

This paper was presented at the symposium 'Integrated Lake and Landscape Management' (18–21 August 1997, Lahti, Finland) under the auspices of the LIFE project 'Integrated System of Drainage Area and Water Rehabilitation' (FIN/A17/FIN/105/PIJ; coordinated by prof. T. Kairesalo)

Restoration of the eutrophicated Köyliönjärvi (SW Finland) through fish removal: whole-lake vs. mesocosm experiences

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Sarvala, J., Ventelä, A.-M., Helminen, H., Hirvonen, A., Saarikari, V., Salonen, S., Sydänoja, A. & Vuorio, K. 2000. Restoration of the eutrophicated Köyliönjärvi, southwestern Finland through fish removal: whole-lake vs. mesocosm experiences. *Boreal Env. Res.* 5: 39–52. ISSN 1239-6095

To improve water quality in a heavily eutrophicated lake (Köyliönjärvi, SW Finland), mass removal of fish was performed in 1992–1998. The fish stock declined from an estimated 170–250 kg ha⁻¹ in 1991–1992 to 40–90 kg ha⁻¹ in 1996–1998 or to 12%–25% of the initial biomass. The biomass of the larger cladocerans slightly increased in 1991–1996 but decreased again in 1997, and chlorophyll *a* levels varied inversely with the cladoceran biomass. Cyanobacteria initially declined, but altogether the water quality effects of fish removal remained small up to the summer 1997. The roles of phosphorus, submerged macrophytes (*Elodea*) and fish were further explored in a factorial enclosure experiment. Significant treatment effects were only observed in the earliest phase of the experiment, when the presence of macrophytes decreased and that of fish increased phytoplankton chlorophyll *a*; later fish treatments were lost. Phosphorus additions had no effect on water quality, but at the end of the experiment phytoplankton chlorophyll *a* was negatively correlated with the biomass of large cladocerans and positively correlated with total phosphorus concentration. The enclosure effect was strong, all enclosures having much lower nutrient and chlorophyll levels than the surrounding lake. The experiment suggests that it is possible to improve water quality through removal fishing even in hypertrophic lakes, but the fish stock, including the young-of-the-year fish, must be decimated to a very low level.

Introduction

Increasing eutrophication is a common problem all over the world. Although the primary cause of eutrophication is excessive external loading of nutrients, especially phosphorus, attempts to reverse the eutrophication process by curbing the external load have often failed (Marsden 1989, Jeppesen *et al.* 1991). The dense populations of cyprinid fish in eutrophic lakes maintain a strong internal loading/cycling of nutrients and control herbivorous zooplankton, thus slowing down or preventing the improvement of water quality. Recently, food web manipulation through removal of excess planktivorous and benthivorous fish has become a popular way to speed up the restoration of eutrophicated lakes, usually in combination with reductions in external load (Benndorf 1990, Reynolds 1994, Horppila *et al.* 1998).

Köyliönjärvi, a lake in southwestern Finland, is an example of a culturally eutrophicated lake amidst of an intensively cultivated agricultural area. It is shallow and located in an area of fertile soils and has thus probably always been relatively productive. However, during the last decades it has become hypertrophic mainly due to intensified agriculture (Itkonen and Olander 1997). Total phosphorus levels in water typically increase during the summer and reach very high values in late summer (Sarvala *et al.* 1995). The late summer total phosphorus levels in water seem to have increased exponentially since the 1960s, or probably since the internal loading from the sediments became important. Concomitant with the increasing nutrient levels, phytoplankton biomass and chlorophyll increased to hypertrophic levels, and heavy blooms of cyanobacteria became common. During the 1980s, the steadily deteriorating water quality started to impede all uses of the lake, and motivated the local community to search for means to improve the situation: in 1990, a restoration project was founded to rescue Köyliönjärvi. The long-term goal of the project was a notable reduction of nutrient loading from the surrounding agricultural area, but, in order to reach control over the internal loading, and hoping to achieve more rapid progress, the project also started a food web manipulation through removal fishing (Hirvonen *et al.* 1993, Sarvala *et al.* 1998). Later this was complemented with intensified

stocking of piscivorous fish (young-of-the-year and age 1+ pikeperch and 0+ pike; Salonen *et al.* 1996, 1998). The removal of coarse fish has so far continued from 1992 to 1998 (Hirvonen and Salonen 1995, Salonen *et al.* 1996). In this paper, we describe the results of the removal fishing and the development of water quality in the lake, complementing the presentation of Sarvala *et al.* (1998) with new data. We also examine the future prospects of the restoration project on the basis of a mesocosm experiment.

Study area

Köyliönjärvi (61°05′–61°10′N, 22°18′–22°24′E; Fig. 1) is shallow lake (mean depth 3.0 m, maximum depth 13 m), and therefore does not show any permanent temperature stratification during summer. The lake is normally ice-covered for 6 months from early November to late April or early May. The drainage area is 129 km² and the lake area is 12.5 km². Theoretical water retention time is 1.0 years. The lake is highly eutrophic, the late summer maxima of total phosphorus having reached up to 170 mg P m⁻³ and those of chlorophyll *a* up to 180 mg chl *a* m⁻³ (Sarvala *et al.* 1998). Extensive cyanobacterial blooms have occurred in late summer, and transparency is poor, late summer Secchi depth being 0.3–0.5 m (Sarvala *et al.* 1995). The external phosphorus loading (0.64 g P m⁻² a⁻¹; Wright *et al.* 1993) exceeds the “permissible” limits of Vollenweider (1975) by a factor of five. About 93% of the total phosphorus input comes as diffuse loading from cultivated fields that comprise 32% of the drainage area. Two thirds of the annual phosphorus load is retained in the lake (Wright *et al.* 1993). There is no commercial fishery in the lake, and the local recreational and subsistence fishery utilizes mainly gill nets and wire traps.

Material and methods

Water quality and plankton

Nutrients, chlorophyll, phytoplankton and zooplankton in Köyliönjärvi have been monitored since 1991, mostly from weekly samples (twice a

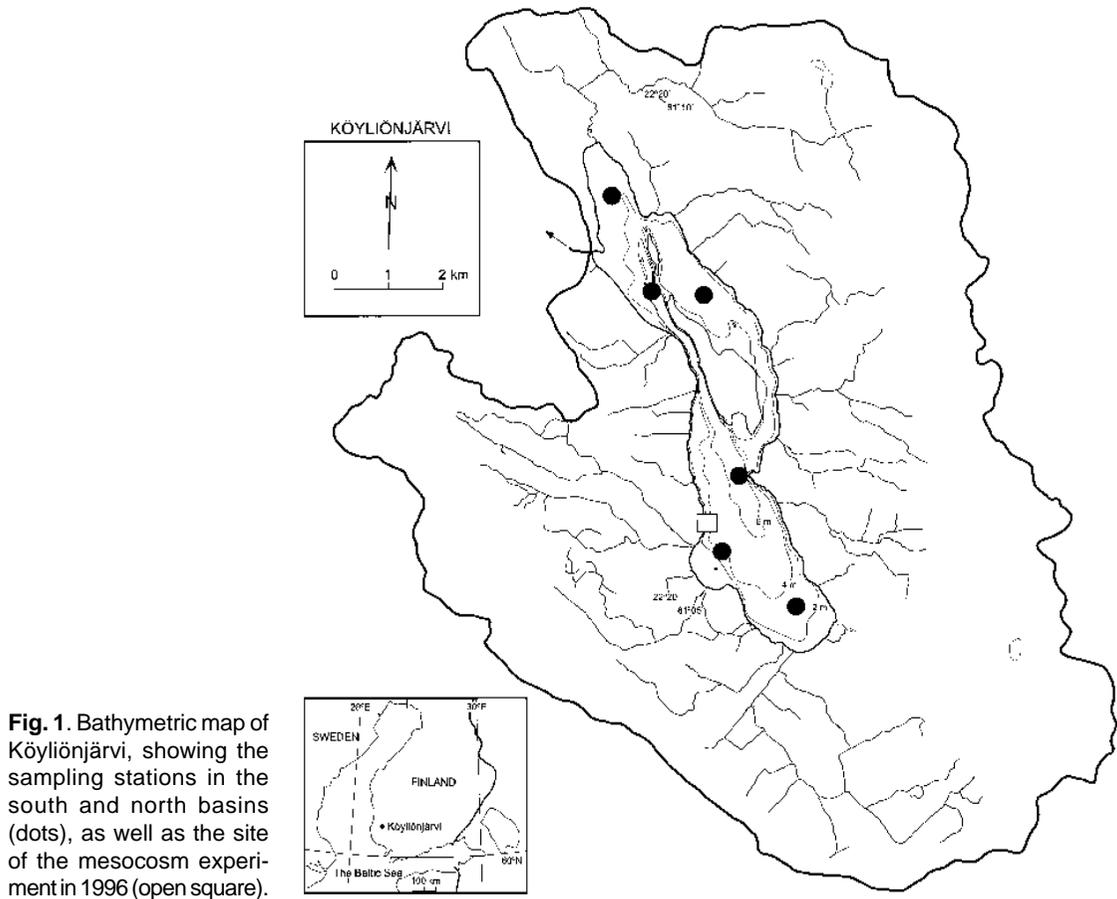


Fig. 1. Bathymetric map of Köyliönjärvi, showing the sampling stations in the south and north basins (dots), as well as the site of the mesocosm experiment in 1996 (open square).

week in 1992). Two water columns from the surface to bottom were sampled with one-metre intervals with a 6.8-l tube sampler (Limnos Ltd., Finland; in 1996 the sampler volume was 2.6 l and in 1997 3.5 l) at each of three sites both in the southern and the northern basin of the lake (Fig. 1) and combined into a single composite sample for each basin and date. Nutrient and chlorophyll analyses were made in the laboratory of the Southwest Finland Regional Environment Centre, those of phytoplankton and zooplankton in the University of Turku. Phytoplankton samples (200 ml) were preserved with acid Lugol solution and counted with an inverted microscope (Utermöhl system). Zooplankton samples were concentrated with a 25 or 50 mm mesh net and preserved with cold 94% ethanol (final concentration 70%). Using an inverted microscope, crustacean zooplankton was identified and counted from subsamples until 50–200 individuals of each dominant spe-

cies had been measured. Length measurements were converted to carbon biomass using carbon to length regressions (as in Sarvala *et al.* 1998).

Additional water chemistry and chlorophyll data were available from vertical sampling series, taken at 2–3 sites usually in late winter and late summer since the 1960s (statutory monitoring and data obtained by the water authorities; unpublished reports of the Water Protection Association of the Kokemäenjoki Watercourse).

Fish

Removal fishing was done in the winters 1992–1998 by commercial fishermen from the nearby lake, Pyhäjärvi, (Sarvala *et al.* 1998) with seine nets operated through holes in the ice. Because of the bottom topography, the fishing concentrated in the southern basin (area 400 ha). In 1996–1998,

seine nets were also used in open water in the autumn, locating the aggregations of fish by echo sounding and sonar. In 1992 and 1996, littoral trap nets, operated by local inhabitants, were also used throughout the open-water season. Harvested fish were sold for animal feed production or directly to fur farms. The average net cost of removal fishing was 2.50 FIM (0.42 ECU) kg⁻¹ or about 150 FIM (25 ECU) ha⁻¹ a⁻¹ (Hirvonen *et al.* 1998).

Changes in the fish community of Köyliönjärvi were studied from two-stage catch samples (procedure described in Salonen *et al.* 1996) taken from 322 (80.1%) of the total of 402 winter seine net hauls during 1992–1998. The samples covered 94.3% of the total winter catch of 355 t. The composition of the trap net and open-water seine net catches (163 t) was similarly assessed. In 1992–1993, the mesh size of the seine cod-end was 8 mm, from 1994 onwards 6 mm. During the winter fishing seasons of 1992, 1993, 1996 and 1998, there was a significant decrease in the catch per seine net haul in the southern basin, allowing estimates of the total catchable fish stock with the removal (DeLury) method (for details of the method, see Hilborn and Walters 1992, and Helminen *et al.* 1993). To reduce random variation, three successive hauls were combined for the final calculations, except in 1992 when only the single haul catches declined significantly. Stock estimates for the southern basin were extrapolated to the whole lake using the ratio of surface areas. Catch-effort estimates provided another way to describe the fish stock development. We regressed the cumulative catch from the southern basin against the log-transformed number of seine hauls each winter. The smallest number of seine hauls in any year from that basin was 26 hauls in 1997; therefore, we calculated the expected catch after 26 hauls for the other years and used the actual total catch for 1997. This method effectively smoothed the random variation of the catches; all regressions were highly significant. Age group analyses of roach (not presented here) allowed us to compensate for the coarser mesh size used in 1992–1993: the stock estimates for 1992 were increased by 15.5% and those for 1993 by 27.0%.

Mesocosm experiment

The roles of nutrients, macrophytes (*Elodea*) and fish (8–10 cm roach (*Rutilus rutilus* (L.))) were

explored in 1996 in a 2 × 2 × 2 factorial enclosure (6 m³) experiment with 3 replicates, following the procedures used earlier in another lake, Vesijärvi (Kairesalo *et al.* 1998). The experimental enclosures were attached to a wooden pier, built at a 50 m distance from the western shore of the south basin. The initial water depth at the site was 1.2–1.4 m, and it declined during the experiment by 20 cm. The pier comprised three contiguous rows of eight 2 × 2.5 m frames parallel to the shore. The enclosures consisted of transparent 0.2-mm plastic, factory-moulded into wide tubes that were attached within the frames. The enclosure walls were sealed into the sediment with sand bags (thirty 2.5-kg bags per enclosure) inserted into a canal welded along the lower ends of the walls. The underwater structures were checked by a diver. The enclosures thus included both water and the underlying natural bottom sediment. Disturbances by birds were prevented by covering the enclosure system with nets. Enclosures were closed on 12 June and checked by diving on 17 June.

The mesocosm experiment followed a randomised block design, each row of enclosures containing all treatment combinations in randomised order. For all factors, zero level denoted no additions. In the nutrient treatments, 70 mg P m⁻³ as KH₂PO₄ was added in the beginning and in the middle of the experiment. In the macrophyte treatments, fresh *Elodea* collected from other parts of the lake were introduced in the beginning and middle of the experiment. In fish enclosures, 16 individuals of 8–10 cm roach, caught with fyke nets from the lake, were introduced in the beginning of the experiment. The first nutrient additions were done on 17 June, and the fish were introduced on 20 June. A total of 5.5 l of *Elodea* per treatment were added on three occasions (1 l on 20 June, 2.5 l on 1 July and 2 l on 18 July; 1 l = 13.8 g dry mass). Sampling from the enclosures started on 23 June and ended 31 July. Very windy weather during the early half of the experiment caused leakages of the wall plastic, and, consequently, the fish and first nutrient treatments were lost. After the leakages had been repaired (by 11 July), the nutrient and macrophyte additions were renewed, but no further fish were added. Nutrients, chlorophyll, bacteria, protozoa, phytoplankton and zooplankton were sampled at 10-day intervals (composite samples from the bottom and

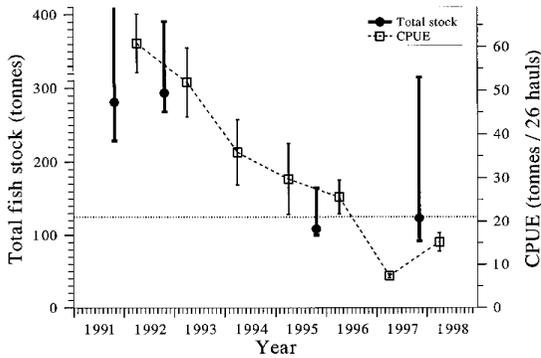


Fig. 2. Development of the total fish stock in Köyliönjärvi in 1991–1998. Dots denote DeLury estimates (vertical bars: 95% confidence limits); open squares denote the cumulative catch per 26 hauls (vertical bars: standard error).

surface layers using a 0.5 m high tube sampler (Limnos; volume 3.5 l). Samples were also taken from the open lake in the immediate vicinity of the enclosures. Periphyton development was assessed from plastic strips suspended vertically into each enclosure (6 strips/enclosure), but no numerical results can be presented because the strips were lost during storage. At the end of the experiment, fish were removed by traps and handnets, and macrophytes collected and weighed.

The experimental results were examined with factorial analysis of variance, multiple regression and partial correlation. The normality of variables was checked with the Wilks-Shapiro test. At the end of the experiment, the values for chlorophyll, total phytoplankton biomass, cyanobacterial biomass, total zooplankton biomass, total phosphorus and total nitrogen did not deviate from normal distributions, and the remaining variables (most of the individual zooplankton and phytoplankton groups) could be normalized with a \log_e -transformation.

Results

Removal fishing

Altogether 518 tonnes (414 kg ha⁻¹) of fish (mainly roach and smelt [*Osmerus eperlanus* (L.)]) were removed from Köyliönjärvi until the end of 1998. Both fish stock indices showed largely similar de-

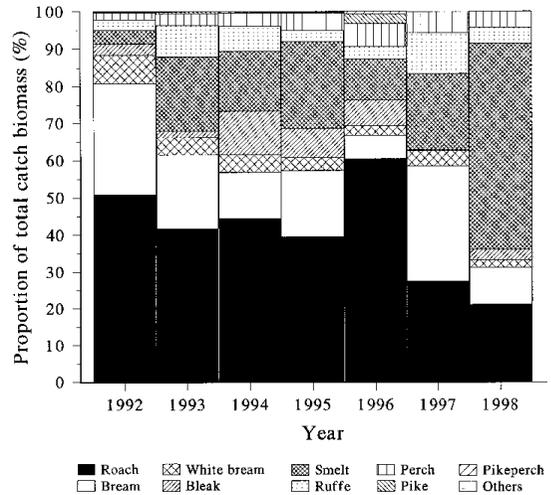


Fig. 3. Proportions of different fish species in the removal fishing catch (winter seine only) in 1992–1998.

crease through the biomanipulation years (Fig. 2). The DeLury estimates for the total fish stock had wide and variable confidence belts (Fig. 2). The point estimates were always close to the lower confidence bound, while the upper confidence belt was much wider. According to DeLury estimates, the fish biomass declined from roughly 170–250 kg ha⁻¹ in 1991–1992 to 40–90 kg ha⁻¹ in 1996–1998 (Fig. 2). The catch-per-unit-effort figures suggested a more regular and somewhat steeper decline of the stock to about 12%–25% of the initial fish stock.

Although there was some fluctuation in the proportions of different species in the catch among the years (Fig. 3), the proportions of roach and bream seemed to decline somewhat (the share of bream in 1997 was inflated by a single large individual in the catch samples), while the proportion of smelt remained largely similar or increased, and perch proportion slightly increased, except for the last year. Altogether the proportion of piscivorous fish (pikeperch, pike and large perch [> 10 cm]) remained very low ($< 5\%$) throughout the period. There were some changes in the size distribution of the fish stock. Even correcting for the effect of the larger mesh size in 1992–1993, the proportion of > 10 cm roach decreased during the period, especially because of strong year-classes hatched in 1996 and 1997 (Fig. 4); simultaneously the mean age of roach declined from

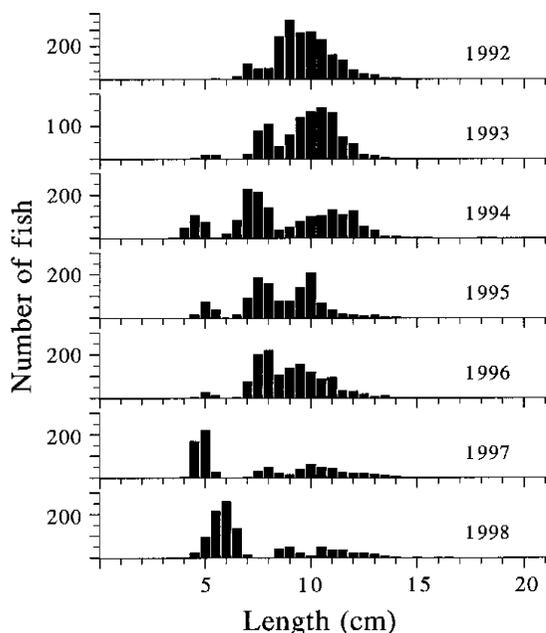


Fig. 4. Length distribution of the roach caught with winter seines in 1992–1997.

3.3 to 2.1 years (J. Sarvala unpubl. data). However, the only species showing a significant trend in size was bream, the mean size of which at least halved during the period.

Water quality development

The late summer phosphorus concentrations increased exponentially since the 1960s, but during the food web manipulation the values have started to decrease (Fig. 5). The decreasing trend was most pronounced in late summer (Fig. 6). Late summer chlorophyll levels did not show any consistent trend during the biomanipulation period, but in the later years there was an inverse relationship with the herbivorous crustacean biomass (Fig. 7).

The total phytoplankton biomass increased during the 1970s concomitant with the phosphorus concentrations, and simultaneously the proportion of cyanobacteria increased, during the 1980s to 70%–80% of total phytoplankton biomass in July–August (Fig. 8). There may be a slight declining trend in the late summer total phytoplankton biomass and in the contribution of cyanobacteria during the biomanipulation period,

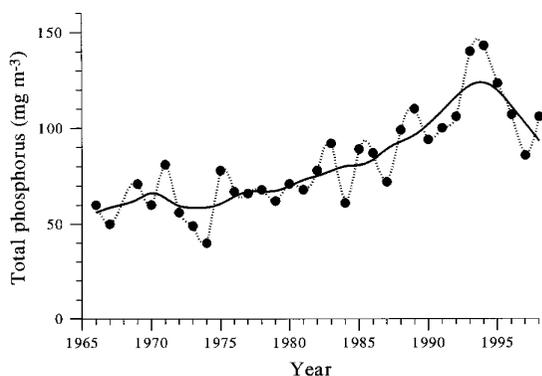


Fig. 5. Average total phosphorus concentration in August in the south basin of Köyliönjärvi in 1966–1998. Sources: Water Protection Association of Kokemäenjoiki Watercourse and Southwest Finland Regional Environment Centre.

but the between-year fluctuations, caused by e.g. weather differences, were too wide to allow definite conclusions.

Altogether the water quality effects of fish removal were so far small. During the biomanipulation period, chlorophyll levels relative to total phosphorus in water were slightly lower than during the preceding decade (Fig. 9). In the early summers of 1996 and 1997, phytoplankton biomass was clearly lower than in the previous years, and yet crustacean biomass remained high. The late summer crustacean zooplankton biomass may have slightly increased up to the year 1996, but in 1997 there was a clear decline again (Fig. 7). Largest between-year variation was due to small cladocerans, mainly *Chydorus sphaericus* (Müller). In both years, phytoplankton chlorophyll level and the biomass of cyanobacteria increased again by autumn. From the moderately decreased fish biomass levels, larger water quality improvements might have been expected in the summer 1997, but the exceptionally high temperatures in that summer probably counteracted any positive development (cyanobacterial blooms were then extremely common in most watercourses in southern Finland; unpublished data base of Finnish Environment Institute). However, there were important changes within the cyanobacterial community in summer 1997: the *Microcystis* species, which had been dominant in previous years, were replaced by *Anabaena*. As a result, there were almost no surface blooms of cyanobacteria in Köy-

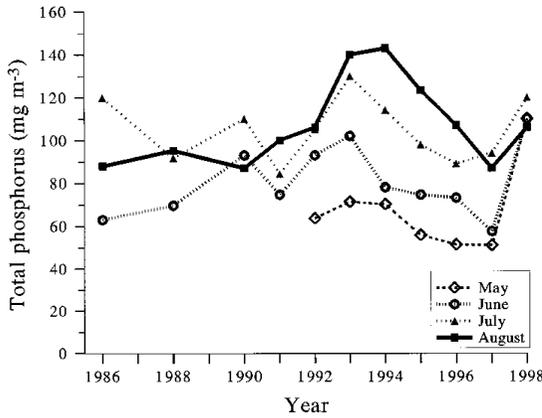


Fig. 6. Average total phosphorus concentrations in the south basin of Köyliönjärvi in May, June, July and August in 1986–1998. Sources as in Fig. 5.

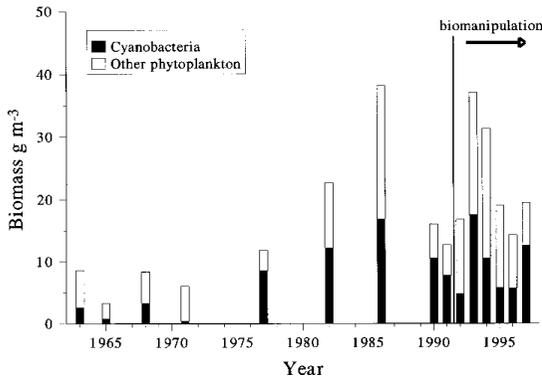


Fig. 8. The average biomass of total phytoplankton and the cyanobacteria in the south basin of Köyliönjärvi in July–August 1963–1997. Data for 1963–1990 from the Finnish Environment Institute.

liönjärvi in 1997 and the cyanobacterial toxins declined to a fraction of previous levels (J. Hietala, pers. comm.).

Mesocosm experiment

Soon after the start of the experiment, water quality in the enclosures began to diverge from the surrounding lake (Fig. 10). This development was reversed due to the leakages, and by 11 July when the leakages were repaired, most enclosures showed phosphorus, nitrogen and chlorophyll values approaching those of the surrounding water. During the next 20 days, different enclosures

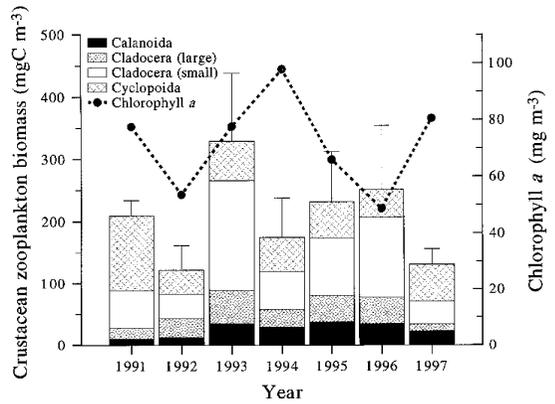


Fig. 7. Late summer (26 July–15 September) concentration of chlorophyll *a* and the biomass of the main crustacean zooplankton groups in the south basin of Köyliönjärvi in 1991–1997 (Sarvala *et al.* 1998, the year 1997 added). Cladocera (“small”) denote *Chydorus cf. sphaericus* and *Bosmina longirostris* (Müller); Cladocera (“large”) include all other non-predatory cladoceran species.

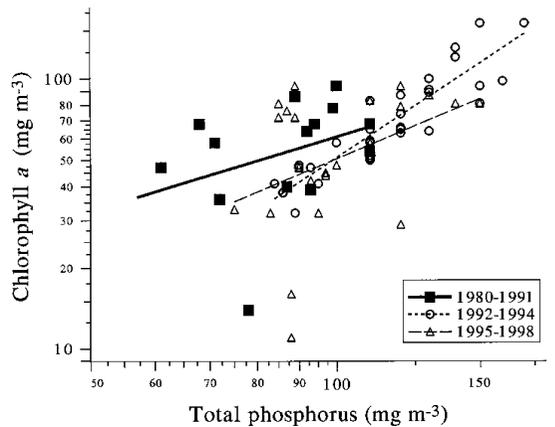


Fig. 9. The average chlorophyll *a* concentration vs. total phosphorus in late summer in the south basin of Köyliönjärvi in 1980–1991 (before biomanipulation), 1992–1994 (early biomanipulation years) and 1995–1997 (late biomanipulation years). Data for 1980–1990 from the Water Protection Association of Kokemäenjoki Watercourse and Southwest Finland Regional Environment Centre.

showed widely divergent development. Differences were largest in chlorophyll and smallest in nitrogen (Fig. 10). The relative homogeneity among the enclosures on 11 July, and the divergence on later dates, were also evident in the chlorophyll: phosphorus relationship (Fig. 11). Total

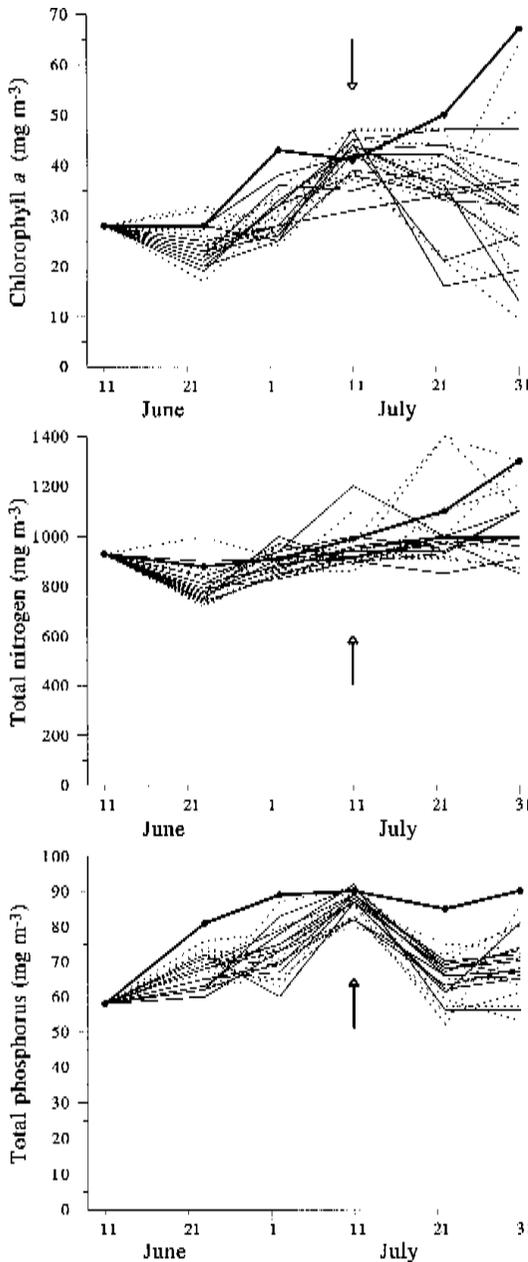


Fig. 10. Development of the total phosphorus, total nitrogen and chlorophyll *a* concentrations in the 24 experimental enclosures (macrophyte treatments shown with thin solid lines) and the surrounding lake (thick lines with dots) during a mesocosm experiment in Köyliönjärvi in summer 1996. Vertical arrows show the date of repair.

phosphorus in the open lake increased mainly during early stages of the experiment and later

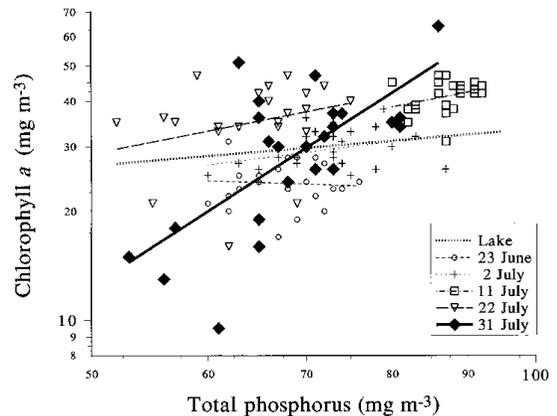


Fig. 11. Chlorophyll *a* vs. phosphorus in different enclosures and in the surrounding lake during the mesocosm experiment in Köyliönjärvi in 1996.

remained almost constant (range 58–90 mgP m⁻³), while most of the enclosures showed decreasing phosphorus levels. Total nitrogen in the lake increased throughout the period, but the relative increase was slightly less than in phosphorus. In most of the enclosures nitrogen remained more stable, but some showed similar increase as in the lake. In general, compared to the situation in phosphorus or chlorophyll, the total nitrogen levels in the enclosures followed more closely the conditions in the lake. In the lake, chlorophyll levels increased considerably in late July, but decreased instead in most enclosures.

At the end of the experiment, the total zooplankton biomass was much higher in all enclosures than in the lake. The largest differences were in the biomass of herbivorous cladocerans (especially *Daphnia cucullata* Sars and *D. cristata* Sars, sometimes also *Ceriodaphnia pulchella* Sars) and calanoids (*Eudiaptomus graciloides* Lilljeborg). *Chydorus sphaericus* showed often the highest biomass; there was negative correlation between the *Chydorus* and *Daphnia* biomasses.

A significant effect of the fish (positive) and plant treatments (negative) on the chlorophyll level of water was observable on the first sampling occasion when the enclosures were still intact (23 June; ANOVA, Table 1; neither the block effect nor any of the interactions were significant and their sums of squares were therefore pooled into the error term). During the rest of the experiment, the fish treatments must be ignored because

most fish escaped through the leakages and no further fish were added. Plant and nutrient treatments were valid after 11 July, but they did not then affect water quality (chlorophyll or nutrient concentrations) to any significant extent. Although the added amount of phosphorus was theoretically sufficient to double the total phosphorus concentration in the enclosures, no significant effects could be traced in any of the analyses. *Elodea* was able to increase appreciably in only one enclosure; in most enclosures the plant biomass decreased. In contrast, the enclosure effect was strong, most enclosures having lower phosphorus, nitrogen and chlorophyll levels than the surrounding lake. This was likely due to the thick mat of periphyton that rapidly developed on the plastic walls; changed sediment-water interactions in the enclosures may also have been involved. However, the difference between the lake and the enclosures was much larger in chlorophyll than in phosphorus or nitrogen, showing that factors other than nutrients were also involved. This was also shown by the notable changes of chlorophyll at a certain phosphorus level (Fig. 11); changes relative to nitrogen were similar.

At the end of the mesocosm experiment, phytoplankton biomass in the lake and in most enclosures was dominated by cyanobacteria. Enclosures with low total biomass also had low proportion of cyanobacteria. Chlorophyll *a* concentration was a good measure of phytoplankton abundance, being tightly correlated with both total biomass ($r = 0.91$) and cyanobacterial biomass ($r = 0.88$). Positive correlations between chlorophyll and pH ($r =$

0.79) and chlorophyll and oxygen concentration of water ($r = 0.82$) were likewise highly significant, confirming that chlorophyll level was also a good indicator of primary productivity in the enclosures. The chlorophyll *a* concentrations in the enclosures showed significant negative correlations with the biomasses of total crustaceans and the large herbivorous crustaceans (the larger cladocerans *Daphnia*, *Ceriodaphnia*, *Diaphanosoma*, *Sida*, *Limnospira* plus the calanoid *Eudiaptomus graciloides*), and significant positive correlations with the total phosphorus and nitrogen concentrations (Table 2). Among the negative correlations of chlorophyll with the major zooplankton groups, those with the calanoid and, unexpectedly, cyclopoid biomass were significant. The latter correlation either indicates herbivorous feeding by cyclopoids or the effect of a confounding factor. Simple correlations between total nitrogen and large herbivorous crustaceans as well as between

Table 1. Analysis of variance table for chlorophyll *a* in the enclosure experiment on 23 June 1996. DF = degrees of freedom, SS = sum of squares, MS = mean square.

Source of variation	DF	SS	MS	F	P
Fish (A)	1	60.17	60.17	5.47	0.030
Phosphorus (B)	1	13.50	13.50	1.23	0.281
Macrophytes (C)	1	54.00	54.00	4.91	0.039
Block (D)					
Error (A·B·C·D)	20	220.17	11.01		
Total	23	347.83			

Table 2. Simple correlations between phytoplankton chlorophyll *a* and various zooplankton and nutrient variables at the end of the enclosure experiment (31 July 1996). Log_e-transformation used throughout (* = $P < 0.05$; ** = $P < 0.01$; $N = 24$).

	CHL	Clado	Cyclo	Calan	Lherbi	Z	TP	TN	CQ2
Chlorophyll <i>a</i> (CHL)	1.00								
Cladoceran biomass (Clado)	-0.24	1.00							
Cyclopoid biomass (Cyclo)	-0.42*	0.12	1.00						
Calanoid biomass (Calan)	-0.52**	0.39	0.55**	1.00					
Large herbivore biomass (Lherbi)	-0.57**	0.56**	0.42*	0.80**	1.00				
Total crustacean zooplankton biomass (Z)	-0.42*	0.90**	0.47*	0.68**	0.77**	1.00			
Total phosphorus (TP)	0.68**	0.25	0.03	-0.15	-0.16	0.14	1.00		
Total nitrogen (TN)	0.83**	-0.14	-0.16	-0.38	-0.51*	-0.28	0.75**	1.00	
Median of cladoceran length (CQ2)	-0.55**	0.04	-0.09	0.10	0.42*	0.06	-0.60**	-0.56**	1.00
Third quartile of cladoceran length	-0.59**	0.13	0.02	0.23	0.54**	0.21	-0.60**	-0.62**	0.79**

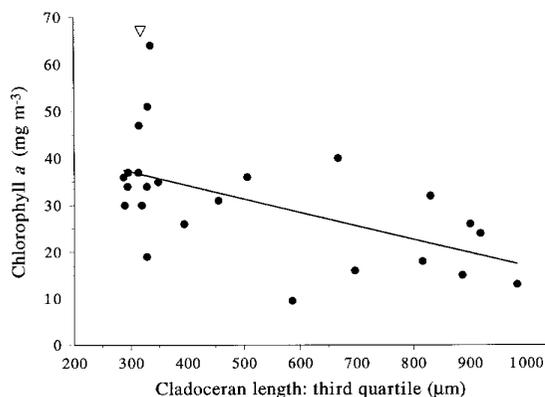


Fig. 12. Chlorophyll *a* vs. the third quartile of cladoceran length distribution at the end of the mesocosm experiment in Köyliönjärvi in 1996. Triangle = lake outside enclosures.

both phosphorus and nitrogen and the median or third quartile of the cladoceran length distribution were significant (Table 2, Fig. 12).

The relationships between different zooplankton and phytoplankton groups showed interesting variation (Table 3). The large herbivores *Daphnia* and *Eudiaptomus* as well as cyclopoids all showed similar negative correlations (although not all exceeding the 0.05 significance level) with cyanobacteria and diatoms, *Daphnia* also with chlorophytes. *Bosmina* likewise had a negative correlation with chlorophytes, while the biomass of *Chydorus* was negatively correlated with chrysophytes. There was an almost significant positive correlation between *Daphnia* and cryptophytes, also manifest at the composite “large herbivore” group level. These correlations might reflect differing

feeding preferences of the crustacean groups.

Multiple regression analyses showed that phytoplankton chlorophyll *a* at the end of the experiment was predictable from the biomass of total crustacean zooplankton, large herbivorous crustaceans, and the total phosphorus and total nitrogen concentrations (Table 4, Fig. 13). The importance of each nutrient in these regressions varied according to the other variables included. Multicollinearity arising from the high mutual correlations between the independent variables makes it difficult to judge the relative role of each explanatory variable. When the effect of the other two independent variables was removed, the highest partial correlation with chlorophyll was shown by total crustacean zooplankton biomass (-0.54 ; large herbivores: -0.42), and total phosphorus showed higher partial correlation (0.47) than total nitrogen (0.40) (ln-transformed values). Among the different zooplankton variables, the large herbivore biomass explained the largest fraction (30%) of chlorophyll variation. The correlations between chlorophyll and the median or third quartile of the cladoceran zooplankton length distribution (Table 2) disappeared when nutrient variables were included. The final concentration of nitrogen in the enclosures was also inversely correlated with the biomass of large herbivores. These results suggest that zooplankton grazing controlled phytoplankton abundance and that phosphorus was the primary nutrient affecting phytoplankton abundance, the correlation between chlorophyll and nitrogen arising secondarily, because increases in nitrogen-fixing blue-green algae simultaneously lead to elevated total nitrogen.

Table 3. Simple correlations between major crustacean zooplankton groups and the main phytoplankton groups at the end of the enclosure experiment (31 July 1996). Log_e-transformation used for all variables except cyanobacterial biomass. Phytoplankton groups: Cyano = Cyanobacteria, Crypto = Cryptophyceae, Chryso = Chrysophyceae, Diatomo = Diatomophyceae, Chloro = Chlorophyceae. The zooplankton group “Other Cladocera” mainly consists of *Chydorus*.

	Cyano	Crypto	Chryso	Diatomo	Chloro
<i>Bosmina</i>	-0.25	0.17	-0.10	-0.37	-0.43*
<i>Daphnia</i>	-0.37	0.38	-0.15	-0.49*	-0.55**
Other Cladocera	-0.01	-0.16	-0.51*	0.17	0.05
Cyclopoida	-0.45*	-0.02	0.04	-0.47*	-0.21
<i>Eudiaptomus</i>	-0.43*	0.17	0.02	-0.39	-0.10
Large herbivores	-0.52*	0.38	-0.07	-0.55**	-0.45*
Total zooplankton	-0.40	0.16	-0.39	-0.30	-0.37

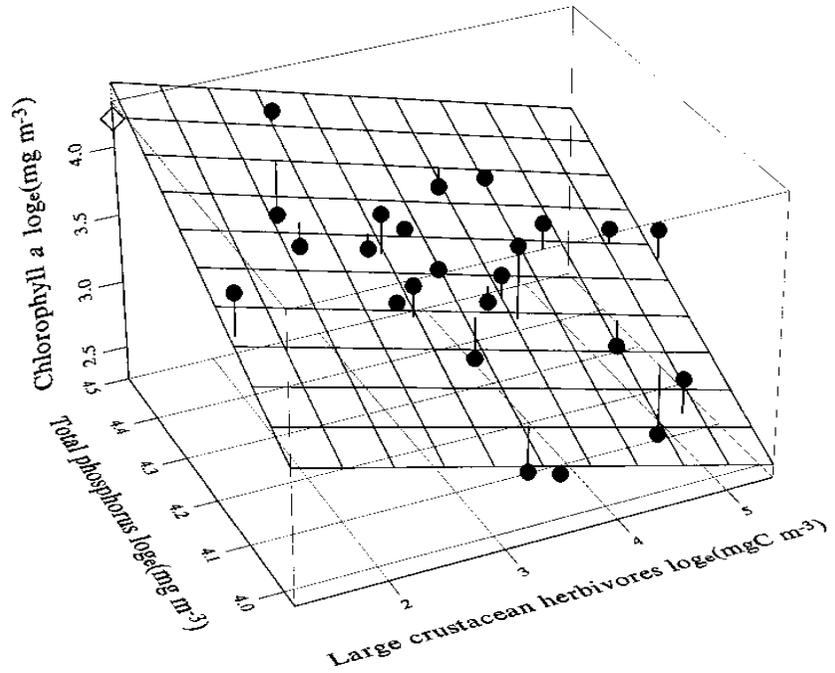


Fig. 13. Chlorophyll *a* vs. total phosphorus and crustacean zooplankton biomass at the end of the mesocosm experiment in Köyliönjärvi in 1996. Diamond = lake outside enclosures.

Discussion

Our long-term study indicated only slight changes in the water quality of eutrophic Köyliönjärvi,

although removal fishing had reduced the total fish biomass to 12%–25% of the initial level. However, a mesocosm experiment showed that abundant herbivore crustacean zooplankton had the

Table 4. Regressions of phytoplankton chlorophyll *a* on the zooplankton biomass, total phosphorus concentration and total nitrogen concentration (\log_e -transformation used throughout) at the end of the mesocosm experiment in Köyliönjärvi in 1996. (1) Total crustacean zooplankton biomass used, (2) herbivore crustacean biomass used, (3) same as (2), but without nitrogen. SD = standard deviation; $N = 24$.

Variables	Regression coefficients	SD	Student's <i>t</i>	<i>P</i>	Fraction explained
(1)					
Total crustacean zooplankton	-0.36	0.13	-2.87	< 0.01	0.14
Total phosphorus	1.72	0.73	2.36	< 0.03	0.58
Total nitrogen	1.50	0.78	1.93	< 0.07	0.03
Overall <i>F</i> = 23.80	$P \ll 0.001$	Adjusted $R^2 = 0.75$			
(2)					
Large herbivorous crustacean zooplankton	-0.13	0.06	-2.06	0.05	0.30
Total phosphorus	1.11	0.71	1.58	0.13	0.36
Total nitrogen	1.81	0.84	2.16	0.04	0.05
Overall <i>F</i> = 19.47	$P \ll 0.001$	Adjusted $R^2 = 0.71$			
(3)					
Large herbivorous crustacean zooplankton	-0.21	0.06	-3.84	0.001	0.30
Total phosphorus	2.31	0.47	4.89	0.0001	0.36
Overall <i>F</i> = 22.89	$P \ll 0.001$	Adjusted $R^2 = 0.66$			

potential to control phytoplankton development even in this lake.

Scheffer (1990) and Scheffer *et al.* (1993) hypothesized that shallow lake ecosystems possess two alternative stable states. At low nutrient levels submerged macrophytes abound and water is clear, while at high nutrient concentrations macrophytes disappear and water remains turbid. Over a range of intermediate nutrient concentrations the system might switch between these states depending on its history and recent perturbations. Our experiences from entire Köyliönjärvi confirm the strong resistance to change of turbid, highly eutrophic lakes (Jeppesen *et al.* 1991). Submerged macrophytes were not able to grow well in the turbid water neither in the enclosures nor in the open lake, and thus they could not affect water quality. However, data collected so far from a number of southern Finnish lakes (Sarvala *et al.* 1997, 1998, and unpublished) suggest that lakes may switch between turbid and clear state irrespective of their nutrient levels. This result agrees well with the literature survey of Mazumder (1994) showing that the water quality responses of lakes formed a wide belt over a range of nutrient concentrations. For example, during a period of 17 years, phytoplankton chlorophyll in Pyhäjärvi, a lake in southwestern Finland, did not oscillate between two alternative end states, but, depending on the strength of the planktivorous fish stock, varied in a continuum between extremely high and extremely low values relative to the phosphorus level (Sarvala *et al.* 1997, 1998). Nothing in the behaviour of Pyhäjärvi suggests that any of the annual situations would be an equilibrium state, rather, the food web structure was continuously changing as a response to external (natural and anthropogenic) fluctuations; the nature of the responses is affected by the different characteristic time scales of the system components, e.g. due to their long generation times, fish buffer changes and cause delayed responses. At the microbial level the responses become evident within a couple of days (e.g. A.-M. Ventelä unpubl.), while a strong year-class of fish may dominate the system over several years. Like Persson *et al.* (1993), we are sceptic about the existence of any real alternative stable states in lake ecosystems.

One interesting result from our mesocosm

experiment was that the enclosure effects were so dominant over other factors affecting water quality. The plastic enclosure walls provided a suitable firm surface for prolific growth of attached algae, which were then able to assimilate a notable part of the nutrients in water into periphyton biomass. Although rarely indicated in published reports, such strong enclosure effects can be expected to be common in comparable experiments. A negative correlation between periphyton and phytoplankton has often been documented (Sand-Jensen and Borum 1991, Harris 1995). It is conceivable that part of the macrophyte effects in such experiments might be mediated through epiphytic growth on the submerged plants (Van Donk *et al.* 1995, Brock *et al.* 1995). In any case, the periphyton development should be taken into account when interpreting experimental results.

In contrast to several earlier studies (e.g. Schriver *et al.* 1995, Kairesalo *et al.* 1998), in our experiment the submerged macrophytes had only minor water quality effects. This was probably due to the high turbidity of water that prevented the growth of *Elodea* through light limitation. In the experiments of Kairesalo *et al.* (1998) in Vesijärvi, the initial transparency of water was much better than in our experiment in Köyliönjärvi. Thus, although macrophytes clearly have the potential to enhance water quality, this will not come into effect until the transparency has first improved and remained good for a relatively long time to allow for macrophyte development (Irvine *et al.* 1989, Jeppesen *et al.* 1990).

Although our mesocosm experiment was technically only partially successful, it suggested that the phytoplankton biomass was regulated not only by nutrients (phosphorus) but also to an almost similar extent by the abundance of herbivorous crustacean zooplankton. The resulting multiple regression equation was almost identical with the corresponding equation obtained from a long-term field data series for the neighbouring Pyhäjärvi (Sarvala *et al.* 1998), which is only weakly mesotrophic. It seems therefore justified to conclude that probably the same mechanisms are regulating water quality in both lakes, although complications may arise from the fact that the crustacean zooplankton abundance also affected in several ways the microbial food web in the enclo-

tures (K. Wiackowski unpubl.). Thus, although the fish removal has not yet resulted in any dramatic water quality changes in Köyliönjärvi, such changes are likely when the crustacean zooplankton becomes more abundant. That crustacean zooplankton has not yet increased as much as one might have expected from the decimated fish populations, can most probably be attributed to two conditions. First, the remaining fish biomass consists mostly of very small-sized fish, which are the most efficient plankton-feeders. Second, exceptionally large year-classes of roach and other coarse fish were probably born during the very warm summer of 1997. It is known that the young-of-the-year fish often account for a major part of total fish production (Chadwick 1976) and food consumption (Helminen *et al.* 1990, Helminen and Sarvala 1994), and, consequently, are also most important in controlling the crustacean zooplankton (Langeland 1982, Lescher-Moutoué *et al.* 1985, Cryer *et al.* 1986, Whiteside 1988, Helminen *et al.* 1990, Helminen and Sarvala 1994).

Based on our results, we conclude that it is possible to improve water quality through removal fishing even in hypertrophic lakes, but the planktivorous fish stock must be reduced to a very low level, and the piscivorous fish stocks should simultaneously be enhanced to decimate the numbers of fish that are too small to be controlled by fishing.

Acknowledgements: This paper is part of a series of studies financed by the Academy of Finland (grants 1071292, 4158, 31365, 35425 and 35619 to JS). We thank Ilkka Blomqvist, Hannu Koponen, Marianne Moilanen, Marjo Tarvainen, Krzysztof Wiackowski and Olli Ylönen, the laboratory personnel of Southwest Finland Regional Environment Centre, Satakunta Environmental Research Centre, and Hannu Uusi-Laurila, the manager of the Räpi Experimental Farm in Köyliö, who all helped in various ways with the field and laboratory work. Lake Köyliönjärvi Protection Association and an Engineering Unit from the Finnish Army helped with the construction of the field enclosures. Dr. Arto Itkonen, Department of Geology, University of Turku, kindly provided the map template for Fig. 1. The removal fishing was financed by the municipality and fisheries district of Köyliö, Köyliö Fish Farm Ltd, the Turku Fisheries District, Southwest Finland Regional Environment Centre, Lake Köyliönjärvi Protection Association and the local farmer and village associations.

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Received 29 June 1999, accepted 8 November 1999