

Lake Restoration by Fish Removal: Short- and Long-Term Effects in 36 Danish Lakes

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ABSTRACT

During the past 10–15 years removal of plankti- and benthivorous fish (mainly roach, *Rutilus rutilus*, and bream, *Abramis brama*) has commonly been used as a method to improve the ecological quality of Danish lakes. Here, we examine the general and long-term effects obtained after the removal of 41–1360 kg fish ha⁻¹ in 36 mainly shallow and eutrophic lakes. In lakes in which less than 200 kg fish ha⁻¹ were removed within a 3-year period only minor effects were observed, but at higher removal rates both chemical and biological variables were markedly affected. The concentrations of chlorophyll *a* (Chla), total phosphorus (TP), total nitrogen (TN), and suspended solids (SS) decreased to 50–70% of the level prior to removal. The most significant and long-lasting effects were found for SS and Secchi depth, whereas the most modest effects were seen for Chla. This probably reflects an efficient and persistent reduction of the bream stock which reduced resuspension and SS, while the biomass of roach returned to former levels, decreasing the zooplankton grazing with less con-

trol on Chla. Total algal biomass also declined after fish removal, particularly that of cyanobacteria, whereas the biomass of cryptophytes increased, indicating enhanced grazing pressure by zooplankton. The abundance and species number of submerged macrophytes increased in the majority of the lakes. For most variables the effects of the fish removal were significant for 6–10 years, after which many lakes tended to return to pre-restoration conditions, probably mainly because of consistently high external and internal phosphorus loading. We conclude that a sufficiently extensive removal of plankti- and benthivorous fish is an efficient tool to create clear water; however, repeated fish removal is presumably required to obtain long-term effects in the most nutrient rich lakes.

Key words: lake; biomanipulation; nutrients; phosphorus; fish; zooplankton; phytoplankton; macrophytes; resuspension; sediment.

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INTRODUCTION

World-wide, many lakes located in densely populated or intensively cultivated areas have become eutrophic and turbid (Edmondson 1972; Coveney and others 2005; Yang and others 2008). This also applies to Denmark where decades with excessive

nitrogen and phosphorus loading have created ideal conditions for phytoplankton production with turbid water and decreased biological diversity as the result (Jeppesen and others 2000; Søndergaard and others 2007). Submerged macrophytes have either disappeared or been markedly reduced in most lakes, and the fish stock has changed toward dominance by zooplanktivorous and benthivorous roach (*Rutilus rutilus*) and bream (*Abramis brama*), whereas the abundance of predatory fish such as perch (*Perca fluviatilis*) has declined (Jeppesen and others 1999).

To remedy this undesired development, massive investments have been made during the past 30–40 years, not least in improved wastewater treatment, but also in other nutrient reducing initiatives (Kronvang and others 2005; Jeppesen and others 2007). This has led to a more than 50% decline in the total loading of phosphorus to the aquatic environment in Denmark and to improved lake water quality. However, in many lakes nutrient loading is still too high to trigger a shift to a permanent clear water state (Jeppesen and others 2007; Søndergaard and others 2007). Furthermore, as evidenced in all parts of the world (Sas 1989; Jeppesen and others 2005), lakes tend to respond slowly to reduced phosphorus loading, implying that the reduction-triggered improvement in ecological state is not as substantial as could be expected. The delayed recovery may be due to chemical resistance conditioned by internal loading of phosphorus from a pool accumulated in the sediment at high loading (Welch and Cooke 2005; Spears and others 2007). High internal phosphorus loading is typically recorded in formerly heavily wastewater impacted lakes, and examples show that many years, and in some instances even decades, may pass before such internal loading abates (Søndergaard and others 2003; Phillips and others 2005). The modesty of improvements may also be due to resistance caused by biological mechanisms, such as the development of a large fish stock dominated by zooplanktivorous species inhibiting top-down control of phytoplankton (Benndorf 1990; Jeppesen and others 1990; Hansson and others 1998). A large stock of benthivorous fish—not least bream—may also create turbid water and nutrient release as their search for food at the lake bottom increases the amount of suspended matter in the water column (Breukelaar and others 1994; Tarvainen and others 2005). Another delay factor may be slow re-establishment of the submerged macrophyte communities that are of vital importance for maintaining the clear water state in shallow lakes (Moss 1990; Scheffer and others 1993; Jeppesen and others 1997).

Unsatisfactory lake water quality, despite reduced loading, has made lake restoration a common management practice in most parts of the world for the past 30–40 years, and a multitude of restoration methods have been developed (Perrow and Davy 2002; Cooke and others 2005). In the future management of European lakes, lake restoration could also be regarded as an important tool to precipitate the development toward ‘good ecological state’ stipulated by the EU Water Framework Directive (European Union 2000). In Denmark, since the mid-1980s, and particularly during the 1990s, attempts have been made to improve the ecological state of about 80 nutrient-impacted lakes via various restoration projects using different techniques such as stocking of pike (*Esox lucius*), hypolimnetic oxygenation, alum treatment, and sediment removal. However, the most common method has been ‘biomanipulation’ involving reduction of the zooplanktivorous and benthivorous fish stock (mainly roach and bream) (Søndergaard and others 2007).

Numerous case studies and reviews on biomanipulation have appeared over the years, including recommendations for how to undertake successful biomanipulation (see for example, Hansson and others 1998; Mehner and others 2002). However, reviews based on a large number of lakes are often marred by limited access to comparable and high-quality data, precluding more detailed ecosystem analyses. Furthermore, documentation on long-term effects (>5 years) is still relatively limited, and descriptions are usually restricted to single lake studies (Van de Bund and Van Donk 2002; Hansel-Welch and others 2003; Loughheed and others 2004; Ibelings and others 2007; Søndergaard and others 2007). General conclusions about the potential of using biomanipulation as a restoration tool to create more permanent effects must therefore be drawn with care.

In this article we examine the overall effects of the use of fish removal as a lake restoration tool in 36 Danish lakes. Our analyses are based on a number of central chemical and biological variables at all main trophic levels and involve comparisons of pre- and post-restoration values. The objective was to identify general patterns and investigate long-term effects.

METHODS

Study Sites

For the analyses we used data from 36 Danish lakes in which removal of plankti- and benthivorous fish

has been undertaken during the last 10–20 years. Between 41 and 1360 kg fish ha⁻¹ were removed within a 1–19-year period, but in most lakes removal was concentrated within 2–4 years. In some of the lakes pike fingerlings were stocked, but recent studies conclude that this method generally has no significant effect on lake water quality (Skov and Nilsson 2007). Most of the manipulated lakes were relatively small and shallow (median size: 32 ha; median mean depth: 1.8 m (Table 1)). Nutrient concentrations differed considerably, but the lakes were generally eutrophic and the concentration of total phosphorus (TP) prior to removal varied between 0.061 and 0.437 mg P l⁻¹ (median = 0.157 mg P l⁻¹) and that of chlorophyll *a* (Chla) between 0.026 and 0.208 mg l⁻¹ (median = 0.084 mg l⁻¹). A more detailed description of the lakes can be found in Liboriussen and others (2007).

The 36 lakes were divided into two categories according to the extent of the removal: (1) 27 lakes in which more than approximately 200 kg fish ha⁻¹ were removed within 3 years in the beginning of the removal period (mean: 410 kg ha⁻¹, range: 190–706 kg ha⁻¹), and (2) 9 lakes in which less than 200 kg fish ha⁻¹ were removed within 3 years (mean: 91 kg ha⁻¹, range: 41–160 kg ha⁻¹). For the latter category data are only shown for nutrients, chlorophyll, and Secchi depth. The limit of 200 kg fish ha⁻¹ was set arbitrarily, but based on former empirical analyses of European lake restoration projects in which a distinction was made between lakes characterized by extensive removal with cascading effects, and lakes characterized by less extensive removal with less probability of inducing effects (Jeppesen and Sammalkorpi 2002; Olin and others 2006).

Sampling and Analyses

Data were mainly collected by local county authorities and mostly by the use of standard sampling techniques and analyses, as described in the Danish national monitoring program (Kronvang and others 1993). In most lakes samples for water

chemistry, zooplankton, and phytoplankton were collected once-twice monthly during summer at a mid-lake station. Mean summer values (1 May–30 September) were calculated for each year.

TP, total nitrogen (TN), suspended solids (SS), and Chla were analyzed according to standard procedures (Jespersen and Christoffersen 1987; Søndergaard and others 1992). Phytoplankton and zooplankton were fixed in Lugol's iodine and identified to the lowest feasible taxonomic level. Phytoplankton biomass was calculated as biovolume by fitting each species/genus to simple geometric forms. Zooplankton biomass was calculated on the basis of length–weight relationships according to Dumont and others (1975) and Bottrell and others (1976). Quantitative measurements of the fish stock were limited to the three most frequently occurring species: bream, roach, and perch, and were expressed as catch per unit effort (CPUE) of weight or numbers based on catches in 42-m long multiple mesh-sized gill nets with 14 different mesh sizes ranging from 6.25 mm to 75 mm (Jeppesen and others 2004). In most lakes, 6–24 nets were used, depending on lake size. The nets were set in late afternoon and retrieved after approximately 18 h the following morning. Submerged macrophytes were estimated during maximum abundance in July or August on 50–400 sampling locations in each lake depending on lake size. On each sampling location species, water depth and macrophyte coverage were recorded. Macrophyte data are only available from 20 lakes in total (species number from 15 lakes, maximum depth distribution from 11 lakes and coverage from 10 lakes).

ANALYSIS OF DATA

Definition of Pre- and Post-Restoration Data

To enable uniform estimation of removal effects between lakes, various definitions were elaborated. Thus, the 'pre'-condition was defined as the aver-

Table 1. Morphological and Chemical Data for the 36 Lakes in which Fish Removal was Undertaken

Variable	Mean	Min	Median	Max
Area (ha)	92	2	32	862
Mean depth (m)	2.0	0.8	1.8	4.3
Max depth (m)	4.2	1.1	3.3	10
TP (mg l ⁻¹)	0.172	0.061	0.157	0.437
TN (mg l ⁻¹)	2.03	0.97	1.93	4.09
Chlorophyll <i>a</i> (mg l ⁻¹)	0.089	0.026	0.084	0.208

The chemical values are total phosphorus, total nitrogen, and chlorophyll a as time-weighted summer means from 1–3 years prior to the fish removal.

age 1–3 years prior to the fish removal. In three lakes, the average 4–5 years prior to removal were applied due to lack of data.

The 'post'-condition comprises all years following the start of the removal process. In most lakes the fish removal lasted more than 1 year, implying that removal may still have been conducted in the first few years of the 'post'-period. Therefore, the effect measured for a particular year may not be a 'post'-effect only, but rather the combined effects of potential ongoing removals and removals undertaken in previous years. To allow a direct comparison between the different lakes we calculated the effects relative to the pre-removal situation. Thus, if the relative value is 1, the parameter remains unchanged relative to the pre-removal situation.

The starting date of the fish removal during its first year was used to distinguish between the 'pre-' and the 'post'-situation. If the fish removal was initiated in October–April the 'pre'-situation comprises data from the previous summer, whereas the first 'post'-situation or first year of effect is the subsequent summer. If, instead, the removal was conducted in May–September, this year cannot be defined as either 'pre' or 'post' and was therefore removed from all analyses. In such cases the last 'pre'-data derive from the year before the fish removal, whereas the first 'post'-data derive from the first year after initiation of the fish removal. As quantitative measurements of the fish community are relatively few and less frequent, the data were grouped into 2-year intervals, implying merging of investigations: 1–2 years, 3–4 years, 5–6 years, and so on after the first year of removal.

Correction of the General Reduction of TP Due to Reduced External and Internal Loading

Corrections had to be made for the reduced nutrient concentrations recorded also in non-biomanipulated lakes resulting from the reduced nutrient loading from external and internal sources (Søndergaard and others 2005). Otherwise, the effects of removal would appear too positive, particularly in lakes where the fish removal was undertaken in the 1980s or in the beginning of the 1990s when the nutrient loading to Danish lakes was considerably reduced. The correction was made by applying data from a national lake monitoring program using 10 intensively monitored lakes as references for the development in non-restored lakes (Kronvang and others 1993). Common to those lakes was a TP level above $0.050 \text{ mg P l}^{-1}$ (summer mean) and the fact that no significant additional interventions were

undertaken to impact chemical and biological variables in the lakes.

The general development was defined for each parameter via a log-linear regression curve based on the annual measurements from the reference lakes, yielding a smoothed reflection of the lakes' annual mean values. On average, the TP concentration decreased by 3% each year. In the analyses this was accounted for by correcting the measurements from the restored lakes for the general development, implying that the impact of the general development for each individual lake was 'deduced' from the measurements. In the survival analyses (see next section) the correction was included as a common value for all lakes as a time-varying explanatory variable rather than correcting the measurements (Kalbfleisch and Prentice 1980). The data corrections were made for all parameters on which annual measurements existed, that is, all chemical parameters, the biomass of phytoplankton and zooplankton and the relative contribution of each phytoplankton and zooplankton group.

For fish a slightly different method of correction was applied as fish investigations are usually only conducted every fifth year, implying that only 3–4 investigations were conducted in each lake during the period 1989–2005. First, for each variable the average was calculated for each of the 10 reference lakes for the two 5-year periods 1989–1993 and 1999–2004. Subsequently, for each 5-year period the average among the lakes was calculated for the given variable, and the percentage change during the 10-year period was distributed evenly across the years. It was assumed that the reference lakes and the fish removal lakes exhibited the same percentual change, also beyond the 10-year period.

Survival Analyses

Statistical survival analyses are applied, for instance in health investigations, to describe the survival potential of patients following surgical intervention and/or initiation of medicinal treatment (Kalbfleisch and Prentice 1980). Survival analysis is similar to other statistical regression methods but is distinguished by its ability to treat right-censored observations, which cannot be analyzed by other regression methods without bias. In health investigations, a survival time is unknown if the patient was still alive at the termination of the investigation or if contact to the patient was somehow lost during the investigation. The observed survival time, however, still contains information about the patients' survival because it constitutes a lower limit for the actual survival time. The actual sur-

vival time is said to be right-censored at the observed survival time. Eliminating such observations would reduce the sample size and introduce selection bias in the data set, for instance exclusion of strong survivors. Treating right-censored survival times as actual survival times in, for example, a standard regression analysis would bias the results in terms of underestimated survival potential.

In our study, survival analysis was used to describe the duration of the effects of fish removal in lakes, 'duration' being defined as the number of years passing until the summer mean of a given parameter returned to the level before the removal. If the fish removal was non-effective, the duration is 1 year, whereas an 'eternal' effect corresponds to a very long, unknown duration still being traceable at the cessation of the investigation period as a right-censored duration. In particular, this means that it is not a prerequisite of survival analysis that the lake at some point returns to the state prior to removal. There are some limitations in the data set as annual measurements are not available in many lakes. This implies that the observed duration may be overestimated, as several years may have passed before the relapse was discovered. On the other hand, in other cases where the effect does not appear until several years after the actual removal the observed duration may be underestimated because it then seems as if the fish removal was not effective.

To overcome some of the heterogeneity among lakes, corrections were made for the differences in mean depth and the pre-values of TP by the use of explanatory variables (Cox-regression; Kalbfleisch and Prentice 1980). Reference values for the explanatory variables were a mean depth of 1 m and a TP of 0.1 mg P l^{-1} , whereas the general loading level corresponds to 2006. Thereby, the survival curve is assumed to represent only the effect of the fish removal, as the general development of the parameter in Danish lakes was eliminated.

Statistical Tests

Statistical significance between pre- and post-treatment values was tested by *t*-tests ($P < 0.05$) using SAS. Each post-treatment year was tested relative to the pre-treatment value for each variable.

RESULTS

Nutrients, Chlorophyll, and Secchi Depth

In the nine lakes in which less than $200 \text{ kg fish ha}^{-1}$ were removed within 3 years no clear effects on nutrient concentrations and turbidity were seen (Figure 1). The only significant effect was observed for Chl a during the first year after removal.

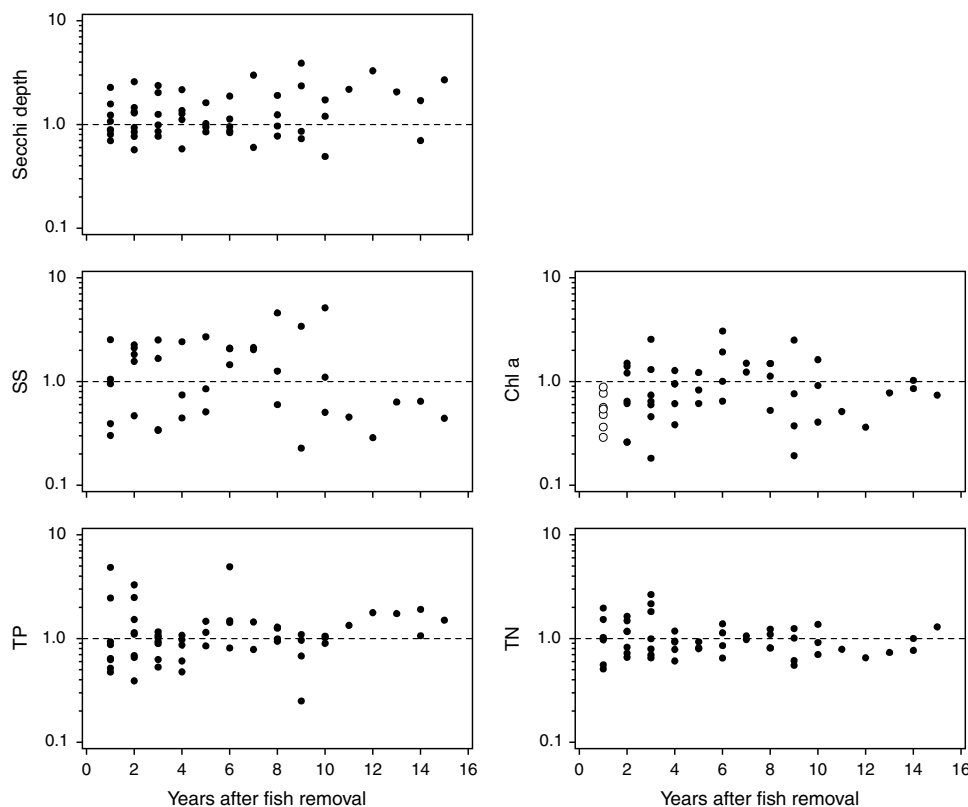


Figure 1. The relative effect at removal of less than $200 \text{ kg fish ha}^{-1}$ over 3 years on Secchi depth, SS, Chl a, TP, and TN in 9 lakes. Time-weighted summer means. Open circles: group of lakes significantly different from the pre-removal situation.

In the 27 lakes in which more than 200 kg fish ha^{-1} were removed during a 3-year period, marked effects on Secchi depth and on all four water chemical variables appeared (Figure 2). The effects were most distinct for Secchi depth, Chl a and SS, but a substantial impact was also observed for TP and TN. The effects occurred already during the first year of removal, but grew stronger in the subsequent years. Typically, Chl a and SS decreased to 50–70%, whereas Secchi depth almost doubled during the first 8–10 years after the initiation of removal. Despite large variations among lakes, an

effect was observed in more than 75% of the lakes and it remained statistically significant for several years. Most variables differed from the pre-situation during the first 6–8 years after the removal, but after approximately 10 years all variables, excluding Secchi depth and partly also SS, exhibited a tendency to return to pre-removal conditions. However, this tendency is based on data from a limited number of lakes. After 14 years SS and Secchi depth also returned to pre-removal conditions, but data are only available for 1–3 lakes.

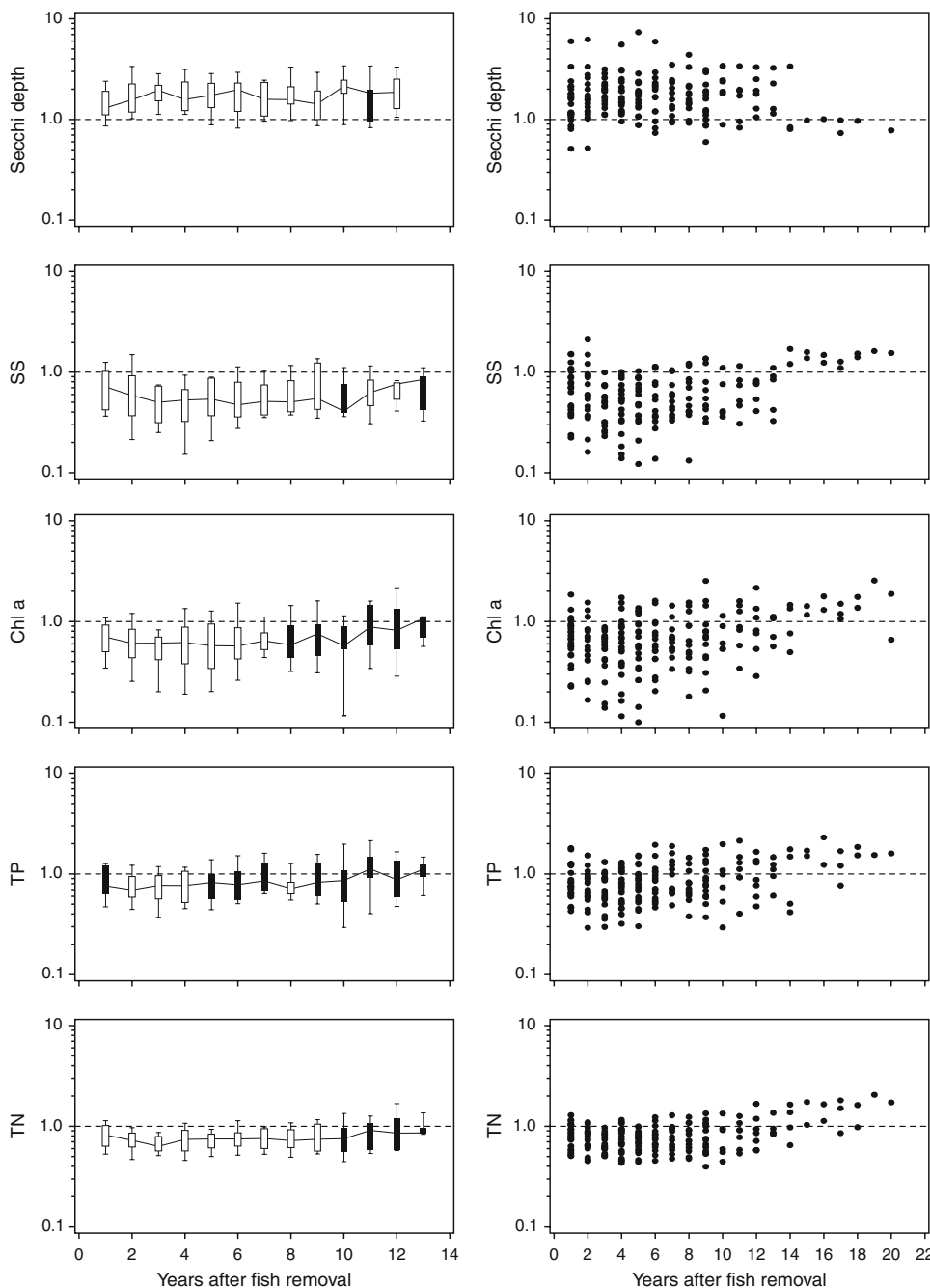


Figure 2. The relative effect at removal of more than 200 kg fish ha^{-1} during 3 years on Secchi depth SS, Chl a, TP, and TN in 27 lakes (time-weighted summer means). Light boxes: significant different from the pre-removal situation. The boxes show 10 and 90% fractiles (*outer lines*), 25 and 75% fractiles (*boxes*). The right-hand side of the figure depicts data from individual lakes.

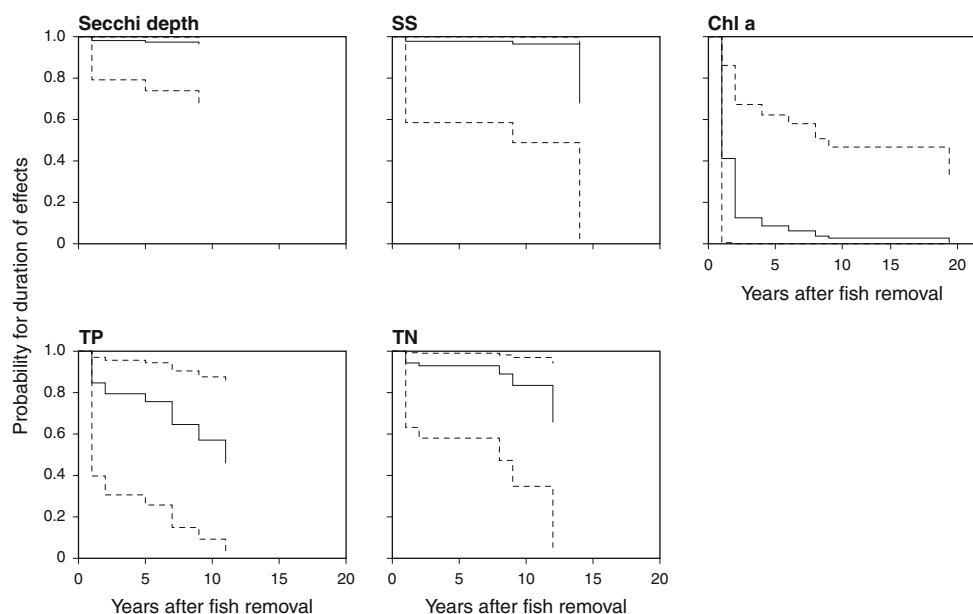


Figure 3. Estimated survival curves (*lines*) with 95% certainty limits (*broken lines*) for Secchi depth, SS, Chl a, TP, and TN in lakes with a mean depth of 1 meter and a pre-value of TP of 0.1 mg P l^{-1} . The general loading level corresponds to that of 2006.

The ‘survival analyses’ for Secchi depth and the four chemical parameters follow the same tendencies (Figure 3). The capability of the lakes to maintain a change in Secchi depth (increase) and SS (reduction) for a prolonged number of years—and perhaps permanently—seems relatively high with a mean ‘survival’ exceeding 90% after more than 10 years (high uncertainty hereafter due to limited data availability). Mean survival of TN is also relatively high, whereas TP and particularly Chl a exhibit a more rapid decline, their mean survival being only 10% after 5 years—both with large confidence intervals, however. It should be emphasized that large inter-annual fluctuations may contribute to low survival, as a single year with high values will imply that the lake, in survival terminology, is considered ‘dead’ even though its state may improve in the subsequent years. In no cases were the explanatory variables found to be statistically significant (significance level 5%).

Phytoplankton

Total algal biovolume generally paralleled the trend seen for Chl a, that is, a 30–50% reduction after initiation of removal. In contrast to the water chemical variables, no significant effect was observed during the first year (Figure 4).

There was substantial variation in the contribution of different algal classes, which partly also reflects a different phytoplankton community found in lakes with different nutrient concentrations. Fish removal led to marked shifts for some of the classes; most notable was the greater than 50% reduction

in mean abundance of cyanobacteria after 3–7 years, it being, however, only statistically significant during the first 2–5 years. Another very notable effect was a substantial increase in most lakes in the abundance of cryptophytes, particularly during the first 3–6 years following removal. With the exception of a few lakes the proportion of cryptophytes was substantially higher during the first 10 years after removal, but the change was only statistically significant during year 3 and 4 after removal. The relative biomass contribution of other algal classes did not change significantly after the fish removal.

Zooplankton

Fish removal did not have significant effects on total zooplankton biomass, although shifts occurred in the abundances of the various zooplankton groups (Figure 5). Particularly the biomass of *Daphnia* increased during the first approximately 5 years, although the changes were not significant. In contrast, the contribution of small-sized cladocerans (other cladocerans) declined, in some years significantly so, although variations among lakes were pronounced. Apart from this, no marked general effects occurred for any of the main groups.

The ratio between the biomass of zooplankton and phytoplankton (here calculated on the basis of both phytoplankton biomass and Chl a converted to dry weight) increased considerably after removal, not least the ratio based on Chl a which more than doubled in nearly all lakes after 3–8 years. The changes were only statistically significant for a few

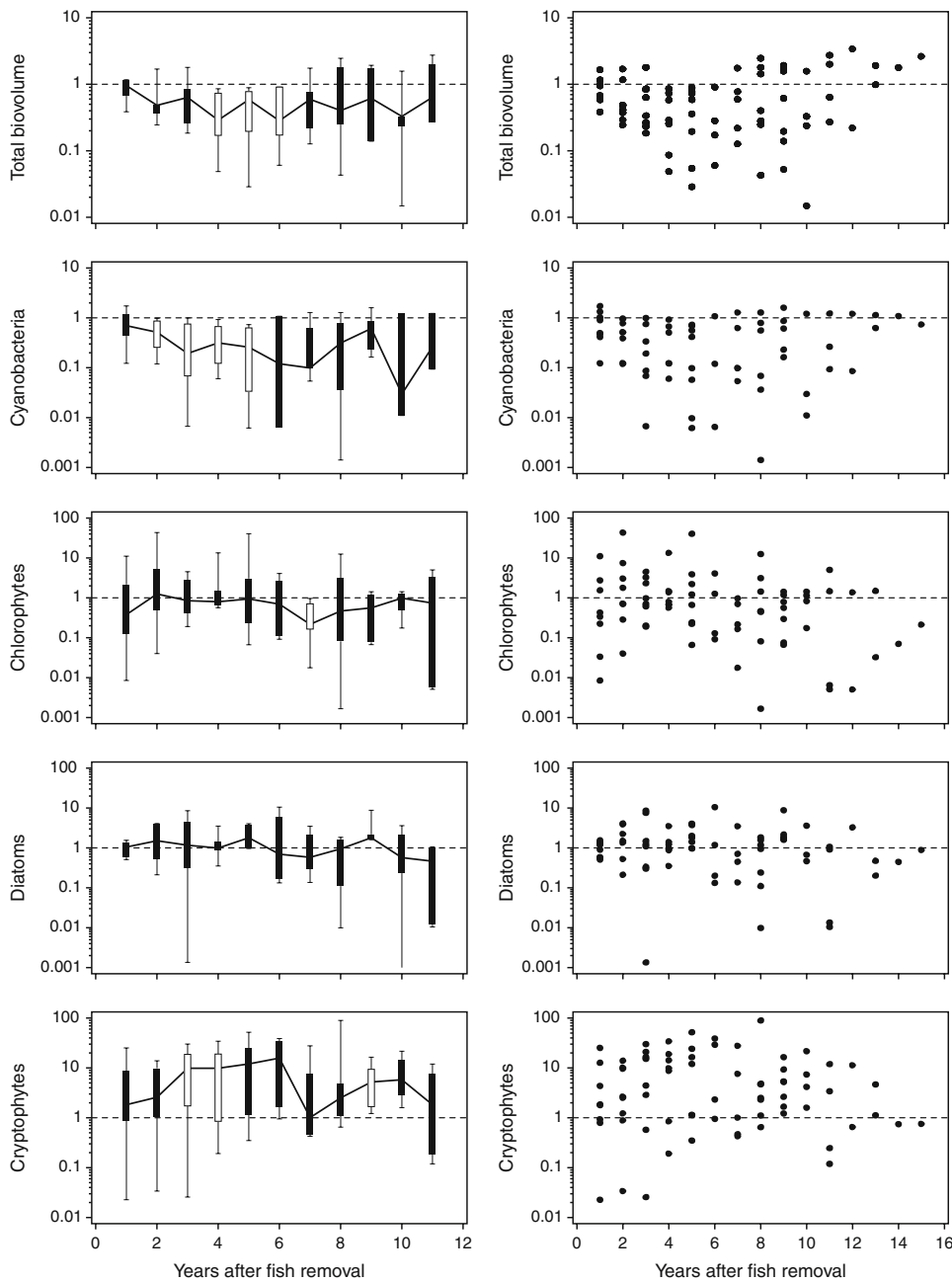


Figure 4. Phytoplankton biomass and the relative share of the most important algal classes relative to the pre-removal situation (number of lakes = 10). See also Figure 2.

years, though. After 8 years the effect seemed to abate, but only few data were available to substantiate this finding.

Fish

Catch per unit effort of the fish stock, both in terms of total number and total biomass, did not change consistently following removal (Figure 6). On a per species basis, marked changes were recorded, however. Apparently bream is the species most notably impacted by removal in the long-term, showing a considerable and maintained significant

decrease in biomass. Initially bream numbers declined, but after 7–8 years a tendency toward increased abundance was observed, without influencing the decrease on weight basis, however. Roach biomass tended to increase (not significantly) after the fish removal, whereas roach abundance tended to decrease (not significantly) during the first years, followed by an increase. The number of perch increased during the first years after removal (not significantly), but then declined again in many lakes. Perch biomass increased (albeit not significantly) after removal and remained

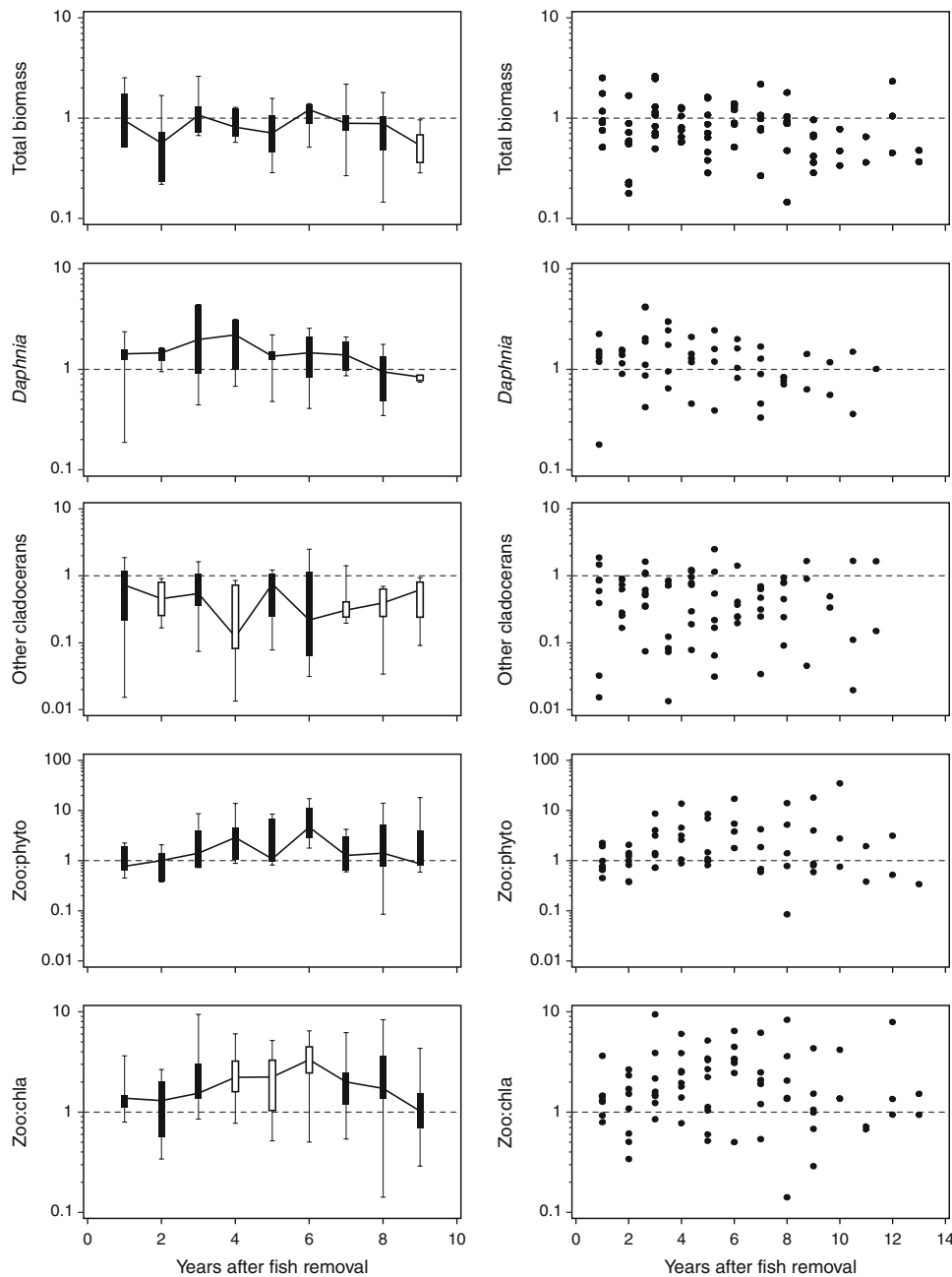


Figure 5. Total zooplankton, *Daphnia* and other cladoceran biomass, (dry weight) and the ratio between zooplankton and phytoplankton biomass, and between zooplankton biomass and chlorophyll *a* (number of lakes = 10). See also Figure 2.

high in most lakes, even after the decrease observed after 5–6 years. There was, though, a tendency to a further decrease after 9–10 years.

Submerged Macrophytes

The abundance of submerged macrophytes increased in most lakes, but in some lakes no changes were recorded (Figure 7). In total, the number of species increased in 13 out of 15 lakes and remained unchanged in two lakes. The dominant species were tall species such as *Elodea canadensis*, *Myriophyllum spicatum*, *Ceratophyllum demersum*, and

Potamogeton species (*P. crispus*, *P. pectinatus*, and others). The maximum depth distribution increased in nine lakes, but did not change in two lakes. The coverage of macrophytes increased in seven lakes and was unaffected in three lakes.

DISCUSSION

Our study confirms the findings from many investigations around the world that significant effects on lake water quality can be obtained by an adequate fish removal (Carpenter and others 1985; Jeppesen and others 1990; Hanson and Butler

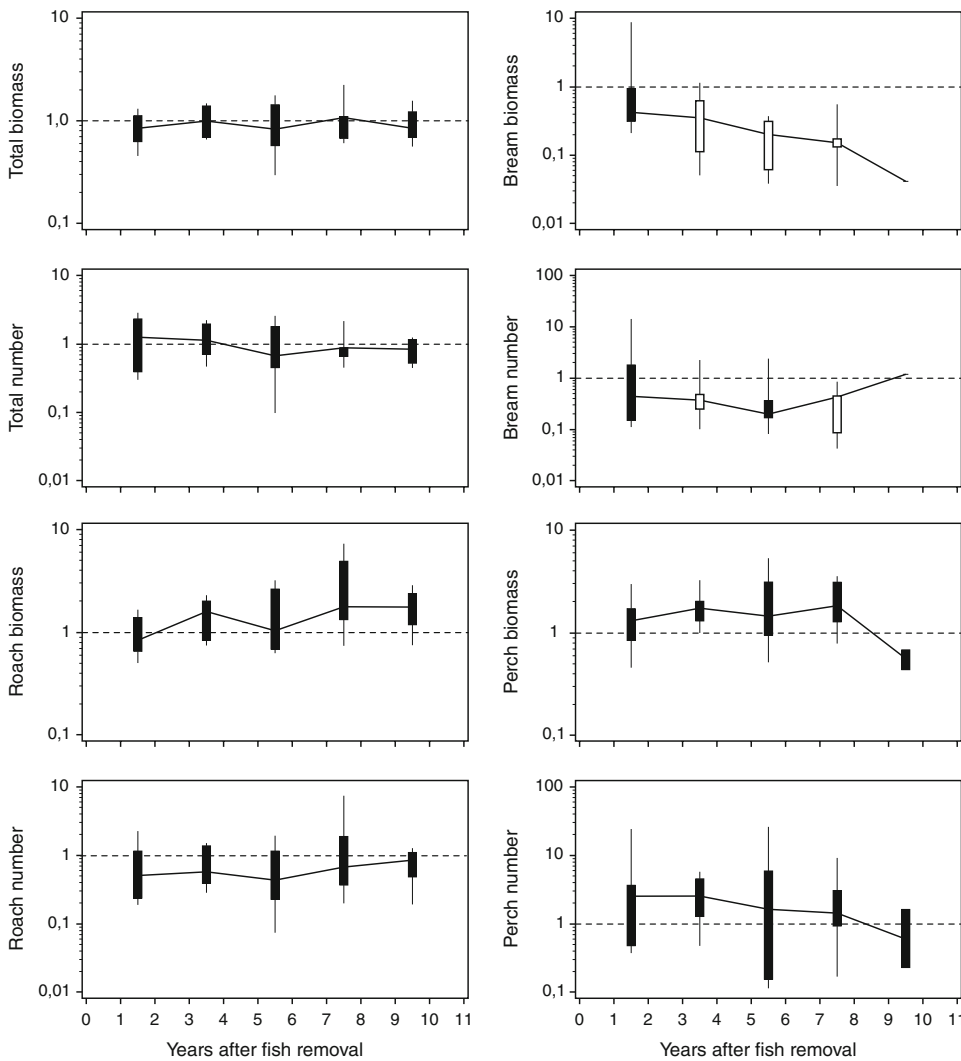


Figure 6. The relative changes in fish stock based on catch per unit effort (CPUE) on weight (kg fish per net) and number (number of fish per net) following removal of more than 200 kg fish ha⁻¹: (upper left): total CPUE; (upper right): bream; (lower left): roach, (lower right): perch (number of lakes = 14). See also Figure 2.

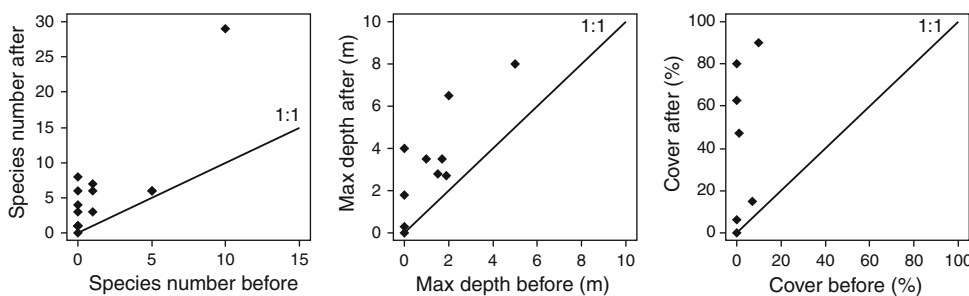


Figure 7. Changes in the number of species, maximum depth distribution, and cover of submerged macrophytes after the fish removal (number of lakes = 10–15).

1994; Meijer and others 1999; Mehner and others 2002). The relatively large number of lakes included in our study exhibit various general patterns that may, though, be restricted to shallow, nutrient rich Northern temperate lakes. Also, in other lake types other mechanisms may prevail (Jeppesen and others 2007). Although our study does not determine the required extent of removal to establish strong cascading effects, it does support the

recommendations by Jeppesen and Sammalkorpi (2002) and Olin and others (2006) that preferably more than 200 kg ha⁻¹ fish should be removed within a few years from nutrient rich lakes to obtain notable effects. However, as fish removal was frequently conducted for more than 3 years in our study lakes, it cannot be excluded that the observed effects were triggered by continued fish removal for some lakes.

Suspended solids and Secchi depth were the variables most significantly affected by fish removal. This confirms that the reduction of benthivorous fish should be an important target in biomanipulation projects (Drenner and Hambricht 1999), because benthivores increase sediment resuspension and the concentrations of SS as well as phytoplankton biomass via their search for food in the sediment (Breukelaar and others 1994; ter Heerdt and Hootsmans 2007; Roozen and others 2007). As most of the Danish study lakes were shallow and easily influenced by wind the effect of bream removal may also be indirect, as suggested by Scheffer and others (2003) who found that the presence of benthivorous fish in a large Dutch lake could prevent sediment consolidation that would otherwise decrease resuspension in windy periods. The persistently lower bream biomass after the fish removal may thus be the main reason why the concentrations of SS remain low in most lakes and why improvements in Secchi depth seem to last longer than a reduction in Chla. In contrast, the return of roach may explain the short impact period recorded for zooplankton with fewer *Daphnia* and reduced phytoplankton grazing (as indicated by reduced zooplankton:phytoplankton ratios) after some years with high *Daphnia* abundance and high grazing. The faster recovery of the roach population after biomanipulation compared to bream may be related to successful breeding of roach in most years, whereas the success of bream fluctuates more in Danish lakes (authors' unpublished results). Moreover, bream typically dominate in hypertrophic lakes and roach at intermediate nutrient concentrations (Jeppesen and others 2000), and in the long-term roach are therefore expected to be less sensitive to biomanipulation-related changes in the fish stock at the prevailing nutrient levels in the study lakes.

Chlorophyll *a* and the biomass of phytoplankton were significantly affected the first 6–8 years after removal, but then approached pre-restoration levels. The biomass of cyanobacteria and hence also the potential toxin production declined markedly in several lakes, which is often regarded as a specific criterion for successful biomanipulation (Hansson and others 1998). Cyanobacteria are considered resistant to zooplankton grazing when abundant (Fulton and Pearl 1988; Chen and others 2007), but our results and similar data from Finnish biomanipulation projects (Olin and others 2006) suggest that cyanobacteria dominance is not an obstacle to successful biomanipulation of lakes. The relative importance of cryptophytes increased after the fish removal, supporting the observation that

the grazing impact on phytoplankton was stronger in the initial years following fish removal, as cryptophytes tend to dominate in systems characterized by high zooplankton grazing (Schriver and others 1995).

Recovery of submerged macrophytes is important for maintaining a clear water state in shallow lakes and it is regarded as one of the main reasons that biomanipulation seems to be more successful in shallow than in stratified lakes (Benndorf and others 2002; Mehner and others 2002). In this study the coverage and the maximum depth of submerged macrophytes increased in most, but not all, lakes. Delayed recovery despite improved light conditions may be due to grazing by waterfowl—and possibly also by fish—impeding macrophyte recolonization (Søndergaard and others 1996; Lauridsen and others 2003; Hilt 2006). From investigations in a Dutch peat lake ter Heerdt and Hootsmans (2007) concluded that high turbidity caused by benthivorous fish in combination with waterfowl grazing were the main causes for the absence of submerged macrophytes. How often waterfowl grazing acts as a limiting factor for colonization of submerged macrophytes after fish removal cannot be determined and is probably also lake specific and influenced by morphometry and the duration of the eutrophication period. However, the relatively fast recolonization of macrophytes seen in many lakes in this study indicates that waterfowl usually do not prevent their reestablishment.

An important side effect of biomanipulation in shallow lakes where clear water is established is decreased concentrations of both phosphorus and nitrogen. In our study the concentrations were reduced to about 50% of the previous levels. This has also been seen in other shallow lakes shifting between the clear and turbid state (Søndergaard and others 1990; Hargeby and others 2007; Ibelings and others 2007). There are several potential mechanisms behind the increased retention. Thus, with reduced phytoplankton biomass the concentrations of organic bound nitrogen and phosphorus decrease as well (Jeppesen and others 1998), impacting TP and TN concentrations and therefore also the retention percentage. If submerged macrophytes re-establish enhanced growth of periphyton may increase phosphorus retention (Dodds 2003) and the co-precipitation of phosphorus with CaCO_3 (Hartley and others 1997). Another mechanism is increased benthic primary production (Jeppesen and others 1998; Søndergaard and others 2005; Tarvainen and others 2005; Spears and others 2007), resulting in an increasing uptake of

phosphorus and nitrogen from the sediment, which reduces the pool of nutrients that may be released to the water column (Hansson 1989). Larger benthic primary production will also more easily establish well-oxidized conditions at the sediment surface, leading to a higher phosphorus retention capacity due to increased presence of oxidized iron hydroxides (Mortimer 1941; Penn and others 2000). Increased retention is important not only for the lake itself, due to the creation of self-reinforcing effects, but also for the loading of possible downstream aquatic areas. On the other hand, high phosphorus retention constitutes a potential risk that the lake may be more heavily influenced by internal release of phosphorus from the sediment if a return to turbid conditions should occur (Søndergaard and others 2007). This is because the sediment stores more phosphorus during the period with improvements than it would have done without biomanipulation.

An important question concerning biomanipulation is the long-term perspective. Is biomanipulation a one-time intervention or must it be repeated? Some case studies clearly demonstrate that short-term effects may be easier to obtain than long-term maintenance of clear water effects (Van de Bund and Van Donk 2002; Søndergaard and others 2007). In our study the effects were highly positive for most of the investigated variables during the first 2–6 years; however, long-lasting or permanent effects seem more difficult to obtain as only a few variables showed significant effects for more than 8–10 years. The number of lakes with data series exceeding 10 years is, however, modest, rendering the prediction of long-term perspectives uncertain. Particularly Chla tends to increase again, which reduces the probability of a permanent shift to a clearwater state. Also, the ‘survival analyses’ show a relapse after a number of years and indicate that maintenance of lower concentrations of SS and increased Secchi depth is more probable than lower phosphorus concentrations and reduced phytoplankton biomass. The tendency to a return to turbid water has also been found in other studies (Mehner and others 2002), suggesting that repetitive removals may be required to maintain the clearwater state, at least in lakes with relatively high nutrient concentrations as those included in our study. However, the follow-up removals may likely be more moderate, as the bream stock, on a weight basis, seems to be affected in the long-term and as the body size of perch and roach increases after removal, this being a typical sign of a more healthy fish community in north European temperate lakes (Jeppesen and others 2000). Given the

positive effects of submerged macrophytes on lake water quality in shallow lakes (Jeppesen and others 1997), the establishment of a substantial coverage of a stable macrophyte community most likely will increase the chance of more permanent improvements. However, we do not have sufficient data from this study to determine whether the occurrence or absence of long-term effects can be related to the disappearance of macrophytes.

A reduction of the phosphorus concentration and the external phosphorus input has been deemed essential to obtain enduring effects, as the probability for obtaining and maintaining positive effects increases at decreased phosphorus concentrations. Equilibrium concentrations below 0.05–0.1 mg P l⁻¹ have been recommended (Jeppesen and others 1990; Jeppesen and Sammalkorpi 2002). Unfortunately, the data from our study do not allow us to determine the level to which loading should be reduced to obtain longer lasting or enduring effects, as all fish removals, except four, were undertaken in lakes with phosphorus concentrations above 0.1 mg P l⁻¹. Consequently, the main reason for the relatively poor long-term success and the tendency to a return to pre-restoration phosphorus levels is probably that nutrient input levels are too high. At a sufficiently strong reduction of the external loading the actual necessity of conducting fish removal ought to be carefully considered as fish communities often respond relatively fast to lowered loading by a decline in fish biomass and an increase in the proportion of piscivores (Jeppesen and others 2005). The mobile phosphorus pool in the sediment and the probability that internal phosphorus loading will regulate lake concentrations likely also decide whether permanent effects can be created, as demonstrated by the increased phosphorus concentrations at the shift from clear to turbid water (Søndergaard and others 2007). Another reason for unstable clear water conditions after biomanipulation in shallow lakes is the risk that the community of submerged macrophytes—provided that they return—will be dominated by a few, nutrient tolerant and fast growing species, such as *Elodea canadensis* which is known to exhibit large inter-annual fluctuations (Rørslett and others 1985; Strand and Weisner 2001; Søndergaard and others 2007). Such macrophytes may be less suited to stabilize permanent clear water in the long term. As demonstrated by long-term studies in Northern Europe, only 1 year of unfavorable conditions for macrophytes, where they miss their ‘window of opportunity’, may lead to their disappearance and a return to turbidity

(Blindow and others 1993; Van de Bund and Van Donk 2002; Søndergaard and others 2007).

In sum, the results from 36 shallow Danish lakes in which fish removal has been conducted clearly demonstrate that substantial effects on all trophic levels may be achieved for multiple years if an adequate amount of planktivores is removed. Our results also suggest that fish removal mainly should be regarded as a management tool to be repeated rather than as a one-time intervention—at least at the nutrient levels exhibited by the lakes in our investigation. As time series beyond 10 years after biomanipulation are only available for a limited number of lakes, our conclusions as to long-term effects are relatively uncertain.

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