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ECOSYSTEMS

MINIREVIEW

Biomanipulation as an Application of Food-Chain Theory: Constraints, Synthesis, and Recommendations for Temperate Lakes

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ABSTRACT

The aim of this review is to identify problems, find general patterns, and extract recommendations for successful biomanipulation. An important conclusion is that the pelagic food chain from fish to algae may not be the only process affected by a biomanipulation. Instead, this process should be viewed as the "trigger" for secondary processes, such as establishment of submerged macrophytes, reduced internal loading of nutrients, and reduced resuspension of particles from the sediment. However, fish reduction also leads to a high recruitment of young-of-the-year (YOY) fish, which feed extensively on zooplankton. This expansion of YOY the first years after fish reduction is probably a major reason for less successful biomanipulations. Recent, large-scale biomanipulations have made it possible to update earlier recommendations regarding when, where, and how biomanipulation should be performed. More applicable recommendations include (1) the reduction in the biomass of planktivorous fish should be 75% or more; (2) the fish reduction should be performed efficiently and rapidly (within 1–3 years); (3) efforts should be made to reduce the number of benthic feeding fish; (4) the recruitment of YOY fish should be reduced; (5) the conditions for establishment of submerged macrophytes should be improved; and (6) the external input of nutrients (phosphorus and nitrogen) should be reduced as much as possible before the biomanipulation. Recent biomanipulations have shown that, correctly performed, the method also achieves results in large, relatively deep and eutrophic lakes, at least in a 5-year perspective. Although repeated measures may be necessary, the general conclusion is that biomanipulation is not only possible, but also a relatively inexpensive and attractive method for management of eutrophic lakes, and in particular as a follow-up measure to reduced nutrient load.

Key words: biomanipulation; lake; restoration; food chain; phosphorus; nutrient; fish; cyprinid.

INTRODUCTION

Despite considerable reduction in external nutrient loading, many lakes affected by urban and agricultural activities have remained eutrophic with algal

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blooms and fish kills. One of many methods for improving the conditions in such lakes is *biomanipulation*, a term coined in 1975 (Shapiro and others 1975) and since embraced as one of the more controversial applications of ecological theory. Generally, the word refers to manipulation of the fish community to reduce predation pressure on herbivorous zooplankton, supposedly followed by an increased abundance and size of zooplankton, particularly *Daphnia*. This, in turn, theoretically leads to higher grazing pressure on phytoplankton and, subsequently, to clear water.

The logic behind this chain of causes and consequences is appealing and easy to understand (Hairston and others 1960). The simplicity of the theory, and the clear predictions derived from it, have attracted considerable interest from researchers, especially freshwater ecologists, making the *food-chain theory* one of the most thoroughly tested theories in aquatic ecology [for example, see Carpenter and Kitchell (1993) and Polis and Winemiller (1996)]. Numerous laboratory, enclosure, and whole-lake studies have, at least partly, corroborated the hypotheses derived from the theory. However, many studies have failed to show any effects on zooplankton and algae following perturbations in the fish community [for a review, see Lyche (1989), Walker (1989), DeMelo and others (1992), Phillips and Moss (1994), Reynolds (1994), and Moss and others (1996a)].

The road from basic science to application is generally winding and the progress laborious. This, however, has not been the case in applying the food-chain theory to biomanipulation. In the early stages of theory application, several biomanipulations were performed (Shapiro and Wright 1984; Benndorf and others 1988) in an attempt to eliminate nuisance algal blooms from eutrophic lakes. Despite improved technical capabilities, the theoretical foundation used by lake managers when conducting biomanipulations often remains similar to that in 1975, regardless of the substantial progress made in food-chain theory since then (Carpenter and others 1985; Persson and others 1988; Scheffer 1990; Moss and others 1996a). Because recent biomanipulations have failed to prove that the simple fish–zooplankton–algae food chain is the only process involved in biomanipulation, the exclusive use of food-chain theory for explaining observed patterns has been drastically criticized: “To some extent, the original idea of biomanipulation (increased zooplankton grazing rate as a tool for controlling nuisance algae) has become a burden” (Horppila and others 1998). Removal of planktivorous fish or addition of piscivorous fish to a lake clearly affects lower trophic levels, but the effects may not necessarily be the ones predicted by the simple and appealing food-chain theory. The importance of other processes besides pure food-chain dynamics has been demonstrated mainly in shallow lakes (Jeppesen and others 1990a, 1990b, 1997, 1998; Moss 1990, 1996a; Scheffer 1990, 1998), where theoretical development has progressed in closer cooperation with lake managers than in the case of deeper lakes. Consequently, theoretical advances were implemented early in the management of shallow lakes [for example, see Jeppesen and others (1990a, 1990b, 1997), Moss (1990), Hosper and Meijer (1993), Moss and others (1996a), Perrow and others (1997), and Scheffer (1998)].

In this review, we discuss processes, derived from results of recent whole-lake biomanipulations, that are likely to confound and support, respectively, a successful rehabilitation of eutrophic lakes. Our aim is also to reevaluate earlier reviews on biomanipulation and to provide updated recommendations for biomanipulation as a lake-management tool. Moreover, we aim to provide a useful guide for lake managers, meaning that we focus more on applications, synthesis, and recommendations, that is, on the connection between basic and applied research, than on theoretical background. For a more thorough description of the theory behind biomanipulation, see Carpenter (1988), Carpenter and Kitchell (1993), and Polis and Winemiller (1996)

Results from Whole-Lake Biomanipulations

Most studies performed to test food-chain theory are conducted in small-scale laboratory or field enclosures. The restricted spatial and temporal scales of such studies cause problems in extrapolation to the whole-lake scale. We therefore focus exclusively on whole-lake studies, including the removal of planktivorous fish and the addition of piscivorous fish, as well as unintentional major fish kills. Among whole-lake manipulations, the quality of available data varies widely from occasional samplings to long-term monitoring before and after the biomanipulation. To avoid dubious conclusions, we have established criteria that a study should fulfill to be included in the evaluation:

1. The manipulation has been intensive; that is, carried out over a limited period (generally 1–3 years).

2. Data are available for at least 5 years after the manipulation was initiated (exceptionally a briefer period was accepted). Although, this criterion excluded many short-term biomanipulations from this

review, the value of lake responses after only 1 or 2 years is limited in making future recommendations. Most agencies involved in biomanipulations are interested in longer-lasting effects. Short-term studies are reviewed by Benndorf and others (1988), Lyche (1989), Walker (1989), Shapiro (1990), Phillips and Moss (1994), and Reynolds (1994).

To focus the discussion and allow valid comparisons, we have standardized the evaluations by quantifying selected diagnostic variables and comparing them during June to September the year before the manipulation began (year 0) and 5 years after the manipulation (year 5). One problem with this standardization is that if one or even both of the years 0 and 5 happen to be "exceptional" in one way or another, so conclusions drawn from that specific case study will be affected. Despite this, we believe that a large number of well-documented studies treated in a standardized way is a powerful tool in extracting general conclusions. The selected variables are Secchi depth, chlorophyll-*a* concentration, submerged macrophyte cover, *Daphnia* biomass, total phosphorus concentration, and blue-green algal density.

Below, we briefly describe some recent biomanipulations that fulfill the criteria just outlined. For details about the measures undertaken, we refer to the references given for each study. The effort and methods differ among the case studies, but all aimed to reduce cyprinid fish numbers. The methods used include cyprinid fish removal or piscivore addition or a combination of both. Also "nonselective" fish removals, such as major fish kills, are included. Some of the studies presented are well documented, allowing for extraction of more details, including additional diagnostic variables, as well as discussion of temporal changes.

In most of the case studies discussed, the external nutrient loading had been reduced prior to biomanipulation so that, for the majority of the lakes, the total phosphorus concentration was below 200 µg L^{-1} at the start of the biomanipulation. Data presented are all summer means (June to September inclusive).

Cyprinid Removal in Combination with Piscivore Addition

Cyprinids were generally removed by trawling. Piscivorous fish caught were returned to the lake, whereas the cyprinids were removed. As a complement to the fish removal, young piscivorous fish were added to the lakes to increase the predation pressure on remaining cyprinids.

Bleiswijkse Zoom is a small, shallow (14.4 ha; mean depth, 1 m), wind-exposed lake in the Netherlands (Meijer and others 1990, 1994). Five years after biomanipulation, the phosphorus concentration had not changed, but the Secchi depth had increased from 0.1 to 0.5 m and the chlorophyll concentration was reduced by about 50% (Table 1). The biomass of *Daphnia* was lower, whereas the cover of submerged macrophytes had increased considerably (Table 1).

Lake Zwemlust, in the Netherlands, is a small, urban, swimming lake (1.5 ha) that was drained, refilled, and biomanipulated in 1987 (Ozimek and others 1990; van Donk and others 1990b). The results were dramatic, including an increase in Secchi depth from 0.1 to 1.9 m, a reduction in chlorophyll concentration of 95%, and a 50% reduction in total phosphorus concentration (Table 1). Moreover, the biomass of large grazers increased sevenfold and the sediment surface was completely covered with submerged macrophytes 5 years after the treatment (Table 1). However, the biomanipulation in Lake Zwemlust should be viewed as an extreme case in that such drastic manipulations are not realistic in larger lakes.

Sövdeborgssjön in southern Sweden is small (11 ha) and shallow (mean depth, 2.5 m). The fish reduction was only 20%, but may have been further reduced by high predation pressure from pike and pike perch (Persson and others 1993). The effects of the biomanipulation were minor, with the exception of *Daphnia* biomass, which showed a modest increase (Table 1).

Lake Vesijärvi, situated close to the city of Lahti in Finland, is large (110 km^2), with a mean depth of 6.8 m. Only one of the three basins, the Enonselkä Basin (26 km^2), was biomanipulated (Horppila 1994; Sammalkorpi and others 1995; Kairesalo and others 1996; Horppila and others 1998). During and after the biomanipulation, there was a decrease in the concentrations of total phosphorus and chlorophyll, whereas Secchi depth doubled (Figure 1). The percentage of blue-green algae decreased from 67% to about 9% of total phytoplankton biomass. With respect to *Daphnia*, data are scarce or not yet analyzed, but no major changes in abundance seem to have occurred (Figure 1). The coverage of submerged macrophytes increased after the biomanipulation, especially *Elodea canadensis* and *Ceratophyllum demersum*. Before the biomanipulation, *E. canadensis* grew at depths below 2 m, whereas in 1993 it had colonized areas at 4-m depth (Sammalkorpi and others 1995).

Cyprinid Fish Removal

Norddiep is, like Bleiswijkse Zoom, a shallow and wind-exposed lake in the Netherlands [31 ha; mean

Table 1. Summary of Diagnosis Variables of Biomanipulations (Mean Values Based on Data from June to September)

	Secchi			Chlorophyll			Macrophytes			*Daphnia*			Total Phosphorus			Blue-Green Algae					
	0	5	±	0	5	±	0	5	±	0	5	±	0	5	±	0	5	±	Source	Start	End
Fish reduction and piscivores																					
Bleiswijkse Zoom	0.1	0.5	+	95	50	−	0	50	+	1.50	0.60	−	250	230	0				1, 2	1986	1991
Zwemlust	0.1	1.9	+	250	12	−	0	100	+	0.10	0.70	+	1200	750	−				2–4	1986	1991
Sövdeborgssjön	1.4	1.3	0	28	28	0				0.01	0.04	+	62	71^E	+				5	1980	1985
Vesijärvi (Enonselkä)	1.5	2.9	+	21	8	−			$+^K$			0^L	48	32	−	67	9	−	6–8	1989	1994
Fish reduction																					
Norddiep	0.1	0.9	+	55	10	−	30	62	+	1.5	1.4^H	0	200	400	−				2	1987	1991
Vaeng	0.8	1.8	+	78	10	−	0	78	+	0.03	0.3^H	+	150	140	0				2, 9, 10	1986	1991
Finjasjön	0.4	1.9	+	60	20	−	4	23	+	0.05	0.1^H	+	210	50	−	98	18	−	11	1992	1995–96
Sätoftasjön	0.8	1.1	+	58	35	−	15	16	0	0.26	0.20	−	93	75	−	44	51	+	12	1989	1994
Västra Ringsjön	1.9	1.3	0	37	26	−	8	10	0	0.36	0.35	0	56	67	+	39	25	−	12	1991	1996
Cockshoot Broad				37	23	−	0.01^A	13^A	+	24^C	51^C	+	70	170	+				13	1988	1993
Piscivores																					
Bautzen Reservoir	2.3	1.4	−	10^D	20^D	+				1.2^D	5.2^D	+	$170^{B,G}$	448^G	+				14	1980	1985
Gjersjøen				5.5^D	1.8^D	−							20	17	−	60	7	−	15, 16	1981	1986
Lyng	0.6	1.8	+	95	30	−				19^C	6^C	−	790	410	−	61	14	−	17	1989	1994
Nonselective reductions																					
Lake St. George	1.7	2.4	+	9	5	−				0.80	0.83	0	33	25	−				18	1981	1986
Haugtjern				14^F	4^F	−				45^C	74^C	+	45	33	−	14	32	+	15, 19, 20	1980	1984
Östra Ringsjön	0.7	1.7	+	48	28	−	3	3	$+^I$	0.16	0.11	−	114	72	−	72	27	−	12	1987	1992
Helgetjern	0.7	1.1	+	110	55	−				0.00	0.00	0	180	85	−	35	25	−	21	1984	1988

Lakes are divided into the following biomanipulation categories: fish reduction and piscivore addition, only fish reduction, only piscivore addition, and nonselective fish reductions (fish kills or rotenone treatment). Variables are Secchi depth (m), chlorophyll (μg L^{-1}), submerged macrophytes (% cover), Daphnia (mg DW L^{-1}), total phosphorus (μg L^{-1}), and blue-green algae (% of total algal biomass). The signs + and − indicate that the variable increased or decreased at least 15% during the period.

A, g DW m^{-2}; B, DRP 1978 due to no sampling 1980; C, no. L^{-1}; D, mg WW L^{-1}; E, 1983; F, g C m^{-2}; G, DRP, μg L^{-1}; H, 4 years after biomanipulation; I, increase during summers (G. Andersson personal communication), but high numbers of swans and coots affected the macrophytes; K, macrophytes not quantified but a considerable increase was noted (Luokkanen unpublished); L, preliminary data show no major changes (Luokkanen unpublished).

1, Meijer and others 1989; 2, Meijer and others 1994; 3, van Donk and others 1990a, 1990b; 4, Ozimek and others 1990; 5, Persson and others 1993; 6, Sammalkorpi and others 1995; 7, Kairesalo and others 1996; 8, E. Luokkanen unpublished; 9, Jeppesen and others 1990a, 1990b; 10, E. Jeppesen unpublished; 11, Bergman and others 1994; 12, E. Bergman unpublished; 13, Moss and others 1996a, 1990b; 14, Benndorf and others 1988; 15, Olsen and Vadstein 1989; 16, Faafeng 1995; 17, Søndergaard and others 1997; 18, McQueen and others 1989; 19, Reinertsen and others 1990; 20, Langeland 1990; 21, Faafeng and Brabrand 1990.

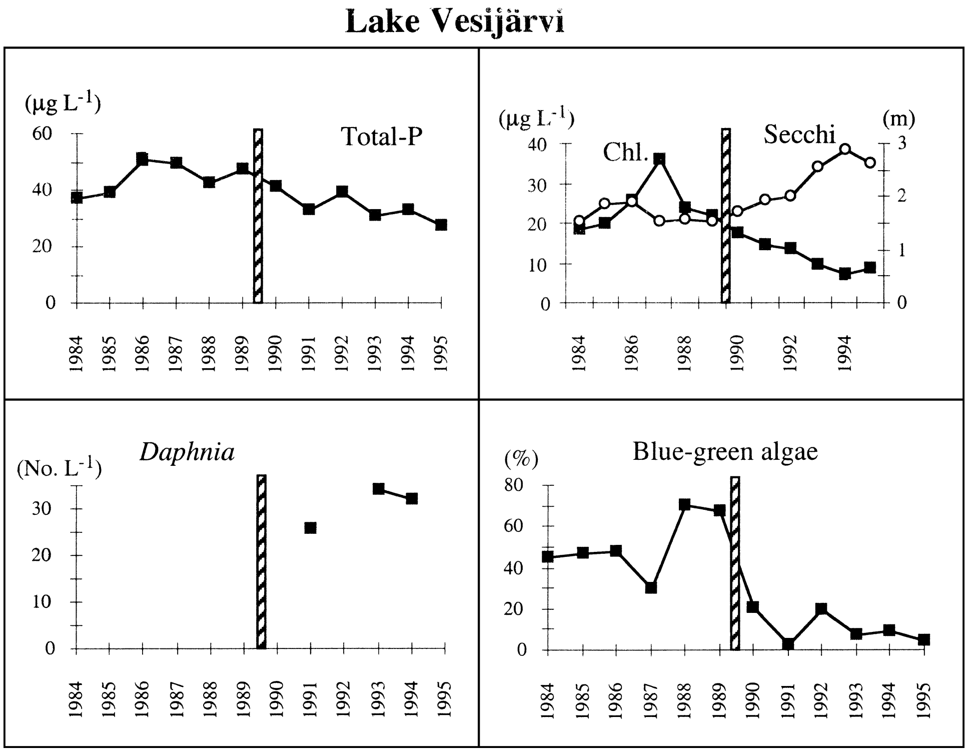

Figure 1. Temporal fluctuations in chemical and biological variables in Lake Vesijärvi (Finland). The striped bar indicates the start of the biomanipulation. The variables are total phosphorus (µg L^{-1}), Secchi depth (m), chlorophyll *a* (µg L^{-1}), *Daphnia* abundance (no. L^{-1}), and blue-green algae as proportion (%) of total algal biomass.

depth, 1.6 m (Meijer and others 1990, 1994)]. The outcome of the biomanipulation was similar to that in Bleiswijkse Zoom except that the concentration of total phosphorus increased markedly (Table 1).

Væng is a small (15 ha) lake situated in Jutland, Denmark (Søndergaard and others 1990; Jeppesen and others 1991, 1998; Meijer and others 1994). As for Vesijärvi, the phosphorus and chlorophyll concentrations decreased, whereas the Secchi depth increased during the first years after the biomanipulation (Figure 2). *Daphnia* biomass showed an increase the year after the biomanipulation, but then decreased to very low values. The percentage of piscivorous fish increased from 20% to almost 80% of total fish biomass 2 years after the biomanipulation, and the submerged macrophytes expanded and covered almost 80% of the sediment surface after 4 years. However, in 1991–92 (about 5 years after biomanipulation), several features started to deteriorate, with increase in total phosphorus, decrease in Secchi depth, increase in chlorophyll, and decline in submerged macrophytes. Since then, the trophic structure of the lake has fluctuated markedly (Figure 2) (E. Jeppesen and M. Søndergaard unpublished)

Finjasjön is a relatively large, shallow lake (1100 ha; mean depth, 2.7 m) in southern Sweden. Cyprinids were removed from October 1992 to June 1994 by trawling (Annadotter and others 1998). Total phosphorus was high and variable before 1993, but decreased after the biomanipulation (Figure 3). The chlorophyll concentration, however, had already started to decrease before the biomanipulation, whereas Secchi depth showed no increase before 1994 (Figure 3). Total zooplankton biomass showed an increasing trend, whereas the portion of *Daphnia* varied considerably following the biomanipulation. Before biomanipulation, cyprinids (roach and bream) constituted about 75% of total fish biomass, whereas piscivores (pike and pike perch) comprised only 10%. If young-of-the-year (YOY) fish are excluded, the proportion of piscivores was 50% in 1995. However, in the first years following fish removal, the YOY biomass (mainly perch) increased considerably (Figure 3). The most pronounced changes in Lake Finjasjön were the increase in submerged macrophyte cover from less than 5% of the lake area to almost 25% (J. Strand personal communication) and the decrease in proportion of blue-green algae from almost 95% to less than 20% (Figure 3).

Sätoftasjön is one of three basins forming Lake Ringsjön in southern Sweden. The lake is relatively shallow (mean and maximum depths are 3 and 17.5 m, respectively). Cyprinid fish removal was initiated in 1989 by means of trawling. Declines in total phosphorus concentration and percentage of blue-green algae began before the biomanipulation and were most probably results of measures in the catchment area, such as improved wastewater treat-

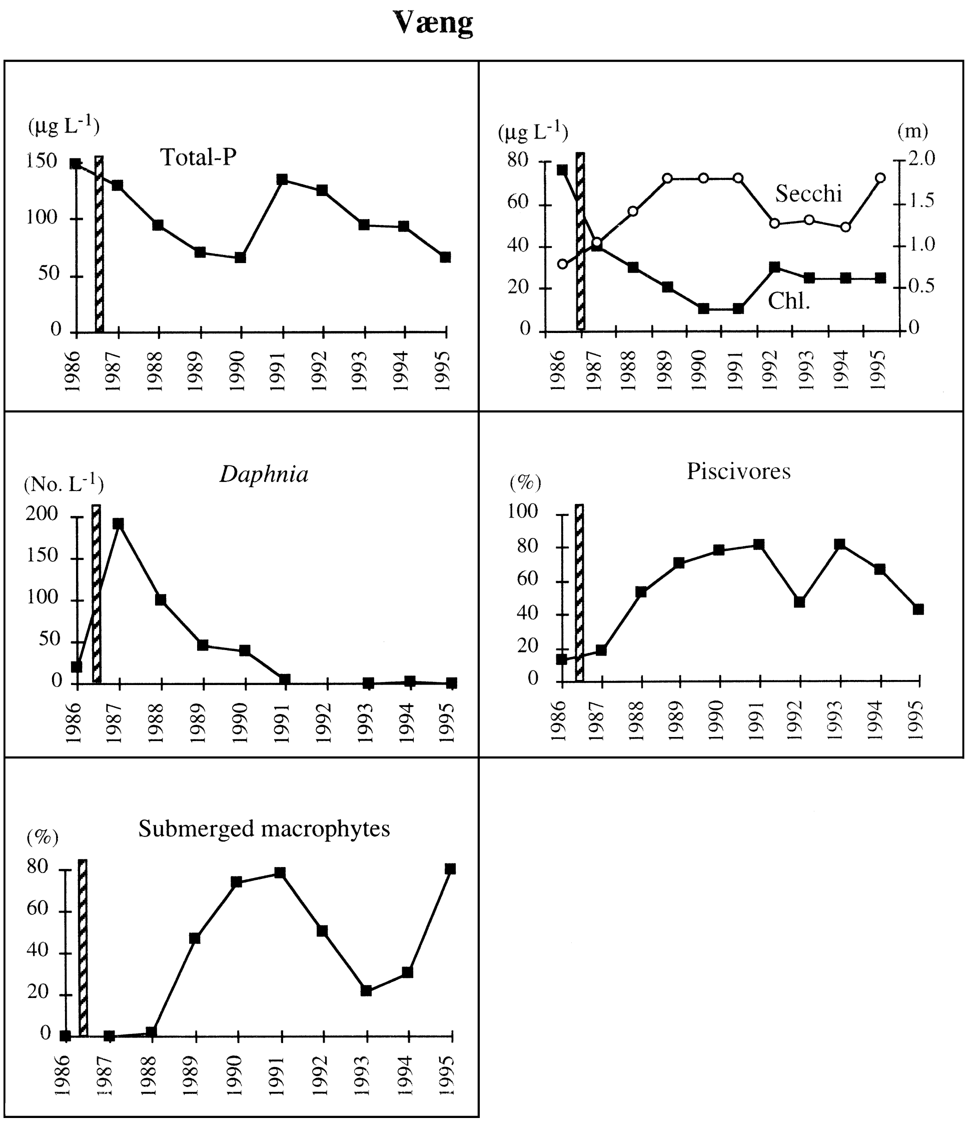

Figure 2. Temporal fluctuations in chemical and biological variables in Lake Væng (Denmark). The striped bar indicates the start of the biomanipulation. The variables are total phosphorus (µg L^{-1}), Secchi depth (m), chlorophyll *a* (µg L^{-1}), *Daphnia* abundance (no. L^{-1}), piscivorous fish as proportion (%) of total fish biomass, and the cover of submerged macrophytes (% of total bottom area).

ment and reduced agricultural fertilization. However, the decrease in chlorophyll concentration, followed by an increase in Secchi depth, occurred immediately after the biomanipulation and were possibly a result of fish reduction (Figure 4). No changes were observed in the zooplankton community, in the percentage of piscivorous fish, or in the overall cover of submerged macrophytes (Figure 4). However, local stands of submerged macrophytes developed in some parts of the basin.

Western Ringsjön is another basin of Lake Ringsjön, southern Sweden. The basin is very shallow (mean and maximum depths are 3.1 and 5.4 m, respectively). Only minor improvements occurred in the basin following fish removal (Table 1).

Cockshoot Broad is one of the small and shallow lakes (mean depth, 1 m) in the Norfolk Broadland in the eastern part of the United Kingdom (Moss and others 1996a, 1996b). About 95% of the cyprinid fish fauna were removed, and 5 years after the removal the number of *Daphnia* had doubled, whereas the chlorophyll concentration was reduced by 40% compared with before the biomanipulation (Table 1). The biomass of the submerged macrophytes had increased considerably, whereas the phosphorus concentration had increased 5 years after the biomanipulation (Table 1).

Addition of Piscivorous Fish

In these lakes, piscivorous fish were added, thereby increasing the predation pressure on cyprinid fish. This measure is cheaper than trawling, but provides highly variable results. *Bautzen Reservoir* is one of the pioneering large-scale biomanipulations in the world. The reservoir is large (more than 500 ha) and situated in the eastern part of Germany. Contempo-

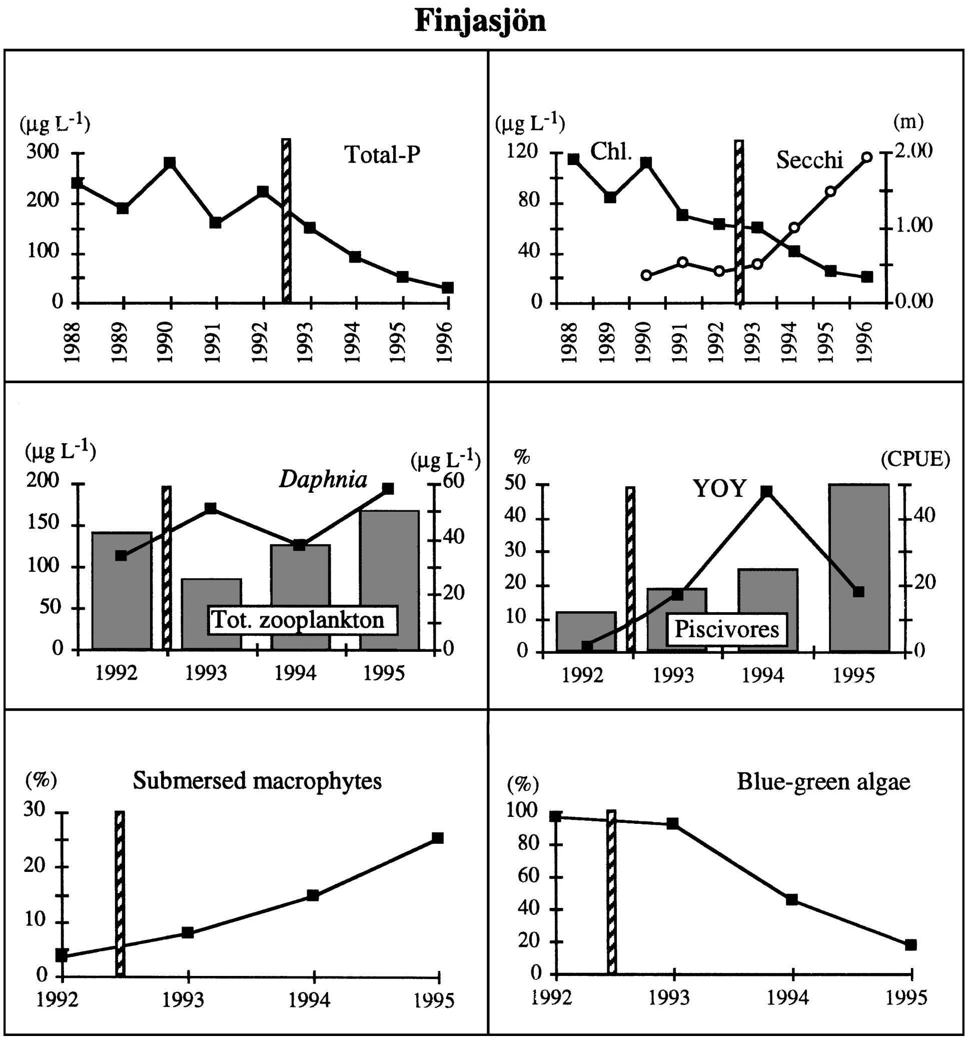

Figure 3. Temporal fluctuations in chemical and biological variables in Lake Finjasjön (Sweden). The striped bar indicates the start of the biomanipulation. The variables are total phosphorus (µg L^{-1}), Secchi depth (m), chlorophyll *a* (µg L^{-1}), *Daphnia* biomass (line; µg DW L^{-1}), total biomass of zooplankton (bars; µg DW L^{-1}), piscivorous fish as proportion of total fish biomass (bars; %), CPUE (catch per unit effort) of YOY (young-of-the-year) fish (kilograms per 20 min trawling), the cover of submerged macrophytes (% of total bottom area), and blue-green algae as proportion (%) of total algal biomass. DW, dry weight.

rary to the biomanipulation, the nutrient load to the reservoir increased, which most probably underlies the negligible improvements in water quality observed (Benndorf 1990). Despite an increase in *Daphnia* abundance, the chlorophyll concentration increased and the Secchi depth decreased (Table 1).

Gjersøen is a relatively large and deep lake (270 ha; mean depth, 23 m) situated close to Oslo, Norway (Brabrand and others 1990). Five years after the addition of pike perch, the chlorophyll concentration had decreased considerably and the blue-green algae had decreased from 60% to 7% of the algal community (Table 1). A minor reduction in the phosphorus concentration was also noted (Table 1).

Lyng is a small, nutrient-rich Danish lake (10 ha; mean depth, 2.4 m). To test the capacity of pike fry to control 0+ cyprinids, pike were stocked in different densities (500–3600 ha^{-1}) in early summer for 4 years (1990–93). Marked changes occurred in both abundance of 0+ fish of cyprinids, total phosphorus, chlorophyll *a*, abundance of blue-green algae, and Secchi depth after stocking, particularly in years with high stocking densities (Berg and others 1997; Søndergaard and others 1997). The lake returned to the turbid state 2 years after the last stocking (Søndergaard and Jeppesen unpublished results).

Nonselective Fish Removal

Lake St. George is small (10 ha) and close to Toronto, Canada. A fish kill in 1981–82 reduced the total number of fish by 60% (McQueen and others 1989). Five years after the fish kill, the Secchi depth had increased from 1.7 to 2.4 m and the chlorophyll concentration had decreased from 9 to 5 µg L^{-1} (Table 1).

Haugatjern is a small, relatively deep lake (9 ha; mean depth, 7.6 m) situated in central Norway. The lake was treated with rotenone in September 1980 and trout fry were introduced in 1982–84 (Langeland 1990; Reinertsen and others 1990). Five years after manipulation, the number of *Daphnia* had increased from 45 to 74/L^{-1} and the phytoplankton

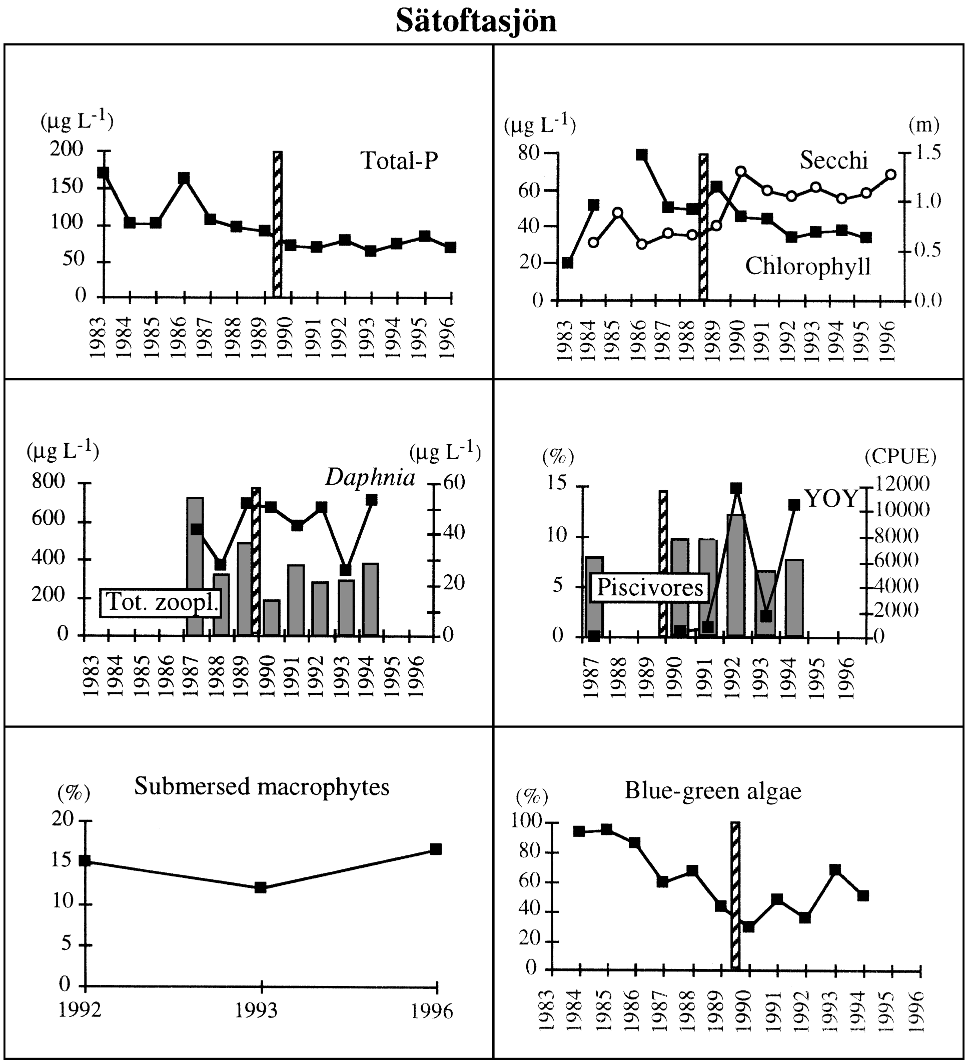

Figure 4. Temporal fluctuations in chemical and biological variables in Lake Sätoftasjön (one of the Lake Ringsjön basins, Sweden). The striped bar indicates the start of the biomanipulation. The variables are total phosphorus (μg L^{-1}), Secchi depth (m), chlorophyll *a* (μg L^{-1}), *Daphnia* biomass (line; μg DW L^{-1}), total biomass of zooplankton (bars; μg DW L^{-1}), piscivorous fish as proportion of total fish biomass (bars; %), CPUE (catch per unit effort) of YOY (young-of-the-year) fish (kilograms per 20 min trawling), the cover of submerged macrophytes (% of total bottom area), and blue-green algae as proportion (%) of total algal biomass. DW, dry weight.

biomass was reduced by 75% (Table 1). The concentration of total phosphorus decreased by 25%, but blue-green algae constituted a higher portion of the algal commuity than before the rotenone addition (Table 1).

In *Eastern Ringsjön* (2000 ha; maximum depth, 16.4 m), southern Sweden, a partial fish kill occurred in winter–spring 1988 that reduced the roach biomass by about 80%. The Secchi depth more than doubled, and the phosphorus concentration and the blue-green algae decreased by 40% and 60%, respectively, 5 years after the fish kill (Table 1).

Helgetjern, in southeastern Norway, is a small, shallow lake (12 ha; maximum depth, 3.5 m) that was treated with rotenone in 1984 (Faafeng and Brabrand 1990). After 5 years, the Secchi depth increased by 40%, and the concentrations of chlorophyll, total phosphorus, and blue-green algae decreased (Table 1). The abundance of *Daphnia*, however, did not increase (Table 1). During later years, the lake returned to a turbid state (B. Faafeng personal communication)

General Experiences from Case Studies

The original argument for most of the aforementioned biomanipulations was that reduced fish predation on zooplankton would lead to higher grazing rates and thereby to reduced algal biomass. In many of the case studies, this was true during the first year or years after the biomanipulation. Generally, however, zooplankton abundances then decreased and often returned to levels observed before biomanipulation (Figure 5). Despite this, the chlorophyll concentration, Secchi depth, and phosphorus concentration continued at low levels in most of the lakes. The conclusion from this is that although the simple food chain is initially important, other processes are

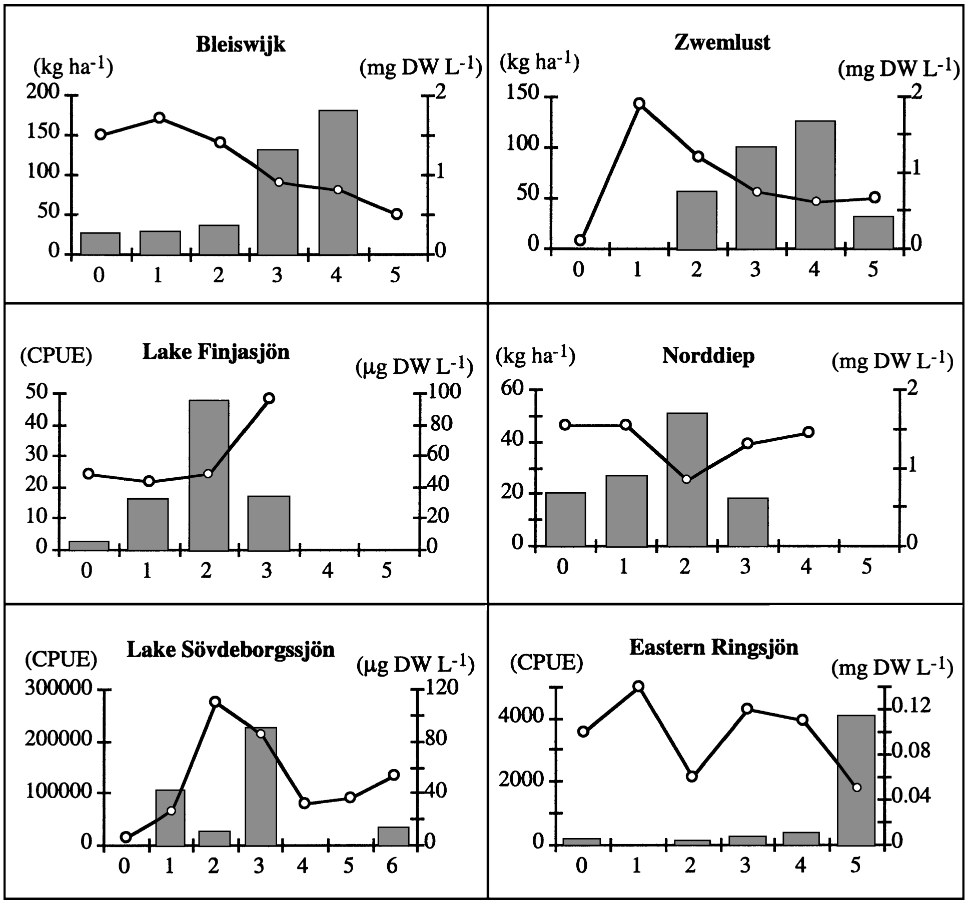

Figure 5. Abundance or biomass of YOY (young-of-the-year) fish (bars) and *Daphnia* (line) in six lakes where biomanipulations have been performed. Year 0 indicates the year before the biomanipulation. The figure indicates that high *Daphnia* biomasses never occurred with high biomasses of YOY fish in these lakes. Units for YOY quantifications are in Bleiswijk, Zwemlust, and Norddiep: kg ha^{-1}; Lake Finjasjön CPUE (catch per unit effort) expressed as kilograms per 20 min trawling, Eastern Ringsjön CPUE expressed as numbers per 20 min trawling, and Lake Sövdeborgssjön CPUE expressed by total number in the lake. Data are from Meijer and others (1989, 1994), Ozimek and others (1990), van Donk and others (1990a, 1990b), Persson and others (1993), and Bergman (unpublished). DW, dry weight.

of greater importance in the longer term, including maintaining the clear-water state after biomanipulation. In the following sections, we identify some of these secondary effects of fish removals.

SECONDARY EFFECTS OF BIOMANIPULATIONS

Expansion of Submerged Macrophytes

A general feature of the more successful biomanipulations is that submerged macrophyte cover increased (in Væng, Finjasjön, Vesijärvi, and Zwemlust). An important aspect of submerged macrophyte biology is the ability to absorb large quantities of nutrients during the summer season, thereby reducing the possibility of algae growth. Epiphytic algae attached to the macrophytes also bind phosphorus from the water (Kairesalo and others 1985; J. Strand unpublished). Moreover, macrophytes stabilize the sediment surface, reducing resuspension of sediment particles, thereby improving light penetration through the water column (Secchi depth). Although "true planktonic" zooplankton seem to avoid dense stands of macrophytes, possibly because of low concentrations of food, macrophytes may also function as a refuge from fish predation (Timms and Moss 1984). Furthermore, macrophytes tend to favor predatory fish, such as pike (*Esox esox*) and large perch (*Perca fluviatilis*), more than cyprinids, such as roach (*Rutilus rutilus*) and bream (*Abramis brama*) (Winfield 1986; Grimm and Backx 1990). It has been suggested that some macrophytes excrete allelophatic substances that negatively affect blue-green algae (Wium-Andersen and others 1982; Jasser 1995; Scheffer and others 1997). These results are based mainly on laboratory studies and the effect of allelophatic substances in natural systems is still to be demonstrated. However, it is obvious that blue-green algae and submerged macrophytes rarely occur in large concentrations simultaneously (Scheffer and others 1997), unless the density of planktivorous fish is high (Schriver and others 1995).

Reduced Nutrient Concentrations

In a study including 300 Danish lakes, it was shown that at total phosphorus concentrations below 50 µg L^{-1}, the water was clear, macrophytes were numerous, and piscivores were common in the fish community (Jeppesen and others 1991). At phosphorus concentrations between 80 and 150 μg L^{-1}, cyprinids were common, macrophytes were rare, and blue-green algae dominated in 20% of the lakes. At even higher phosphorus concentrations, no submerged macrophytes were present, and the algal and fish communities were dominated by blue-green or green algae and cyprinids, respectively. From these observations, it was concluded that total phosphorus concentration in equlibrium with the present external loading [for example, estimated from the empirical equation by Vollenweider (1968)] should preferably be below 100 μg P L^{-1} to obtain a long-term effect of biomanipulation in shallow lakes unless the nitrogen input is low (Jeppesen and others 1991). *This does not imply, however, that the actual concentration has to be below this threshold. Providing the external phosphorus loading has been reduced, biomanipulation may occur at higher concentrations and still fullfill the aforementioned criteria, as the manipulation often leads to a reduction in total phosphorus*. Such reductions have occurred following several biomanipulations, including those of Lakes Finjasjön, Vesijärvi, Helgetjern (Lyche and others 1990), and Væng (Søndergaard and others 1990). In Lake Finjasjön, the reduction in phosphorus was caused by reduced internal loading (P.-Å. Nilsson unpublished) and by phosphorus absorption by submerged macrophytes and their periphytic algae (J. Strand personal communication). Other factors affecting the phosphorus concentration—such as light climate at the sediment surface, stimulating periphytic algal growth and thereby oxygen production, chemical sorption, and biological uptake of phosphorus at the sediment surface (Boström and others 1982)—may be improved by biomanipulation. Reduced bioturbation, that is, feeding by benthic fish at the sediment surface, may also reduce the phosphorus release from sediment to water (see the section on *The feeding of benthic fishes*).

The Risk of Increased Recruitment of Young-of-the-Year Fish

When the abundance of cyprinid fish is reduced, competition for food decreases and the recruitment of strong year classes of young fish is improved. Although very small, their consumption rate is high. YOY fish may eat their own weight in zooplankton per day (Post and others 1992). Moreover, YOY fish eat and grow rapidly, thereby mobilizing and excreting high amounts of nutrients (Post and others 1997). Hence, high recruitment of YOY fish and their predation on zooplankton may strongly counteract the effect of biomanipulation. This counteractive effort can be shown by plotting YOY fish against *Daphnia* (Figure 5). In three of the lakes investigated (Bleiswijk, Zwemlust, and East Ringsjön), the biomass of zooplankton increased the year after biomanipulation (year 1; Figure 5). However, the increase was replaced with a decrease 2–5 years after biomanipulation, which corresponds with the increase in YOY abundance (Figure 5). Sövdeborgssjön and Finjasjön showed YOY increases 1 and 2 years, respectively, after biomanipulation, which may be the reason the increase in *Daphnia* biomass was delayed until the year after the YOY maximum (Figure 5). Norddiep showed no increase in *Daphnia* biomass, but a considerable decrease in year 2 when YOY abundance was at its maximum (Figure 5). Although the investigated lakes show different patterns, there seems to be an inverse relationship between the biomass of large zooplankton and YOY fish abundance. However, proper quantification of YOY fish is very difficult (Romare and Bergman 1998), which may be one factor behind the oscillations in estimated YOY abundances (Figure 5). Moreover, *Daphnia* biomass is affected by other factors besides YOY predation, such as predation from larger fish, competition, and shortage of food, which may disturb a relationship between YOY and *Daphnia*. If YOY affects *Daphnia*, very high and very low biomass of YOY may be expected to lead to low and high biomasses, respectively, of *Daphnia*. By normalizing all YOY and *Daphnia* values (that is, setting the highest value in each lake to 1.0), data from all lakes can be used together. Then, defining *high YOY* as a normalized value higher than 0.8 and *low YOY* as values below 0.2, comparing the *Daphnia* biomasses in the two groups shows that high *Daphnia* biomass is associated with low biomass of YOY ($Z = -2.204$; $P < 0.028$; $n_{\text{low}} = 8$, $n_{\text{high}} = 6$; Mann–Whitney U test; note that year 0 in figure 5 is not included in the analysis because predation from adult fish then affected the *Daphnia*). Hence, despite methodological problems, two conclusions may be drawn from these data: a YOY "boom" is to be expected 1–4 years after a biomanipulation if the increase in abundance of piscivorous fish is not large enough, and this boom reduces the abundance of large, efficient herbivores. Hence, the very high reproductive potential of fish, manifested in strong year classes, is indeed a problem that has to be considered when planning biomanipulation. Possible solutions are follow-up fish reductions, recruitment prevention by egg destruction, or addition of piscivorous fish to the lake.

The Feeding of Benthic Fishes

As already stated, the theory behind biomanipulation rests entirely on pelagic processes, such as fish predation on zooplankton. The possible importance of bottom-feeding fish species has been acknowledged (Lammens 1989; Meijer and others 1990). Specialized benthic feeding fish are "vacuum cleaning" the sediment surface, searching for invertebrates. This feeding behavior causes *resuspension* of sediment particles, which may, especially in shallow lakes, reduce the light penetration through the water (Meijer and others 1990). Although roach mainly feed on zooplankton, they switch to benthic animals, algae, and plants when zooplankton become scarce, thereby possibly causing bioturbation and resuspension (Horppila and Kairesalo 1992; Horppila 1994). Moreover, the feeding behavior also transfers nutrients to the water, providing phytoplankton with additional resources (Lammarra 1975; Andersson 1984) and possibly reducing submerged macrophyte establishment (Meijer and others 1990). Hence, there is an argument for reducing the abundance of benthic feeding, as well as zooplanktivorous fish.

What Is a Successful Biomanipulation?

Specific criteria for a successful biomanipulation mainly lie in the eyes of the observer, but general criteria would include (a) *decrease in algal turbidity*, (b) *decrease in blue-green algae amounts* [blue-green algae tend to form nuisance "blooms" that may be poisonous (Annadotter and others 1998)], and (c) *stability of the improvement*; that is, if the effects are only temporary or if they last for a longer period. Based on these criteria and on the diagnostic variables used in Table 1, the success of a specific biomanipulation may be roughly quantified. We may consider how many of the diagnostic variables show improvement for each lake. The biomanipulations may be ranked from those where all (100%) of the variables improved, to those where only a few variables improved. The proportion of variables improved for each lake is listed in Table 2. In three lakes, all diagnostic variables were still improved 5 years after biomanipulation, whereas in four lakes less than 50% of the variables were improved 5 years after biomanipulation (Table 2). A reasonable criterion for a successful biomanipulation may be that about 75% of the diagnostic variables remain improved 5 years after the biomanipulation. Thus, we conclude that more than half of the biomanipulations should be categorized as successful, given the 5-year time span (Table 2). This is a judgmental view, but since biomanipulation can be expensive to perform, it is important to provide a quantitative measure of how well the investment is reflected in actual improvements.

Table 2. Number of Improved Diagnosis Variables and the Reduction in Cyprinid Fish Abundance (%)

Lakes	Improvement (%)	Fish Reduction (%)
Finjasjön	100	80
Zwemlust	100	89
Gjersjöen	100	80
Vesijärvi	83	85
Helgetjern	80	99
Lyng	80	—
Vaeng	80	50
Cockshoot Broad	75	95
Haugtjern	75	100
Lake St. George	75	60
Eastern Ringsjön	67	80
Bleiswijkse Zoom	60	75
Norddiep	60	56
Sätoftasjön	50	60
Western Ringsjön	33	49
Sövdebordssjön	25	20
Bautzen Reservoir	25	—

An improvement is here defined as a change by at least 15% (see Table 1). The number of improved variables were then divided with the total number of quantified variables in that specific lake. Diagnosis variables are similar to those in Table 1. In Bautzen Reservoir and Lake Lyng, the fish reduction was not possible to estimate.

Cost–Benefit Analysis: Do Results Repay Effort?

If biomanipulation through fish reduction really has a positive effect on lake status, then the number of diagnostic variables that improve might be expected to be positively related to the intensity of the measure; that is, to the amount of fish removed. This would be a critical test of whether the fish removal is the probable cause of the observed improvements. As seen in Figure 6, there is a relationship between the proportion of improved diagnostic variables and the percentage of the cyprinid fish community that has been removed from the lake. In other words, the intensity of the measure is proportional to how "successful" the biomanipulation is likely to become (Figure 6). If the cyprinid proportion is reduced by less than 50%, for example, due to a restricted budget, the biomanipulation should be avoided since only a limited number of the diagnostic variables outlined in Table 1 would be expected to be improved 5 years after the biomanipulation (Figure 6). However, if the budget allows a reduction of 75% of the cyprinid fish assemblage, the probability is high that the biomanipulation will be viewed as a success 5 years after

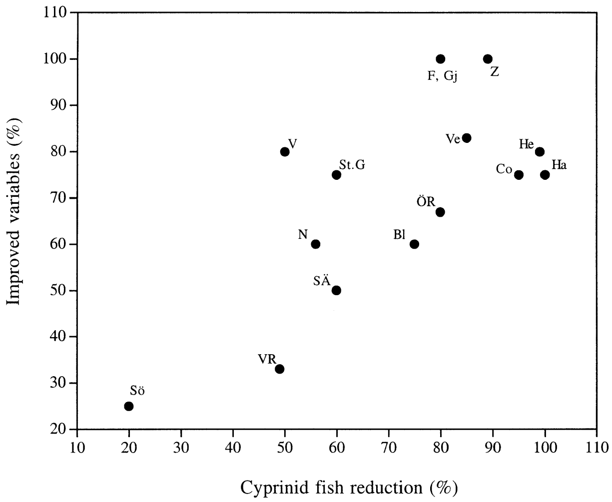

Figure 6. Proportion of the diagnosis variables (%) that were still improved 5 years after the biomanipulation in relation to the amount of fish taken from the lake. Variables are Secchi depth, chlorophyll, cover of submerged macrophytes, *Daphnia* biomass, total phosphorus, and blue-green algae. The correlation is significant: $t_{13} = 3.534$; $P < 0.005$. All lakes in Table 1 are included, except Bautzen Reservoir and Lake Lyng, since data are lacking on the amount of fish taken out. Sö, Sövdeborgssjön; VR, Western Basin (Ringsjön); SÄ, Sätoftasjön (Ringsjön); N, Norddiep; Bl, Bleiswijk Zoom; St.G., Lake St. George; V, Væng; ÖR, Eastern Basin (Ringsjön); Ve, Vesijärvi; Co, Cockshoot Broad; Ha, Haugatjern; He, Helgetjern; Z, Zwemlust; Gj, Gjersjøen; F, Finjasjön.

the measure (Figure 6). This level of reduction was also recommended by Hosper and Meijer (1993), Perrow and others (1997), and Jeppesen and others (1997). It should be noted, however, that this relation is by no means a guarantee of a successful result, but should rather be used as a guideline and a basis for planning discussions. The *intensity* of the fish reduction is also important; that is, a fish reduction of 1 ton each year over 10 years is not the same as 10 tons over 1 year, since the fish community can compensate mortality with reproduction if the intensity is too low.

SYNTHESIS: WHAT HAPPENS AFTER A BIOMANIPULATION?

As stated in the introduction, the main theory behind biomanipulation is still focused on pelagial processes. This evaluation, however, together with those by Moss and others (1996a), Horppila and others (1998), Hosper (1997), Perrow and others (1997), and Jeppesen and others (1998), suggest that littoral and benthic factors, such as submerged macrophytes and benthic feeding fish, strongly affect the success of a biomanipulation and that these should receive equal consideration. Instead of being the *only* mechanism involved, alterations in the food chain may be viewed as triggers that initiate other processes.

Figure 7 summarizes what may happen after a biomanipulation. The hatched line in the middle represents the status of the lake before biomanipulation—a strongly eutrophic lake with repeated algal blooms. All processes above the line force the lake toward clear water and less common algal blooms, whereas processes below the line force the lake toward turbid water with intense algal blooms (Figure 7). At the top of the figure, there is an approximate time axis where the fish reduction denotes year 0. The fish reduction has several *primary effects* that are shown in the grey box (Figure 7). Hence, often, but not always, a biomanipulation leads to an increase in zooplankton abundance within 1–2 years (see also Figure 5). This results in reduced algal biomass, which in turn leads to improved light conditions and improved possibilities for submerged macrophytes to establish. The macrophytes absorb nutrients, leading to a further reduction in algal biomass, and a *positive spiral* is created. Additionally, the reduction in benthic feeding fish results in less resuspension of sediment particles, which improves the light penetration and reduces phosphorus transport from sediment to water, as well as reduced damage to macrophytes. These processes further strengthen the positive spiral. However, another primary effect of a fish reduction is reduced food competition among fish (Figure 7). If the biomanipulation is intense enough and the density of piscivorous fish high enough, the recruitment of YOY fish may not become a problem. However, if insufficient fish are removed, the YOY hatching in the years following the biomanipulation will have access to an almost unlimited food resource, since competition with larger fish is negligible.

However, this *negative spiral* may be avoided by addition of piscivorous fish, a method that has been tested in several lakes (Table 1). If the planktivorous fish biomass is not sufficiently reduced, it will recover to a similar biomass as before the biomanipulation within 2–4 years, a scenario leading to deterioration in the status of the lake (Figure 7). An example of this comes from a comparison of fish catches in Lake Sätoftasjön and Lake Finjasjön, southern Sweden. The fish reductions were carried out over 420 and 610 days, respectively. However, owing to technical problems, only 80 days (19%) were efficient trawling days in Lake Sätoftasjön, whereas the corresponding value for Lake Finjasjön

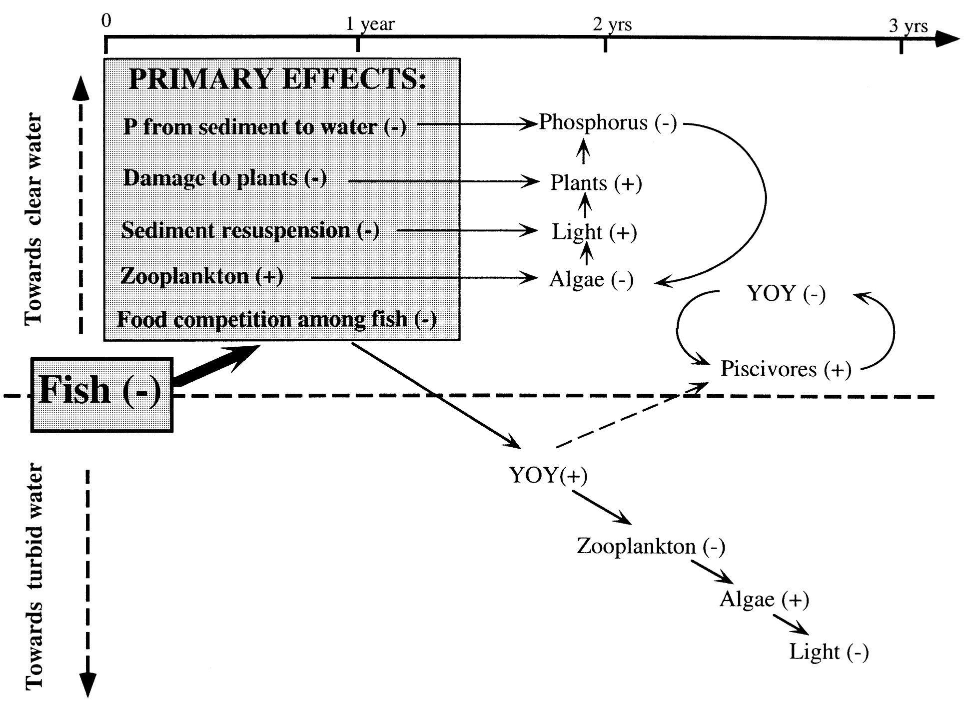

Figure 7. An overview of important processes triggered by a reduction in cyprinid fish abundance (biomanipulation). Primary effects are included in the shaded box. These in turn affect other variables in the system. Processes above the dashed line lead to clear water, whereas processes below the line lead to more turbid conditions. An approximate time scale at the top of the figure indicates when different effects are to be expected. YOY, young-of-the-year fish.

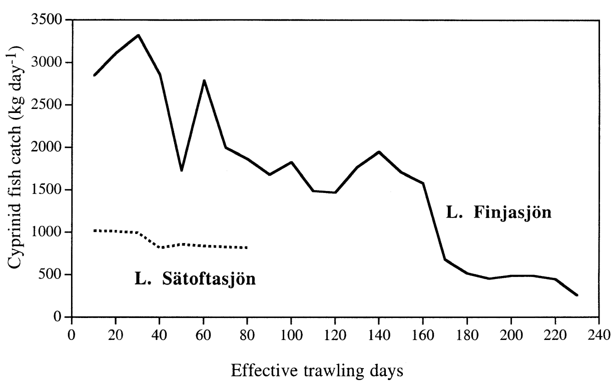

Figure 8. Catch of cyprinid fish (kilograms per day) in Lake Finjasjön and Lake Sätoftasjön. The biomanipulations were performed from October 1992 to May 1994 and from September 1989 to December 1990, respectively.

was 230 days (38%). In Lake Sätoftasjön, the catch per day did not decrease, indicating that the final fish stock after the biomanipulation was not very different from that before the measure (Figure 8). In Lake Finjasjön, however, the trawling was very efficient due to more appropriate methods, such that the catch per day decreased from more than 3 tons to less than 0.5 tons, indicating a considerable decrease in the fish stock. (Figure 8).

Recommendations

Recommendations regarding biomanipulation have been presented several times before, for example the recent reviews by Hosper and Meijer (1993), Phillips and Moss (1994), Reynolds (1994), Moss and others (1996a), and Perrow and others (1997). Despite these relatively recent reviews, new knowledge has emerged from large-scale biomanipulations that were initiated at the end of the 1980s and the beginning of 1990s. Many of the earlier recommendations, especially those outlined in Reynolds (1994) and Phillips and Moss (1994), may now be viewed as too conservative. Hence, the recommendations that lake size should not exceed 4 ha and that the maximum depth should not be more than 4 m (Reynolds 1994) or 3 m (Phillips and Moss 1994) would have argued against the successful biomanipulations in Finjasjön (1100 ha; maximum depth, 12.5 m) and Vesijärvi (2600 ha; maximum depth, 33 m). Similarly, retention times of less than 30 days (0.08 years) were recommended if a biomanipulation were to be successful (Reynolds 1994). Few of the lakes involved in this evaluation have such short retention times. Another recommendation was that phytoplankton must not be dominated by blue-green algae (van Donk and others 1990a; Phillips and Moss 1994; Reynolds 1994). Although biomanipulation is probably easier and cheaper to perform in a shallow, small lake with a short retention time that lacks blue-green algae, these factors may not restrict the success of a biomanipulation (Jeppesen and others 1997; Perrow and others 1997). Although it may be wise to be cautious when presenting recommendations, the problem is that caution may prevent many biomanipulations with excellent odds for success from ever being performed. We have, thus, revised earlier recommendations:

The biomanipulation should be intense and reduce the planktivorous fish stock by at least 75%. Intensive removal increases the probability of a successful biomanipulation by reducing the predation on zooplankton as well as the risk of a "boom" of young fish in the immediately subsequent years. Preferably, fish removal should not take longer than 2 years, although in larger lakes the measure may, due to practical reasons, take longer. A lengthy process at low intensity increases the risk of strong recruitment of young fish. Hosper and Meijer (1993), Jeppesen and others (1997), and Perrow and others (1997) also recommended reducing cyprinid fish stock by 75%.

Benthic fish should be strongly reduced. Benthic feeding fish, such as bream (*Abramis brama*) and gizzard shad (*Dorosoma cepedianum*), resuspend sediment particles and transfer nutrients from sediment to water. They also injure submerged macrophytes during feeding. A strong reduction of benthic fish may therefore affect water clarity in several ways (Meijer and others 1994).

Recruitment of young fish should be reduced. The YOY fish generally increase considerably in biomass 1–3 years after the biomanipulation. They may be kept within acceptable numbers by applying an intense measure or by adding piscivorous fish to the lake during, or the first year after, the biomanipulation, or both (Søndergaard and others 1997).

Establishment of submerged macrophytes should be improved. If large numbers of birds are feeding on vegetation in the lake, macrophyte beds may be protected with nets (Lauridsen and others 1994; Moss 1996a; Søndergaard and others 1997). Earlier reviews (Phillips and Moss 1994; Reynolds 1994; Jeppesen and others 1997; Perrow and others 1997) made similar recommendations. It should, however, be noted that this measure may not always be necessary.

The phosphorus concentration should be lower than about 100 $\mu g\ L^{-1}$. The examples in this report suggest that when providing an efficient reduction of cyprinid fish, a trophic cascade most often occurs in eutrophic lakes irrespective of the nutrient level. Even some of the highly nutrient-enriched lakes dominated by blue-green algae shifted toward a clear-water state (Zwemlust, 1200 μg P L^{-1}; and Lake Lyng, 790 μg P L^{-1}). Less promising results were obtained for the Bautzen Reservoir. However, several of the more nutrient-enriched lakes in our collection have shifted back to the turbid state or deteriorated markedly during recent years: for example, Bleiswijke Zoom [see Meijer and others (1995) and Hosper (1997)], Lake Lyng (M. Søndergaard and E. Jeppesen unpublished results), and Helgetjern (B. Faafeng personal communication). Exceptions are Finjasjön, which today receives low external P input (Annadotter and others 1998), and Zwemlust, which shows considerable instability. The observed drawbacks correspond to the threshold hypothesis described by Jeppesen and colleagues (1990a, 1990b) and Benndorf (1990).

If a long-term effect (more than 2–5 years) is to be achieved, we therefore presently recommend a reduction in the external loading prior to biomanipulation to such a level that the future equlibrium concentration [for example, as estimated by the empirical equation of Vollenweider (1968)] would be below 100 μg P L^{-1} for shallow temperate lakes and possibly even lower for deep lakes (Jeppesen and others 1997). If the N input is low, a clear-water state seems to be maintained at a higher P concentration at least in shallow lakes (Jeppesen and others 1991; Moss and others 1996a). Moreover, if the fish community changes toward a higher proportion of piscivores, the response in chlorophyll is lower at similar nutrient loads than if the lake is planktivore dominated (Carpenter and others 1995). Similar results were found when comparing fishless with planktivore-dominated lakes (Hansson 1992); that is, the increased algal productivity at increasing nutrient availability is transferred into a growing grazer community. Hence, the Vollenweider models on phosphorus load versus chlorophyll concentration may be applicable only in planktivore-dominated systems.

Defining the thresholds in nutrient concentration for different types of lakes is a challenge for the future and awaits more and, in particular, longer-term experiments (more than10 years) than those presented in this review.

Engagement! A factor that generally is underestimated or not mentioned at all is the participants involved. The best results have been achieved when the biomanipulation was supported by politicians, agencies, authorities, and inhabitants around the lakeshores, as in the case in Lake Finjasjön (Sweden) and especially in Lake Vesijärvi (Finland).

Final Remarks

Some of the biomanipulations described in this review have not been as successful as expected, whereas others have been very successful. The reasons underlying the different outcomes are now beginning to emerge, illustrated by the connection between low intensity of fish removal and a less successful result. Recent studies have shown that biomanipulation can also be successful in large, relatively deep lakes with long retention times. Moreover, dominance of blue-green algae may be eliminated by biomanipulation. Although this may suggest that almost any lake can be successfully biomanipulated, it is obvious that some lakes present better conditions than others and that biomanipulations in large, deep lakes consume more resources and funding than small, shallow ones. Low external and internal phosporus loading and large areas suitable for colonization of submerged macrophytes increase the probability of successful biomanipulation. Another important conclusion is that the formerly dominant view that the *only* mechanism involved in biomanipulation is the pelagic food chain (fish–zooplankton–algae) should be revised. Instead, this process may be viewed as the trigger for secondary, mainly benthic and littoral, processes, such as establishment of submerged macrophytes and reduction in benthic feeding by fish. The final conclusion is that well-planned biomanipulation is, in combination with a reduction in the external nutrient input, an attractive method with high odds of improving the water quality in most types of eutrophic lakes, at least in a 5-year perspective.

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