r^2 = 0.55, P < 0.01, n = 10$)].

A grazing equation for the lake based on 31 measurements of clearance rates on ^{14}C -labeled phytoplankton during 1984–91 (Jeppesen and others 1996) revealed the importance of grazing. Zooplankton ingested 1%–2% of the phytoplankton biomass d^{-1} during summer in 1984–85 (2%–4% of phytoplankton production), increasing to 20%–27% (40%–53% of production) in 1988–90. In the

subsequent years, it varied between 9% and 22 % of the biomass d^{-1} (Figure 5). Linear regression revealed a significant negative relationship between estimated zooplankton grazing compared with total phytoplankton biomass and grazing compared with phytoplankton production (Table 2).

Ciliates and Bacterioplankton

The summer mean abundance of ciliates ranged from 299 mL^{-1} in 1985 to 117 mL^{-1} in 1990 (Figure 7). The average maximum length of ciliates ranged from 14.5 to 24 μm and was highest (18–24 μm) in years when *Bosmina longirostris* and rotifers dominated, and was particularly high (24 μm) in 1990 when the biomass of cyclopoid copepods was low.

The biomass of bacterioplankton ranged between 0.21 and 0.41 g C m^{-2} . It was particularly high in years with low zooplankton biomass or high biomass of rotifers and *B. longirostris* (1985, 1990, and 1991). Small bacteria dominated, the average volume ranging from 0.050 $\mu\text{m}^3 \text{cell}^{-1}$ to 0.074 $\mu\text{m}^3 \text{cell}^{-1}$, with the lowest volumes occurring when *Bosmina* and rotifers were abundant. Bacterioplankton production was relatively constant (0.15–0.22 $\text{g C m}^{-2} \text{d}^{-1}$) during most years, but somewhat higher in 1990–91 (0.31–0.32 $\text{g C m}^{-2} \text{d}^{-1}$).

The impact of zooplankton on bacterioplankton was further elucidated by a grazing equation developed by Jeppesen and colleagues (1996) on the basis of grazing experiments in the lake with ^3H -thymidine-labeled bacterioplankton. The calculated ingestion was low in 1985 (less than 0.7% of bacterioplankton biomass), but increased to a maximum of 67% of bacterioplankton biomass and 88% of bacterioplankton production in 1988. Bacterio-

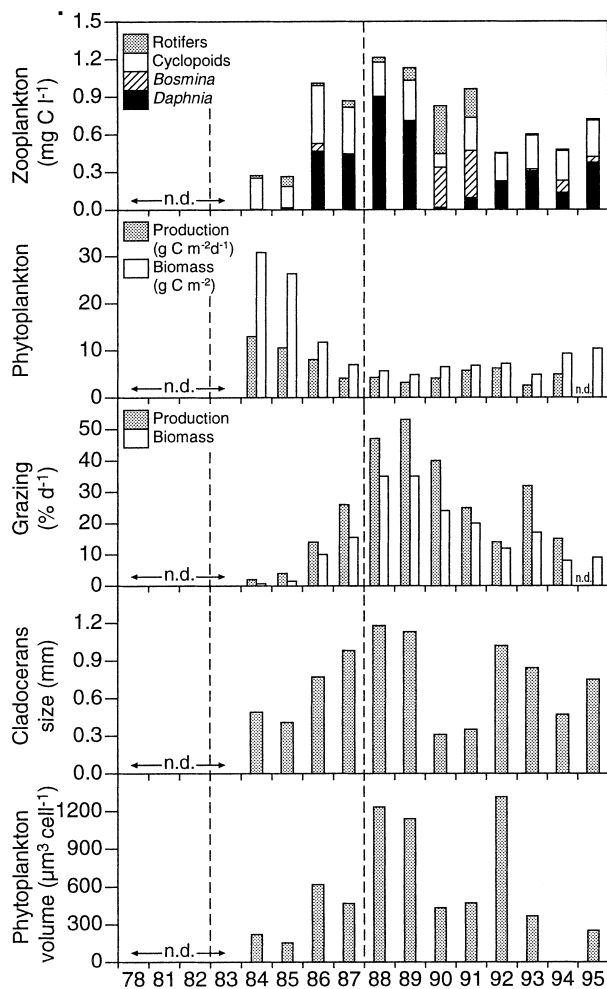


Figure 5. Interpolated summer means of the biomass of various zooplankton, phytoplankton production, and biomass, estimated macrozooplankton grazing in percentage of phytoplankton production and biomass, average size of cladocerans, and average biovolume of phytoplankton during 1984–95 (n.d., no data).

plankton biomass was depressed the same year (Figure 7). Low grazing and high biomass of bacterioplankton were found in 1990–91 (*B. longirostris* and rotifer dominance). However, no significant relationship was found between estimated zooplankton grazing on bacterioplankton compared with either biomass, production, or size of bacterioplankton (Table 2).

Fish

The major changes in the zooplankton community structure and size distribution suggest large variations in fish predation. Quantitative information on fish is available from 1986 to 1996. In 1986, the total biomass of the planktivorous fish population

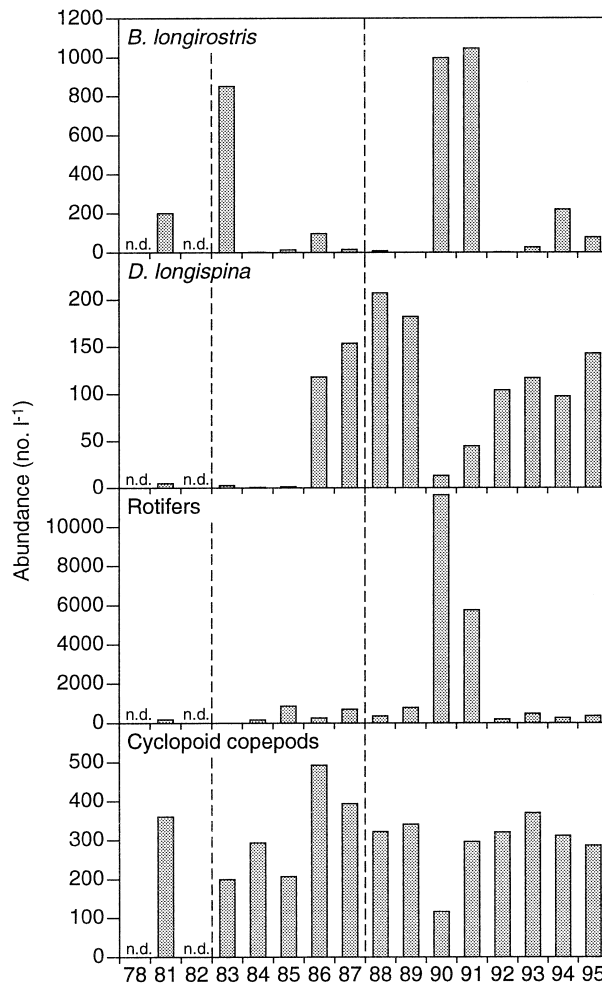


Figure 6. Interpolated summer mean abundance of various zooplankton during 1981–95 (n.d., no data).

was estimated as 67 g wet weight m^{-2} . Roach (*Rutilus rutilus*), rudd (*Scardinius erythrophthalmus*), and bream (*Abramis brama*) constituted 63%, 34%, and 3% of the biomass and 53%, 46%, and 1% of the planktivorous fish density, respectively. For these three species, the age classes 2+ and 8+ represented more than 80% of the fish population in terms of numbers, while fish younger than 2–3 years and older than 8 years were almost absent.

Major changes in catches per net (that is, catch per unit effort, CPUE) in multiple-mesh-sized gill nets were observed since 1987 (Figure 8). The CPUE for roach in terms of numbers ranged from 34 to 205. Rudd and three-spined sticklebacks (*Gasterosteus aculeatus*) were particularly abundant in 1989–90. CPUE of the potentially carnivorous perch was less than 3, but there was a tendency toward increasing abundance from 1988 to 1995. CPUE, as biomass, fluctuated less. Mean CPUE of the fish

Table 2. Linear Regression Relating Various Phytoplankton and Bacterioplankton Variables to Cladoceran Biomass and Estimated Zooplankton-Grazing Rates (All Data Are Interpolated, Log-Transformed Summer Means), SE in parenthesis

	Log _e (Cladoceran Biomass, mg C L ⁻¹)					Log _e (Zooplankton Biomass, mg C L ⁻¹)					Log _e (Zooplankton Grazing, mg C L ⁻¹ d ⁻¹)				
	Inter-cept	Slope	P<	r ²	n	Inter-cept	Slope	P<	r ²	n	Inter-cept	Slope	P<	r ²	n
Log _e (phytoplankton biomass, mg C L ⁻¹)	1.86 (0.13)	-0.32 (0.06)	0.0002	0.76	11	1.97 (0.18)	-0.89 (0.27)	0.01	0.51	11	2.32 (0.115)	-0.82 (0.19)	0.002	0.64	11
Log _e (phytoplankton production, mg C L ⁻¹ d ⁻¹)	1.33 (0.06)	-0.22 (0.06)	0.006	0.59	10	1.44 (0.12)	-0.56 (0.18)	0.03	0.42	10	1.66 (0.11)	-0.57 (0.19)	0.02	0.50	10
Log _e (phytoplankton mean volume, µm ³)	6.59 (0.23)	0.27 (0.10)	0.03	0.43	10	6.55 (0.22)	0.88 (0.34)	0.04	0.42	10	6.22 (0.16)	0.78 (0.26)	0.02	0.49	10
Log _e (bacterioplankton production, mg C L ⁻¹ d ⁻¹)	-1.56 (0.14)	0.07 (0.09)	NS	0.06	10	-1.58 (0.11)	0.16 (0.19)	NS	0.08	10	-1.90 (0.25)	-0.10 (0.08)	NS	0.14	10
Log _e (bacterioplankton biomass, mg C L ⁻¹)	-1.26 (0.13)	-0.13 (0.08)	NS	0.23	10	-1.17 (0.11)	-0.17 (0.18)	NS	0.09	10	-1.47 (0.23)	-0.13 (0.08)	NS	0.25	10
Log _e (bacterioplankton mean volume, µm ³ cell ⁻¹)	-2.84 (0.05)	-0.05 (0.03)	NS	0.26	10	-2.81 (0.04)	-0.12 (0.07)	NS	0.28	10	-2.82 (0.10)	-0.02 (0.03)	NS	0.03	10

NS, not significant.

community ranged between 9.0 and 16.9 kg net⁻¹ in 1990 and 1994–95 (Figure 8), respectively, mainly due to roach (CPUE, 8.1–15.4 kg net⁻¹) and rudd. The biomass of predatory fish was less than 3%. Linear regression revealed a significant negative relationship between total cladoceran biomass and mean length of *Daphnia* spp. compared with cyprinid CPUE numbers and between mean length of *Daphnia* compared with CPUE, while a weak negative relationship between CPUE and the estimated zooplankton grazing on bacterioplankton was observed (Table 3). No significant relationships between CPUE in terms of biomass and any of these variables were found (data not shown).

DISCUSSION

Prolonged Internal Loading of Total Phosphorus

Most studies of recovery following P-loading reduction have shown negative net retention of P for 0–5

years (Sas 1989; Van der Moelen and Boers 1994). Despite the low hydraulic retention time of a few weeks, net retention of P in Lake Søbjerg has remained negative for 13 years now (or 204 water renewal times). Even in 1995, P concentrations still exceeded five times the value predicted by the equation developed by Vollenweider (1976). The high and persistently negative retention reflects a high-P pool in the sediment amounting to 240 g P m⁻² of the upper 23 cm of sediment as measured in 1990 (Søndergaard and others 1993). Immediately following the external loading reduction, TP was released from the surface sediment, but at present it is being released from the 18- to 23-cm sediment level (Søndergaard and others 1993 and unpublished results). Based on iron-TP ratios in the upper sediment, Søndergaard and colleagues (1993) argued that at least 26 g P m⁻² was expected to be released after 1990 before a new equilibrium based on the present P-loading could be obtained. From 1990 to 1995, the net release has been 17 g P m⁻².

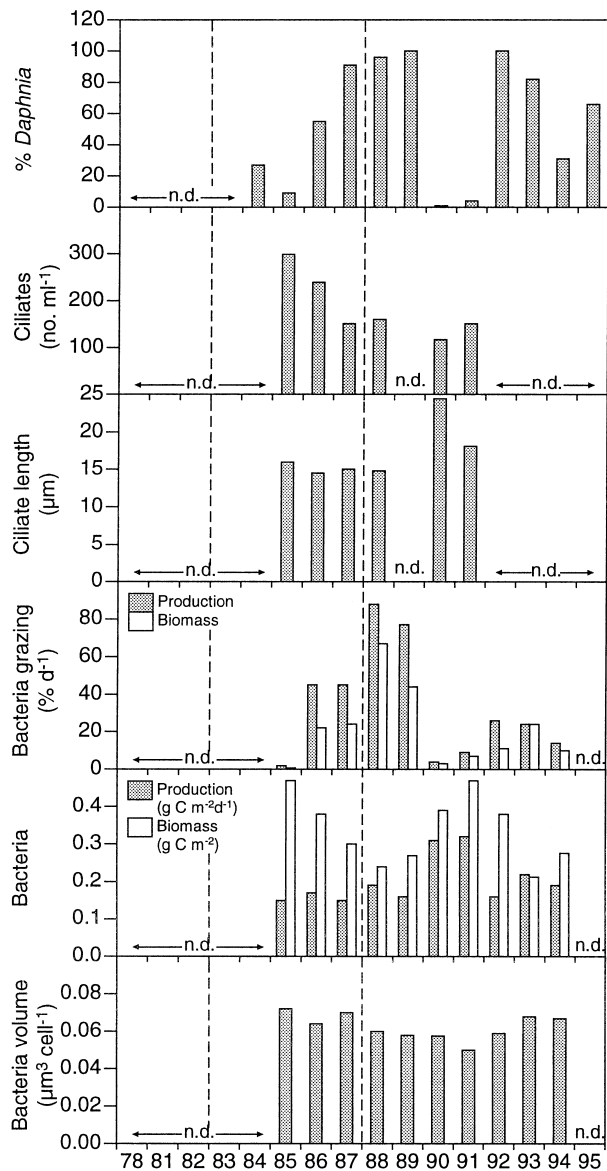


Figure 7. Summer means of the contribution of *Daphnia* as a percentage of total cladoceran abundance (calculated from interpolated means), abundance and mean length of ciliates, estimated zooplankton grazing on bacterioplankton as a percentage of bacterioplankton biomass and production, and mean bacterioplankton volume during 1984–95. (n.d., no data.)

Predictions based on a dynamic P model suggest that another decade will pass before the equilibrium is reached (Jensen and others 1994a).

Net P release was positively related to chlorophyll *a* during 1983 to 1995, indicating benthic–pelagic coupling. The higher net release in years with high chlorophyll *a* was probably caused by higher oxygen consumption in the sediment mediated by a higher sedimentation of phytoplankton. The importance of microbial metabolism for P release from

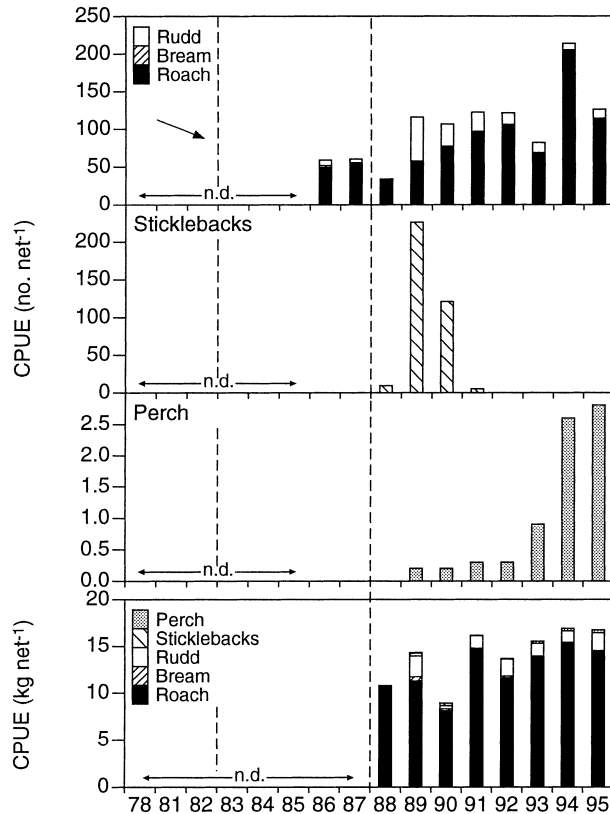


Figure 8. Average catch per unit effort (CPUE) of predominant fish species caught in multiple mesh-sized gill nets (14 sizes between 6.25 and 75 mm; 18 nets) during 16 h (overnight) between 15 August and 15 September of each year (November in 1988). CPUE in terms of numbers and biomass are given; roach, *Rutilus rutilus*, bream, *Abramis brama*, rudd, *Scardinius erythrophthalmus*, perch, *Perca fluviatilis*, stickleback (three-spined), *Gasterosteus aculeatus*. No fish data (n.d.) exist before 1986, but mark-recapture experiments from 1986 suggest higher numbers during the early 1980s, as indicated by the arrow. (n.d., no data.)

sediments in shallow lakes has been demonstrated in several studies [for example, see Gächter and colleagues (1988) and Boström and colleagues (1988)], including Lake Søbygård (Jensen and Andersen 1992). In the years with high chlorophyll *a*, pH was also high. High pH reduced P binding to iron hydroxides in the lake sediments, thereby enhancing P release to the overlying water [for example, see Boström and colleagues (1982)]. Jensen and Andersen (1992) confirmed that high pH may cause an increase in the P-release rate from the sediment in Lake Søbygård in early spring, but that the pH effect is less important compared with the microbial-mediated release during summer. Lower net internal loading due to a grazer-mediated reduction in chlorophyll *a* has also been found in several fish manipulation studies [for example, see

Table 3. Linear Regression of Some Zooplankton Variables and Estimated Grazing on Phytoplankton and Bacterioplankton Compared with the Average Number of Cyprinids Caught in Multiple-Mesh-Size Gill Nets (14 Different Mesh Sizes, 6.25–75 mm) During 16 Hours in Early Autumn (15 August–15 September). The *y*-Variables Are Interpolated Summer Means. All Data Are Log_e Transformed to Stabilize Variance. SE in Parenthesis

	Log _e (CPUE of Cyprinids, No Net ⁻¹)				
	Intercept	Slope	<i>P</i> <	<i>r</i> ²	<i>n</i>
Log _e (cladoceran biomass, mg C L ⁻¹)	1.72 (1.01) ^{NS}	-0.57 (0.04)	0.04	0.45	9
Log _e (zooplankton biomass, mg C L ⁻¹)	1.77 (0.76)	-0.45 (0.17)	0.03	0.48	9
Log _e (<i>Daphnia</i> mean size, mm)	0.90 (0.31)	-0.21 (0.07)	0.02	0.53	9
Log _e (<i>Bosmina</i> mean size, mm)	-0.89 (0.22)	-0.05 (0.05)	NS	0.11	8
Log _e (grazing on phytoplankton, mg C L ⁻¹ d ⁻¹)	1.55 (0.94) ^{NS}	-0.31 (0.21)	NS	0.22	9
Log _e (grazing on bacterioplankton, mg C L ⁻¹ d ⁻¹)	1.26 (1.93) ^{NS}	-0.94 (0.43)	0.06	0.41	8

CPUE, catch per unit effort; NS, not significant.

Reinartsen and Olsen (1984, Shapiro and Wright (1984), Søndergaard and others (1990), and Benn-dorf (1990)].

In contrast to P, the N-loading reduction did not appear to affect the TN retention percentage, suggesting fast equilibration. This suggests that a large part of the N was denitrified, resulting in little accumulation of inorganic N in the sediment (Jensen and others 1992). The observed annual mean TN closely matched the one predicted by the equation of Windolf and colleagues (1996) for 16 shallow Danish lakes (Figure 3). According to this model, water TN is related to discharge-weighted inlet concentrations, hydraulic retention, and mean depth.

The Vollenweider equation predicts that TP_{lake} in equilibrium with the present loading will be 0.105 mg P L⁻¹, which is 21% of the 1995 level. The equilibrium concentration of TP is so high that the lake, in all probability, will remain in a turbid state. Diversion of sewage and a reduction in the diffuse loading from arable land may be necessary to shift

the lake to the clear-water state with extensive growth of submerged macrophytes, which characterized the lake in the previous century, as suggested by paleoecological studies of lake sediment (Anderson and others unpublished; Jeppesen and others unpublished).

Strong Cascading Effects of Fish on Zooplankton

The marked changes found in trophic dynamics, pH, and Secchi depth could largely be attributed to the major variations in the fish population structure and abundance rather than to changes in the external loadings of organic matter, P, and N. The variation in fish abundance most likely reflects variations in oxygen concentration and pH (Figure 9). Hence, the low abundance of fish recruited before 1979 can be attributed to the frequent and severe summer fish kills in the 1970s (Andersen and others 1979; Mathiesen and Christensen 1981), most likely caused by oxygen depletion due to high organic loading as seen in other studies of hypertrophic lakes (Barica 1975; Carvalho 1994). Following the introduction of biological sewage treatment in 1976, the oxygen concentration increased, and the last major fish kill occurred in 1978. Likewise, the low CPUE of rudd and roach during 1986–88 compared with 1989–95 (Figure 8) can be mainly ascribed to the near absence of fish recruitment from 1984 to 1987. This poor recruitment may have resulted from high pHs in those years. In support of this theory, Timmermann (1987) showed that the 1986 spawning of roach and rudd was delayed 1–2 months, and spawning occurred simultaneously with a pH reduction caused by a major phytoplankton collapse. It cannot, however, be excluded that the low CPUE during 1986–88 was influenced by large commercial harvests of roach and rudd that corresponded to 17% of the biomass estimate from 1986.

Changes in the age structure and density of the planktivorous fish population were discernible in zooplankton structure and abundance. We have no quantitative zooplankton data from the 1970s when fish kills were observed. However, the large cladoceran, *D. magna*, occurred in high densities during summer and dominated the efflux of organic matter from the lake (Holm and Tuxen-Pedersen 1975). Furthermore, sediment analyses revealed a high abundance of resting eggs of large daphnids (*D. magna* or *D. pulex*) deposited in the 1970s (Jeppesen and others unpublished data). Large daphnids were apparently abundant in 1978, when chlorophyll *a* was low from late May to September (Andersen and others 1979), the year of the last fish kill.

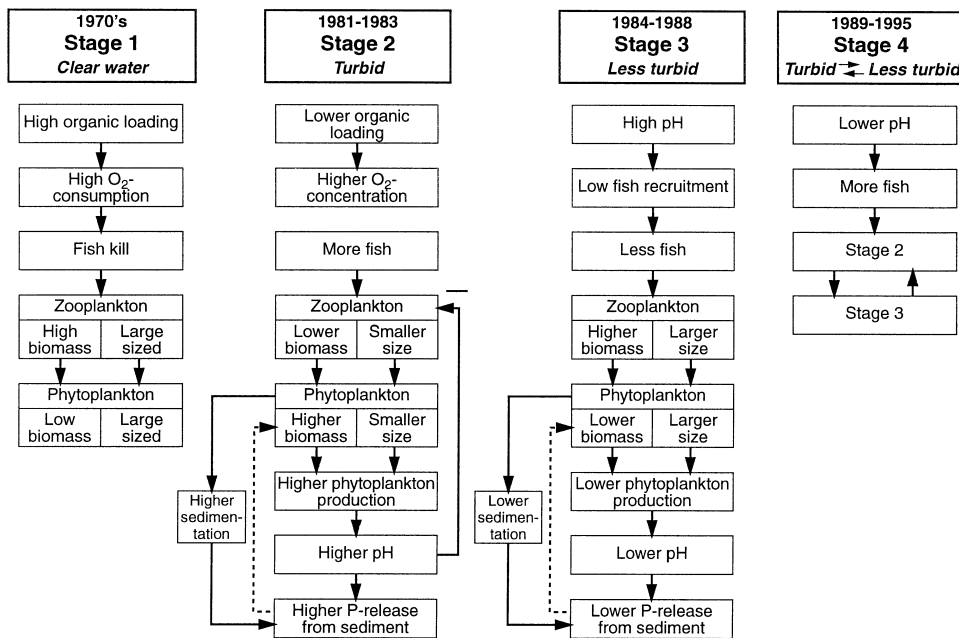


Figure 9. A conceptual model for how organic loading and pH are suggested to have affected the trophic structure and dynamics in the pelagial of Lake Søbygård during 2 decades.

The major changes in zooplankton community structure and size with changes in CPUE numbers of planktivorous fish are in accord with the size-efficiency hypothesis (Brooks and Dodson 1965). The shifts occurred despite relatively minor changes in CPUE biomass, however, which underlines the importance of young fish in structuring zooplankton communities (Cryer and others 1986; Mills and others 1987; He and Wright 1992; Søndergaard and others 1997; Jeppesen and others 1997b). The significant negative relationship between cladoceran biomass and mean size of *D. longispina* to cyprinid CPUE numbers, but not biomass, provides further evidence.

Effects of High pH on Trophic Dynamics

Besides being influenced by fish, the extremely low abundance of cladocerans in 1984 and 1985 may be attributed to high pH. Midmorning pH was above 10.5 approximately half of the time during the summers of 1984 and 1985 [data in Jeppesen and others (1990c)], and field experiments in the lake (Hansen and others 1991) have shown a negative effect on *D. longispina* survival when pH is greater than 10.5. Likewise, laboratory experiments by Vijverberg and colleagues (1996) showed enhanced mortality of juvenile and adult *D. galeata* at pH above 10.5 and of eggs and neonates at pH above pH 10. The pH effect is self-perpetuating, as a pH-mediated reduction in cladoceran abundance reduces the zooplankton-grazing pressure on phytoplankton (Figure 9). This reduction facilitated an increased growth of phytoplankton and higher pH

with negative feedback on cladocerans. Results from the enclosure experiments also indicate that high pH may increase the P release from the sediment and inhibit nitrification and accordingly uncouple nitrification-denitrification leading to increased ammonium release (Hansen and others 1991), which, in turn, may potentially stimulate phytoplankton growth. As just described, however, high pH seemed to have a negative influence on the spawning success of the fish (Mortensen and others unpublished manuscript). Reduced abundance of fish resulted in lower predation on cladocerans. In 1986, cladoceran densities reached high enough densities to reduce phytoplankton biomass and production, as well as pH values. The resultant lower pH levels, in turn, improved conditions for fish recruitment, which caused enhanced predation on cladocerans (Figure 9). Accordingly, the marked variations in the biological structure in Lake Søbygård seemed partly influenced by pH-mediated effects on biological structure and nutrients: pH-provoked variations at the top (fish and zooplankton) and at the bottom (N and P) of the food web that, at least for the former, influenced phytoplankton and Secchi depth.

Strong Cascading Effect of Zooplankton on Phytoplankton

The fish-mediated and pH-mediated changes in zooplankton had a major impact on the phytoplankton composition, size distribution, and production. Our data strongly suggest that the marked interannual variations in the contribution of the various

phytoplankton species to the total biovolume were largely determined by the changes in zooplankton composition, size, and grazing pressure. When cladoceran biomass was low, *Scenedesmus* dominated. When small *B. longirostris* and rotifers became abundant, a shift occurred to small or intermediate-sized green algae (mainly *Chlorella* spp. and *Oocystis*). When intermediate-sized *Daphnia* (*D. longispina*) dominated, algae shifted to intermediate-sized *Pediastrum* spp. Finally, when large *D. magna* dominated, there was a shift from large flake-forms of *Aphanizomenon flos-aqua*, as observed in other studies of highly eutrophic lakes (Lynch 1980; Fott and others 1980; Andersson and Cronberg 1984). The shift to large algae caused a marked decrease in the volume-specific P_{\max} and total phytoplankton production. These changes all support the trophic cascade hypothesis (Carpenter and others 1985). However, strong support for the hypothesis has only been found in some cases (Carpenter and Kitchell 1993). Kerfoot (1987) demonstrated a tendency toward a unimodal relationship between grazing pressure and algal size, large algae being dominant at intermediate *Daphnia* densities. Our data indicate that phytoplankton mean volume correlated more strongly with zooplankton size than with zooplankton-grazing pressure (Figure 5).

The high cascading effect of fish on zooplankton contradicts "the intermediate hypothesis" (Carney and Elser 1990; Carney 1990), which claims that herbivory declines from mesotrophic to hypertrophic lakes because the phytoplankton community becomes dominated by less nutritious and less palatable algae. Our results show that, in hypertrophic Lake Søbygård, the phytoplankton community was dominated by edible green algae and that the intensity of herbivory seems mainly influenced by changes in the abundance of planktivorous fish. This is in accord with results from a cross-analysis of data from 39 shallow Danish lakes showing a close negative relationship between the zooplankton-phytoplankton biomass ratio and the abundance of planktivorous fish, while percent cyanobacteria in terms of biovolume did not contribute significantly to the relationship (Jeppesen and others 1997b). Moreover, in eutrophic Danish lakes alternately dominated by blue-green and green algae, the zooplankton-phytoplankton biomass ratio showed no significant year-to-year variation (Jeppesen and others unpublished), suggesting that top-down control is the key factor in such lakes. Leibold (1989) and Sarnelle (1992) have already suggested that fish play a key role for herbivory in eutrophic lakes.

In 1983–85, when the phytoplankton biomass reached extremely high values (maximum chloro-

phyll *a*, 1400–1500 $\mu\text{g L}^{-1}$), the phytoplankton community was completely dominated by small algae (*Scenedesmus* spp. and *Chlorella* sp.). Small green algae have been reported to dominate in many other hypertrophic, freshwater lakes with dense phytoplankton communities (Nygaard 1949; Pavoni 1963; Leah and others 1980; Jensen and others 1994b). These results are not in agreement with the hypothesis of Agustí and Kalff (1989), Duarte and colleagues (1990), and Agustí (1991) that predicts that the average size of phytoplankton generally increases with increasing phytoplankton biomass. There may be several advantages of being small in dense, shallow lake communities. First, small algae have a higher chlorophyll content per unit of volume (Reynolds 1984; Enriquez and others 1996), maximizing light exploitation in a light-limited system. Second, the small size facilitates nutrient uptake (Hein and others 1995), which may be important in an environment characterized by pulse loading of nutrients as normally occurs in shallow lakes due to, for instance, wind-induced resuspension and diel changes in water temperature. The data from Lake Søbygård suggest that a shift to larger algae occurs only when larger zooplankton dominate (Figure 5). Low grazing pressure mediated by high fish predation may thus contribute to the frequently observed dominance by small algae in hypertrophic freshwater lakes, although exceptions can be found from less eutrophic, cyanobacteria-dominated lakes [for example, see Barica (1975) and Gulati and others (1992)].

Phytoplankton and Nutrients

According to most studies, the environmental conditions found in Lake Søbygård [high pH, low N–P ratios, low euphotic–mixing zone ratios (low Secchi depth) (Figure 2), and periodically low inorganic N concentrations (see below)] should favor cyanobacteria (Schindler 1977; Smith 1983; Shapiro 1990; Van Liere and Gulati 1992; Scheffer and others 1997). In addition, Sterner and colleagues (1992) and Hessen (1997) argued that cyanobacteria are favored in lakes with low *Daphnia*–copepod ratio, because the TN–TP ratio of matter excreted by copepods is lower than for *Daphnia*. Except in 1978, the phytoplankton community was, however, dominated by green algae and diatoms, even in years with a low biomass ratio of cladocerans–copepods. This pattern can be observed in many temperate shallow hypertrophic lakes (Jeppesen and others 1990a; Jensen and others 1994b). In previous reports, we have argued that high external loading of nutrients along with a high internal loading of CO_2 and nutrients from the sediment may explain the

dominance of green algae in these lakes (Jeppesen and others 1990b; Jensen and others 1994b).

The slight reduction in lake TN and TP during the study may have influenced phytoplankton succession. The reduction in TP concentrations and organic matter loading after the implementation of biological waste water treatment (Holm and Tuxen-Pedersen 1974) may have caused the shift in the early 1980s from *Chlorella* sp. to *Scenedesmus* spp. Both genera are favored in nutrient-rich and often highly organically loaded ponds and lakes (Jeppesen and others 1990b; Jensen and others 1994b), but *Chlorella* sp. seems more tolerant of high ammonia concentrations and is better adapted to utilize organic substances for growth (Niewolak 1971). The shift to dominance by *Scenedesmus* spp. occurred concomitantly with a major decrease in the density of *Bosmina* and this could potentially indicate an interdependent relationship. However, *Chlorella* sp. densities did not increase after the return of *Bosmina* dominance in 1990–91, suggesting that changes in nutrients and organic loading are more likely to be the decisive factor for the decreased abundance of *Chlorella* sp. Likewise, the gradual increase in importance of diatoms may reflect a reduction in nutrient concentrations. The duration of the period with low inorganic N concentrations (below, for instance, 50 $\mu\text{g L}^{-1}$ during summer) increased from an average of 8 days in 1984–87 to 38 days in 1989–95 (unpublished results), and average TN–TP ratio decreased from 3–7 before 1987 to 2–5 after (Figure 2). This may have improved the competitive capacity of diatoms. Enrichment experiments with natural phytoplankton from the hypertrophic Grosser Binnensee (Sommer 1989) revealed that the Monod saturation coefficient for inorganic N was 6–10 times higher for *Scenedesmus* than for *Stephanodiscus*, which is the most abundant diatom genus in Lake Søbygård. Accordingly, the phytoplankton species composition in Lake Søbygård seems influenced by the reduction in nutrient loading and nutrient concentration. Superimposed upon that, however, substantial fluctuations occurred, reflecting changes propagated from fish via zooplankton.

Modest Cascading Effects on the Microbial Community

The cascading effects of fish-stock changes seemed less significant on the abundance of ciliates and bacterioplankton than on zooplankton and phytoplankton, supporting several observations that cascading effects diminish downward through the food web (McQueen and others 1986; Pace 1993). The response in 1990–91, when *B. longirostris* and rotifers dominated the zooplankton community, was

significantly different from the other years. Bacterioplankton biomass and especially production were high, average bacteria volume was low, and ciliate mean size was high, particularly in 1990–91 (Figure 7). A multiple-regression analysis on summer data from 1985 to 1992 showed that bacterioplankton abundance and production were positively related to the biomass of rotifers, *B. longirostris*, and cyclopoid copepods and negatively related to the biomass of *D. longispina* (Jeppesen and others 1997a). The apparent positive effect of the small cladocerans, rotifers, and cyclopoid copepods may be explained by increased organic substrate for bacteria through excretion in combination with predation on potential bacterivores, flagellates, and ciliates. As for *Daphnia*, predation seems to overrule the potential positive effects on bacterioplankton, as demonstrated in other studies of eutrophic lakes (Riemann 1985; Christoffersen and others 1993; Jürgens 1994; Christoffersen and Bosselmann 1997). Annual bacterioplankton production amounted to only 2%–6% of phytoplankton production, the highest percentages being obtained in 1990 and 1991 when *B. longirostris* and rotifers dominated (Jeppesen and others 1997a). The low values compared with Cole and colleagues' (1988) mean of 17% for a number of aquatic systems may be attributed to high loss by sedimentation due to the shallowness of the lake (low mean depth) and to dominance of phytoplankton with high specific settling rates (Kristensen and Jensen 1987) and low grazing rates in some years (Jeppesen and others 1997a). Our results support the conclusion by Cole and colleagues (1988) that the bacterioplankton–phytoplankton production ratio declines from oligotrophic to eutrophic lakes.

The multiple regression analysis also showed a significant negative effect of pH on bacterioplankton production, when pH was higher than 10.2. This effect was supported by laboratory experiments (Jeppesen and others 1997a) and implies that recycling of dissolved organic matter back to the food web via bacteria is reduced at high pH. Pace and Cole (1996) found a similar negative effect of pH on bacterioplankton production at low pH.

In conclusion, the results from the long-term study of Lake Søbygård suggest that shallow hypertrophic lakes with short retention times may be highly resistant to external P-loading reduction. In addition, sewage-loading reduction may create substantial perturbations at the top of the food web that may have major cascading effects on zooplankton and phytoplankton community structure, biomass, size, and production, with more minor effects on the pelagial microbial community. Changes in oxygen concentration and pH mediated by changes in

external loading of organic matter and internal biological processes seemed to be the most important factors determining the perturbations. The results obtained are in accord with the trophic cascade hypothesis (Carpenter and others 1985), but can not confirm (a) that dense phytoplankton communities are dominated by large phytoplankton (Agustí and Kalff 1989), (b) that herbivory declines from mesotrophic to hypertrophic lakes because of an increase in biomass of large cyanobacteria (Carney and Elser 1990), or (c) that cyanobacteria are favored at low N-P ratios and high pH (Smith 1983; Shapiro 1990). In contrast, small green algae dominated when zooplankton-grazing pressure was low and phytoplankton biomass extremely high, large green algae dominated at higher grazing pressure, and herbivory seemed mainly influenced by the abundance of planktivorous fish.

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REFERENCES

- Agustí S. 1991. Light environment within dense algal populations: cell size influences on shelf-shading. *J Plankton Res* 13:863-71.
- Agustí S, Kalff J. 1989. The influence of growth conditions on the size dependence of maximal algal density and biomass. *Limnol Oceanogr* 34:1104-8.
- Andersen JM, Jensen J, Kristensen Aa, Kristensen K. 1979. Investigation of the environmental state of Lake Søbygård in 1978 [In Danish]. Århus (Denmark): Report from Århus County, 29 p.
- Andersson G, Cronberg G. 1984. *Aphanizomenon flosaqua* and *Daphnia*: an interesting plankton association in hypertrophic waters. In: Bösheim S, Nicholls M, editors. Interactions between different trophic levels in freshwater [In Norwegian]. Oslo (Norway): Norsk Limnologförening, Blindern. p 63-76.
- Barica J. 1975. Collapses of algal blooms in prairie pothole lakes: their mechanisms and ecological impact. *Verh Int Ver Limnol* 19:606-15.
- Boers P, Van Ballegooijen L, Uunk J. 1991. Changes in phosphorus cycling in a shallow lake due to food web manipulations. *Freshwater Biol* 25:9-20.
- Benndorf J. 1990. Conditions for effective biomanipulation: conclusions derived from whole-lake experiments in Europe. *Hydrobiologia* 200-201:187-203.
- Boström B, Andersen JM, Fleischer S, Jansson M. 1988. Exchange of phosphorus across the sediment-water interface. *Hydrobiologia* 170:457-74.
- Boström, Jansson M, Forsberg C. 1982. Phosphorus release from lake sediments. *Ergeb Limnol* 18:5-59.
- Brooks JL, Dodson SI. 1965. Predation, body size and composition of plankton. *Science* 150:28-35.
- Carney HJ. 1990. A general hypothesis for the strength of food web interactions in relation to trophic state. *Verh Int Ver Limnol* 24:487-92.
- Carney HJ, Elser JJ. 1990. The strength of zooplankton-phytoplankton coupling in relation to trophic state. In: Tilzer MM, editor. Ecology of large lakes. New York: Springer-Verlag. p 613-31.
- Carpenter SR, Cottingham KL, Schindler DE. 1992. Biotic feedbacks in lake phosphorus cycles. *TREE* 7:332-6.
- Carpenter SR, Kitchell JF, editors. 1993. The trophic cascade in lakes. Cambridge: Cambridge University. 385 p.
- Carpenter SR, Kitchell JF, Hodgson JR. 1985. Cascading trophic interactions and lake productivity. *Bioscience* 35:634-9.
- Carvalho L. 1994. Top-down control of phytoplankton in a shallow hypertrophic lake: Little Mere (England). *Hydrobiologia* 275-276:53-64.
- Christoffersen K, Bosselmann S. 1997. Zooplankton: growth, grazing and interactions with fish. In: Sand-Jensen K, Pedersen O, editors. Freshwater biology: priorities and development in Danish research. Copenhagen (Denmark): GEC GAD p 162-82.
- Christoffersen K, Riemann B, Klysner A, Søndergaard M. 1993. Potential role of zooplankton in structuring a plankton community in eutrophic lake water. *Limnol Oceanogr* 38:561-73.
- Cole JJ, Findlay S, Pace ML. 1988. Bacterial production in fresh and saltwater ecosystems: a cross-system overview. *Mar Ecol Prog Ser* 43:1-10.
- Cooke GD, Welch EB, Peterson SA, Newroth PR. 1993. Restoration and management of lakes and reservoirs. Boca Raton (FL): Lewis.
- Cryer M, Peirson G, Townsend CR. 1986. Reciprocal interactions between roach, *Rutilus rutilus*, and zooplankton in a small lake: prey dynamics and fish growth and recruitment. *Limnol Oceanogr* 31:1022-38.
- Cullen P, Forsberg C. 1988. Experience with reducing point sources of phosphorus to lakes. *Hydrobiologia* 170:321-36.
- Duarte CE, Agustí S, Canfield DE. 1990. Size plasticity of freshwater phytoplankton: implications for community structure. *Limnol Oceanogr* 35:1846-51.
- Edmonson WT. 1985. Recovery of Lake Washington from eutrophication. In: Proceedings from lakes pollution and recovery, Rome, 15-18 April 1985. p 228-34.
- Elser JJ, Elser MM, Carpenter SR. 1986. Size fractionation of algal chlorophyll, carbon fixation and phosphatase activity: relationships with species-specific size distributions and zooplankton community structure. *J Plankton Res* 8:365-83.
- Enriquez S, Duarte CM, Sand-Jensen K, Nielsen SL. 1996. Broad-scale comparison of photosynthetic rates across phototrophic organisms. *Oecologia* 108:197-206.
- Fott J, Pechar L, Prazaková M. 1980. Fish as a factor controlling water quality in ponds. In: Barica J, Mur LR, editors. Hypertrophic ecosystems. *Dev Hydrobiol* 2:255-61.

- Fuhrmann JA, Azam F. 1982. Thymidine incorporation as a measure of heterotrophic bacterioplankton production in marine surface waters: evaluation and field results. *Mar Biol* 66:109–20.
- Gächter R, Meyer JS, Mares A. 1988. Contribution of bacteria to release and fixation of phosphorus in lake sediments. *Limnol Oceanogr* 33:1542–58.
- Gulati RD, Lammens EHHR, Meijer M-L, van Donk E. 1990. Biomanipulation, tool for water management. *Hydrobiologia* 200–201:1–628.
- Gulati RD, Ooms-Willems AL, Tongeren OFR, Postma G, Siwertsen K. 1992. The dynamics and role of limnetic zooplankton in Loosdrecht lakes (The Netherlands). *Hydrobiologia* 233:69–86.
- Gulati RD, Siewertsen K, Postema G. 1982. The zooplankton: its community structure, food and feeding, and the role in the ecosystem of Lake Vechten. *Hydrobiologia* 95:127–63.
- Hansen A-M, Christensen JV, Sortkjær O. 1991. Effect of high pH on zooplankton and nutrients in fish-free enclosures. *Arch Hydrobiol* 123:143–64.
- Hansen A-M, Jeppesen E. 1992. Life cycle of *Cyclops vicinus* in relation to food availability, predation, diapause and temperature. *J Plankton Res* 14:591–605.
- He X, Wright R. 1992. An experimental study of piscivore–planktivore interactions: population and community responses to predation. *Can J Fish Aquat Sci* 49:1176–83.
- Hein M, Pedersen MF, Sand-Jensen K. 1995. Size-dependent nitrogen uptake in micro- and macroalgae. *Mar Ecol Prog Ser* 118:247–53.
- Hessen DO. 1997. Stoichiometry in food webs: Lotka revisited. *Oikos* 79:195–200.
- Hobbie R, Daly J, Jasper S. 1977. Use of nuclepore filters for counting bacteria by fluorescence microscopy. *Appl Environ Microbiol* 33:1225–8.
- Holm TF, Tuxen-Pedersen F. 1975. River Gudenåen 1974 [in Danish]. Århus (Denmark): Report from the Laboratory of Physical Geography, Geological Institute, University of Århus, Denmark. 108 p.
- Hosper H. 1997. Clearing lakes: an ecosystem approach to the restoration and management of shallow lakes in the Netherlands [PhD dissertation]. Lelystad (The Netherlands): RIZA. 168 p.
- Hovmand MF, Grundahl L, Runge EM, Kemp KK, Aistrup W. 1993. Atmospheric deposition of nitrogen and phosphorus [In Danish]. Roskilde (Denmark): National Environmental Research Institute, research report no. 91, 65 p.
- Jensen HS, Andersen F.Ø. 1992. Importance of temperature, nitrate and pH for phosphate release from aerobic sediments of four shallow, eutrophic lakes. *Limnol Oceanogr* 37:577–89.
- Jensen JP, Jeppesen E, Bøgestand J, Roer Petersen A, Søndergaard M, Windolf J, Sortkjær L. 1994a. Action Plan for the Aquatic Environment; Survey Programme 1993; Freshwater; Lakes (In Danish). Roskilde (Denmark): National Environmental Research Institute, Research Report no. 121, 93 p.
- Jensen JP, Jeppesen E, Kristensen P, Christensen PB, Søndergaard M. 1992. Nitrogen loss and denitrification as studied in relation to reductions in nitrogen loading in a shallow, hypertrophic lake (Lake Søbygård, Denmark). *Int Rev Gesamten Hydrobiol* 77:29–42.
- Jensen JP, Jeppesen E, Olrik K, Kristensen P. 1994b. Impact of nutrients and physical factors on the shift from cyanobacterial to chlorophyte dominance in shallow Danish lakes. *Can J Fish Aquat Sci* 51:1692–9.
- Jeppesen E, Erlandsen M, Søndergaard M. 1997a. Can simple empirical equations describe the seasonal dynamics of bacterioplankton in lakes? An eight year study in shallow hypertrophic and biologically highly dynamic Lake Søbygård Denmark. *Microb Ecol* 34:11–26.
- Jeppesen E, Jensen JP, Kristensen P, Søndergaard M, Mortensen E, Sortkjær O, Olrik K. 1990a. Fish manipulation as a lake restoration tool in shallow eutrophic lakes. 2. Threshold levels, long-term stability and conclusions. *Hydrobiologia* 200–201: 219–27.
- Jeppesen E, Jensen JP, Søndergaard M, Lauridsen TL, Møller PH, Sandby K. 1998. Changes in nitrogen retention in shallow eutrophic lakes following a decline in density of cyprinids. *Arch Hydrobiol*. Forthcoming.
- Jeppesen E, Jensen JP, Søndergaard M, Lauridsen T, Pedersen LJ, Jensen L. 1997b. Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia* 342–343:151–64.
- Jeppesen E, Jensen JP, Søndergaard M, Sortkjær O. 1996. Fish-induced changes in zooplankton grazing on phytoplankton and bacterioplankton: a long-term study in shallow hypertrophic Lake Søbygård. *J Plankton Res* 18:1605–25.
- Jeppesen E, Kristensen P, Jensen JP, Søndergaard M, Mortensen E, Lauridsen T. 1991. Recovery resilience following a reduction in external phosphorus loading of shallow, eutrophic Danish lakes: duration, regulating factors and methods for overcoming resilience. *Mem Ist Ital Idrobiol* 48:127–48.
- Jeppesen E, Søndergaard M, Mortensen E, Kristensen P, Riemann B, Jensen HJ, Møller JP, Sortkjær O, Jensen JP, Christoffersen K, Bosselmann S, Dahl E. 1990b. Fish manipulation as a lake restoration tool in shallow eutrophic lakes. 1. Cross-analysis of three shallow, eutrophic temperate lakes. *Hydrobiologia* 200–201:205–18.
- Jeppesen E, Søndergaard M, Sortkjær O, Kristensen P. 1990c. Interactions between phytoplankton, zooplankton and fish in a shallow hypertrophic lake: a study on short term changes in the trophic relationships in Lake Søbygård, Denmark. *Hydrobiologia* 191:149–64.
- Jeppesen E, Sortkjær O, Søndergaard M, Erlandsen M. 1992. Impact of a trophic cascade on heterotrophic bacterioplankton production in two shallow fish-manipulated lakes. *Arch Hydrobiol* 37:219–31.
- Jespersen A-M, Christoffersen K. 1987. Measurements of chlorophyll *a* from phytoplankton using ethanol as extraction solvent. *Arch Hydrobiol* 109:445–54.
- Jürgens K. 1994. The impact of *Daphnia* on microbial food webs: a review. *Mar Microb Food Web* 8:295–324.
- Kerfoot WC. 1987. Cascading effects and indirect pathways. In: Kerfoot WC, Sid A, editors. *Predation: direct and indirect impacts on aquatic communities*. Hanover (NH): University Press of New England. p 57–70.
- Koroleff F. 1970. Determination of total phosphorus in natural water by means of the persulphate oxidation. *Cons Int Explor Mer; Interlaboratory Report* 3.
- Kristensen P, Hansen HO, editors. 1994. *European rivers and lakes: assessment of their environmental state*. Copenhagen (Denmark): European Environment Agency. 122 p.
- Kristensen P, Jensen P. 1987. *Sedimentation and resuspension in Søbygård Lake [MSc thesis] [in Danish]*. Silkeborg (Denmark): National Agency of Environmental Protection, Freshwater Laboratory. 152 p.

- Kristensen P, Jensen JP, Jeppesen E. 1990. Simple empirical lake models. In: Miljøstyrelsen, editor. Nitrogen and phosphorus in fresh and marine waters. C-abstract. Copenhagen (Denmark): Environmental Protection Agency. p 125–45.
- Lauridsen TL, Jeppesen E, Andersen FØ. 1993. Colonization of submerged macrophytes in shallow fish manipulated Lake Væng: impact of sediment composition and water fowl grazing. *Aquat Bot* 46:1–15.
- Lathrop RC, Carpenter SR, Rudstam LG. 1996. Water clarity in Lake Mendota since 1900: responses to differing levels of nutrients and herbivory. *Can J Fish Aquat Sci* 53:2250–61.
- Leah RT, Moss B, Forres DE. 1980. The role of predation in causing major changes in the limnology of a hyper-eutrophic lake. *Int Rev Gesamten Hydrobiol* 65:223–47.
- Leibold MA. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *Am Nat* 134:922–49.
- Lynch M. 1980. *Aphanizomenon* blooms: alternate control and cultivation by *Daphnia pulex*. In: American Society of Limnology and Oceanography Special Symposium. Volume 3. Hanover (NH): University Press of New England. p 299–305.
- Marsden S. 1989. Lake restoration by reducing external phosphorus loading: the influence of sediment phosphorus release. *Freshwater Biol* 21:139–62.
- Mathiesen H, Christensen J. 1981. The Gudenå investigation. Characteristics of the Lakes [in Danish]. Århus (Denmark): Botanical Institute, Århus University.
- McQueen DJ, Post JR, Mills EL. 1986. Trophic relationships in freshwater pelagic ecosystems. *Can J Fish Aquat Sci* 43:1571–81.
- Messer JJ, Brezonik PL. 1978. Denitrification in the sediments of lake Okeechobee. *Verh Int Ver Limnol* 20:2207–16.
- Mills EL, Forney JL, Wagner KJ. 1987. Fish predation and its cascading effect on the Oneida Lake food chain. In: Kerfoot WC, Sih A, editors. Predation: direct and indirect effects on aquatic communities. Hanover (NH): University Press of New England. p 118–31.
- Moss B. 1990. Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. *Hydrobiologia* 200–201:367–78.
- Murphy J, Riley JP. 1962. A modified single solution method for the determination of phosphate in natural waters. *Anal Chim Acta* 27:21–6.
- Niewolak S. 1971. The influence of living and dead cells of *Chlorella vulgaris* and *Scenedesmus obliquus* on aquatic microorganisms. *Pol Arch Hydrobiol* 18:43–54.
- Nygaard G. 1949. Hydrobiological studies on some Danish ponds and lakes. *Biol Skr K Vidensk Selsk* 7:1–239.
- OECD. 1982. Eutrophication of waters: monitoring, assessments and control. Paris: OECD. 210 p.
- Olrik K. 1991. Phytoplankton methods for lakes and marine areas. Copenhagen (Denmark): Environmental Protection Agency, Ministry of Environment, Environmental Project no. 187, 108 p.
- Pace ML. 1993. Heterotrophic microbial process. In: Carpenter SR, Kitchell JF, editors. Cascading trophic interactions. Cambridge: Cambridge University. p 252–77.
- Pace ML, Cole JJ. 1996. Regulation of bacteria by resources and predation tested in whole-lake experiments. *Limnol Oceanogr* 41:1448–60.
- Pavoni M. 1963. The importance of nanoplankton compared to netplankton. *Schweiz Z Hydrol* 25:219–341.
- Reinertsen H, Olsen Y. 1984. Effects of fish elimination on the phytoplankton community of a eutrophic lake. *Verh Int Ver Limnol* 22:649–57.
- Riemann B. 1985. Potential importance of fish predation and zooplankton grazing on natural populations of freshwater bacteria. *Appl Environ Microbiol* 50:187–93.
- Riemann B, Søndergaard M, Schierup HH, Bosselmann S, Christensen G, Hansen J, Nielsen B. 1982. Carbon metabolism during a spring diatom bloom in the eutrophic Lake Mossø. *Int Rev Gesamten Hydrobiol* 67:145–85.
- Reynolds CS. 1984. The ecology of freshwater phytoplankton. Cambridge: Cambridge University. 384 p.
- Ryding S-O. 1981. Reversibility of man-induced eutrophication: experiences of a lake recovery study in Sweden. *Int Rev Gesamten Hydrobiol* 66:189–207.
- Sarnelle O. 1992. Nutrient enrichment and grazer effects on phytoplankton in lakes. *Ecology* 73:551–60.
- Sas H, editor. 1989. Lake restoration by reduction of nutrient loading: expectation, experiences, extrapolation. Sankt Augustin: Acad Ver Richardz. 497 p.
- Scheffer M, Rinaldi S, Gragnani A, Mur LR, van Nes EH. 1997. On the dominance of filamentous cyanobacteria in shallow turbid lakes. *Ecology* 78:272–82.
- Schindler DW. 1977. Evolution of phosphorus limitation in lakes. *Science* 195:260–2.
- Shapiro J. 1990. Current beliefs regarding dominance by blue-greens: the case for the importance of CO₂ and pH. *Verh Int Ver Limnol* 24:38–54.
- Shapiro H, Wright DI. 1984. Lake restoration by biomanipulation: Round Lake, Minnesota, the first two years. *Freshwater Biol* 14:371–83.
- Smith VH. 1983. Low nitrogen to phosphorus ratios favour dominance by blue-green algae in lake phytoplankton. *Can J Fish Aquat Sci* 43:1101–12.
- Solórzano L, Sharp JH. 1980. Determination of total dissolved nitrogen in natural waters. *Limnol Oceanogr* 25:751–4.
- Sommer U. 1989. Nutrient status and nutrient competition in a shallow, hypertrophic lake. *Limnol Oceanogr* 34:1162–73.
- Søndergaard M, Jeppesen E, Berg S. 1997. Pike (*Esox lucius* L.) stocking as a biomanipulation tool. 2. Effects on lower trophic levels in Lake Lyng, Denmark. *Hydrobiologia* 343–343:319–25.
- Søndergaard M, Jeppesen E, Kristensen P, Sortkjær O. 1990. Interactions between sediment and water in a shallow and hypertrophic lake: a study on short term changes in the trophic relationships in Lake Søbygård, Denmark. *Hydrobiologia* 1991:139–48.
- Søndergaard M, Kristensen P, Jeppesen E. 1993. Eight years of internal phosphorus loading and changes in the sediment phosphorus profile of Lake Søbygård, Denmark. *Hydrobiologia* 253:345–56.
- Sterner RW, Elser JJ, Hessen DO. 1992. Stoichiometric relationships among producers, consumers and nutrient cycling in pelagic ecosystems. *Biogeochemistry* 17:49–67.
- Timmermann M. 1987. Lacking reproduction of roach (*Rutilus rutilus* (L.)), bream (*Abramis brama* (L.)) and perch (*Perca fluviatilis* (L.)) in Lake Søbygård and the density and growth of fish fry in Lake Væng [in Danish]. Silkeborg (Denmark): the

- Freshwater Laboratory, Agency of Environmental Protection; Publication 85. 81 p.
- Van der Molen DT, Boers PCM. 1994. Influence of internal loading on phosphorus concentration in shallow lakes before and after reduction of external loading. *Hydrobiologia* 275/276:479–92.
- Van Liere L, Gulati RD, editors. 1997. Restoration and recovery of shallow eutrophic lake ecosystems in the Netherlands. *Hydrobiologia* 233:1–287.
- Vijverberg J, Kalf DF, Boersma M. 1996. Decrease in *Daphnia* egg viability at elevated pH. *Limnol Oceanogr* 41:789–94.
- Vollenweider RA. 1976. Advance in defining critical loading levels for phosphorus in lake eutrophication. *Mem Ist Ital Idrobiol* 33:53–83.
- Welch EB, Cooke GD. 1995. Internal phosphorus loading in shallow lakes: importance and control. *Lake Reservoir Manage* 11:273–81.
- Windolf J, Jeppesen E, Jensen JP, Kristensen P. 1996. Modelling the seasonal variation in in-lake concentration and retention of nitrogen in 16 shallow lakes: a four-year mass balance study. *Biogeochemistry* 33:25–44.