BIOMANIPULATION IN THE NETHERLANDS

15 years of experience

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Stellingen

1. Verwijdering van meer dan 75% van de visstand leidt vrijwel altijd tot helder water, ook bij hoge nutriënten gehalten.

2. Het sterk uitdunnen van de visstand (Actief Biologisch Beheer) is een effectievere maatregel om de helderheid van het water te vergroten dan fosfaatreducerende maatregelen.

3. Actief Biologisch Beheer is behalve een methode om de algenconsumptie te verhogen ook een methode om de fosfaatconcentratie in een meer te verlagen.

4. Het algemene idee dat in voedselrijke wateren ieder jaar moeten worden afgevist om het water helder te houden is onjuist. Als het water eenmaal helder is geworden en waterplanten zijn opgekomen, dan volstaat een uitdunning in iedere 5-8 jaar.

5. De in Nederland gebruikelijke methode van zooplankton bemonstering (overdag en in het open water) is ongeschikt om in heldere wateren het effect van graas op zooplankton te bepalen.

6. Het bij de waterbeheerders geconstateerde verschil in opvatting over de effectiviteit van Actief Biologisch Beheer, geeft vooral aan dat een mislukking in eigen water zwaarder weegt dan succesverhalen elders.

7. Niet alleen in het Wolderwijd, maar ook in het Veluwemeer heeft een reductie van de visstand het herstel versneld.

8. Vissen in troebel water werkt verhelderend.

9. Wetenschapsbeleid dat is gericht op grote onderzoeksverbanden staat vernieuwend fundamenteel onderzoek in de weg.

10. Genezing van een langdurige ziekte is pas mogelijk, als de energie om weer beter te worden beschikbaar komt.

11. Het totale budget voor het lager onderwijs is in verhouding tot het totale budget voor het hoger onderwijs te laag.

12. Het grote plezier van het hebben van kinderen weegt ruimschoots op tegen de complexiteit van de combinatie van werk en zorg.

Marie-Louise Meijer.
Biomanipulation in The Netherlands, 15 years of experience.
29 mei 2000, Wageningen Universiteit

CONTENTS

ABSTRACT

The objective of lake restoration in the Netherlands is the return of clear water and growth of aquatic plants. This thesis analyses the potential of biomanipulation as a method to restore the clear water state in eutrophic lakes and the mechanisms involved. The existence of alternative stable states is presented as the basis for biomanipulation. Whole lakes experiments varying in scale from 3 ha to 2650 ha are analysed. A comparison of 18 whole lake experiments demonstrates that biomanipulation is effective in creating clear water, even in eutrophic lakes, provided the fish stock removal is substantial. Fish reduction not only affects top-down mechanisms, but appears to reduce bottom-up production as well. Although the clear water state in eutrophic lakes is not stable in the long run, the return time to the turbid water state is long (> 8 years).

CHAPTER 1

INTRODUCTION

INTRODUCTION

Up to the 1950's, most Dutch shallow lakes were characterised by clear water and an abundant growth of submerged macrophytes (Hosper, 1997). The lakes contained low concentrations of nutrients and observers described transparent water and light green meadows of stoneworts (Redeke, 1948; Van Zinderen Bakker, 1948). In the 1960's this situation started to change. Due to the increase in population, agricultural activities and use of fertilizers, the nutrient loading to the Dutch surface waters increased. This led to a higher algal production, a process known as eutrophication (Golterman, 1970) and resulted in turbid water. The turbidity of the water and the increased production of epiphytic algae on surfaces reduced the light availability for the macrophytes and they disappeared (Philips *et al.*, 1978). The elevated production of algae and the decaying macrophytes produced high amounts of detritus, which accumulated on the bottom of the lakes to form loose sediment. Resuspension of this loose sediment by wind, waves and benthivorous fish further enhanced the turbidity of the water (Gons *et al.*, 1986).

Restoration methods such as reduction of the external phosphorus loading had only a limited effect. The decrease of external P-loading was partly compensated by phosphorus release from the sediment (Brinkman & van Raaphorst, 1978; Golterman, 1977). This led lake managers, in later years, to remove phosphorus-rich sediment by dredging (Frinking & Van der Does, 1993). As a result of these measures the chlorophyll-*a* concentrations in many lakes decreased, but the effect was not sufficient to cause a substantial improvement of the transparency of the water (Van Liere & Gulati, 1992; Sas, 1989; Van der Molen & Portielje, 1999). Research showed that the turbid state has various stabilising mechanisms causing it to be resistant to restoration measures centred on nutrient reduction. The problems encountered during the attempts to restore eutrophic shallow lakes spawned an interest in the alternative approaches, especially those involving reduction of the fish stock.

Already in the 1960's it was recognised that planktivorous fish can reduce the potential of zooplankters to graze upon algae, through selective predation of the more efficient large bodied cladocerans (Hrbáček *et al.*, 1961, Brooks & Dodson, 1965). However, it was not until 1975 that Shapiro and co-workers suggested that these predator-prey relationships had implications for lake restoration, as they reasoned that the fish stock of most eutrophic lakes would be dominated by planktivorous fish. They introduced "biomanipulation" as a restoration approach in which components of the ecosystem were manipulated in order to reduce the algal biomass (Shapiro *et al.*, 1975). In addition to control of zooplanktivorous fish, they suggested other means of increasing the mortality rate of algae, such as introduction of filterfeeders like mussels, stimulation of algal viruses or the introduction of refuges for the zooplankton to hide against the predation by fish. Since the mid 1980's, however, the term biomanipulation is generally restricted to fish removal, or the introduction of piscivores, or both (Jeppesen *et al.*, 1990; Hosper & Meijer, 1993; Philips & Moss, 1994; Hansson *et al.*, 1998).

The first biomanipulation experiments were, almost exclusively, carried out in deep lakes (Benndorf, 1988; see review in Walker, 1989) where predation by planktivorous fish on zooplankton was observed to be a dominant process. However, in Denmark, The UK and The Netherlands biomanipulation was mostly carried out in shallow lakes (Jeppesen *et al.*, 1990; Philips & Moss, 1994; this thesis) where sediment-water interactions, the benthic food-web and the potential for the dominance of submerged macrophytes play an important role in the mechanisms involved in restoring the lakes (Jeppesen, 1998; this thesis). Biomanipulation in such lakes involves three phases: a drastic reduction of the fish stock, resulting clearance of the water and the stabilisation of the clear water state (Hosper & Meijer, 1993). Therefore, a successful biomanipulation roughly works as follows: after a drastic fish mass reduction in winter, the large-bodied zooplankters, *Daphnia sp.*, develop in spring causing a high grazing pressure on the algae leading to clear water. In addition the reduction of the biomass of bottom-feeding fish leads to a decrease of resuspension of sediment enhancing the increase in water clarity. The resulting clear-water phase in spring induces the macrophytes to develop, which in turn stabilise the clear water state. The positive effect of vegetation on water clarity is the result of a combination of different mechanisms. Dense vegetation reduces the resuspension of the sediment by wind (Van der Berg *et al.*, 1997; James & Barko, 1990). Plants may also enhance the populations of piscivorous fish, i.e. pike and perch, which can reduce the standing stock of bream (Grimm, 1990). Aquatic plants provide a refuge for zooplankton against planktivorous fish (Timms & Moss, 1984; Schriver *et al.*, 1995). Also, macrophytes create suitable conditions for denitrification and take up nitrogen for their growth, which can lead to nitrogen limitation of the algal production (Gumbricht, 1993;Van Donk *et al.*, 1993). Finally, plants may release allelopathic substances which reduce the algal growth as shown in laboratory studies (Wium-Andersen *et al.*,1982).
Since macrophyte growth is enhanced by clear water, the improvement in the underwater light caused by the plants implies a positive feedback which stabilises the clear-water state once vegetation has invaded the lake (Scheffer, 1998). Whether this feedback stabilises vegetation dominance in the long term, depends among other things upon the nutrient concentrations. A critical phosphate concentration between 0.05 and 0.10 mg P l^{-1} has been suggested, but this level will depend partly on other factors such as lake size and the potential for nitrogen limitation (Jeppesen *et al.*, 1990; Hosper & Jagtman, 1990; Moss *et al.*, 1996; Jeppesen, 1998).

In The Netherlands, the understanding of the way in which biomanipulation can contribute to the restoration of shallow lakes has gradually evolved over the past 15 years from numerous field studies (Van Donk *et al.*, 1990, 1993; Van Donk & Gulati, 1995; this thesis) and model analyses (Scheffer, 1989, 1990; 1993; Scheffer, 1998). The biomanipulation experiments started in 1985 with research on the edibility of cyanobacteria by *Daphnia* in plastic bags as small mesocosms (Rigter,1986). This was followed, in 1986, by experiments in small drainable ponds (Chapter 3). From 1987 onwards biomanipulation was applied in whole lakes, starting in small lakes (< 5 ha) and later upscaling the experience to larger lakes > 2000 ha (Gulati *et al.*, 1990; Van Donk *et al.*, 1990a and 1990b; Chapter 4, 5 and 8; Van Berkum *et al.*, 1995). From 1989 to 1993 a grant from the Dutch Government (REGIWA) stimulated the application of lake restoration methods and the number of biomanipulation projects expanded. By 1998 it was possible to evaluate 18 biomanipulation projects in the Netherlands (Chapter 9).

Most of the data included in this thesis are based on whole lake experiments. A drawback of whole-lake studies is that rigorous analysis of the results is difficult because there is often (but not always) no reference situation and because frequently more than one measure is carried out simultaneously. Comparisons among whole-lake-studies may further be hampered by variation in restoration- and monitoring methods. In mesocosms the impact of fish and/or zooplankton is easier to study than in the field, due to better replication and controll of conditions. On the other hand, it is difficult to translate the observations of mesocosm experiments to whole lakes (Carpenter & Kitchell, 1992; Schindler, 1998), as in a whole lake patterns occur due to processes such as wind resuspension and the active movement of predators and prey (Schindler, 1998), which are absent in mesocosms. Thus, the potential of biomanipulation as a lake-restoration method can only be evaluated by applying the method in real lakes.

In the 1980's many papers on individual whole-lake biomanipulation studies or enclosure experiments were published (Shapiro & Wright, 1984; Reinertsen & Olsen, 1984; Van Donk *et al.*, 1989; Faafeng, 1988; Gulati *et al.*, 1990; Jeppesen *et al.*, 1990; Chapter 3, 4, 5, 8). In the first half of the 1990's several reviewers doubted the effectiveness of biomanipulation as a restoration method, especially in eutrophic lakes (De Melo *et al.*, 1992; Reynolds, 1994; Harris, 1994). However, this thesis and several recent publications demonstrate that biomanipulation is a powerful restoration method even in eutrophic lakes, provided that a substantial fish removal has been carried out (Hansson *et al.*, 1998; Chapter 9; Jeppesen, 1998).

This thesis provides an overview of a series of studies focused on the potential of biomanipulation as a method to restore the clear water state in eutrophic lakes and the mechanisms involved.
After a theoretical outline of the existence of alternative stable states and the principle of biomanipulation (Chapter 2), two biomanipulation experiments are described in more detail, one mesocosm experiment in ten drainable ponds of 0,1 ha (Chapter 3) and one experiment in the small Lake Bleiswijkse Zoom of 3,1 ha (Chapter 4). The mechanisms behind the observed changes in transparency in Lake Bleiswijkse Zoom and in the biomanipulated Lake Noorddiep (4,5 ha) and in particular the role of benthivorous fish in this process are quantified in Chapter 5. When it became clear that biomanipulation could lead to clear water in small biomanipulated lakes the issue of long term stability remained. This aspect is studied in the following chapter, based on five year results from Lake Noorddiep, Lake Bleiswijkse Zoom and Lake Zwemlust in The Netherlands and Lake Væng in Denmark (Chapter 6). Subsequently, the testing of the initial idea that the development of submerged macrophytes will change the fish stock towards more piscivores and more macrophyte-associated fish is analysed in the three mentioned Dutch lakes in Chapter 7. Chapter 8 shows that the biomanipulation experiments were not restricted to small lakes, as this chapter describes the effects of biomanipulation in the large Lake Wolderwijd (2700 ha). In Chapter 9 the results of

eighteen biomanipulation experiments in the Netherlands are evaluated in order to determine the critical conditions for a successful biomanipulation and the mechanisms involved.

In the final chapter, the evolution of hypotheses on the developments of the trophic levels after biomanipulation and the mechanisms that cause the water to become clear and to stay clear, are discussed (Chapter 10).

CHAPTER 2

ALTERNATIVE EQUILIBRIA IN SHALLOW LAKES

M. Scheffer, S.H. Hosper, M.-L. Meijer, B. Moss, E. Jeppesen, 1993
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ALTERNATIVE EQUILIBRIA IN SHALLOW LAKES

ABSTRACT

The turbidity of lakes is generally considered to be a smooth function of their nutrient status. However, recent results suggest that over a range of nutrient concentrations, shallow lakes can have two alternative equilibria, a clear state dominated by aquatic vegetation, and a turbid one characterized by high algal biomass. This bistability has large implications for the possibilities of restoring eutrophied shallow lakes. Nutrient reduction alone may have little effect on water clarity, but an ecosystem disturbance like foodweb manipulation can bring the lake back to a stable clear state. We discuss the reasons why alternative equilibria are theoretically expected in shallow lakes, review evidence from the field, and evaluate some recent applications of this insight in lake management.

INTRODUCTION

The theoretical possibility that ecosystems have more than one equilibrium has been long recognized (Noy-Meir, 1975; May, 1977). Support from field data is less easily obtained. However, recent observations on shallow lakes have led aquatic ecologists to suspect that these ecosystems may indeed possess two alternative stable states, a turbid and a clear one (Hosper, 1989; Timms & Moss, 1984; Scheffer, 1989,1990: Jeppesen *et al.*, 1990). Many ecological feedback mechanisms are thought to play a role in this, but most ideas centre around the interaction between submerged vegetation and turbidity (Figure 2.1). Vegetation tends to enhance clarity of the water, while on the other hand, a high turbidity prevents the growth of submerged plants. The adverse impact of turbidity on vegetation growth is simply a matter of light limitation. Submerged plants can only grow down to a certain turbidity-dependent depth (Figure 2.2) beyond which the light availability becomes too low (Spence, 1982). The positive effect of vegetation on water clarity is the result of a number of different mechanisms: resuspension of bottom material is reduced by vegetation (James & Barko, 1990); aquatic plants provide a refuge against planktivorous fish for zooplankton which grazes phytoplankton (Hosper, 1989); vegetation can suppress algal growth due to a reduction of nutrient availability (Van Donk *et al.*, 1990); and plants can release allelopathic substances that are toxic to algae (Wium-Andersen, 1987).
Although the quantitative importance of each of these submechanisms is often hard to assess and may vary between lakes, analysis of large data sets supports the view that there is an overall positive

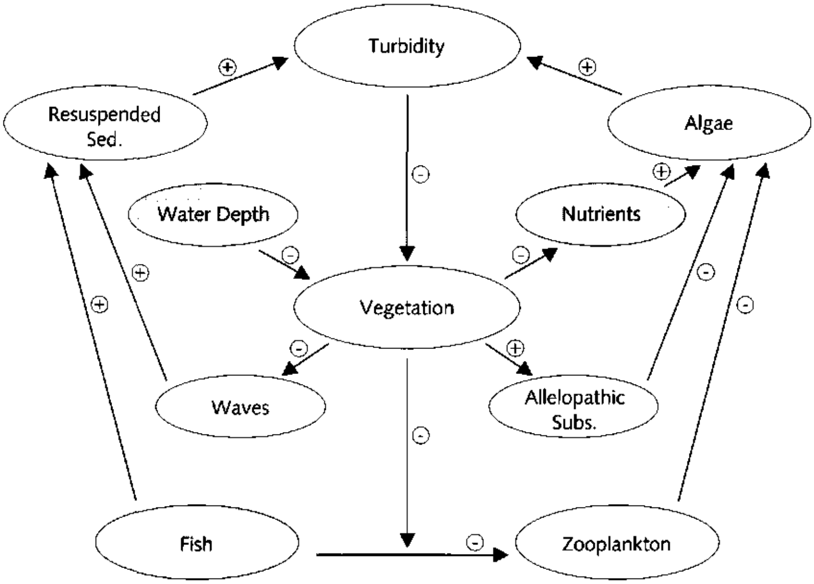


Figure 2.1: *Main feed-back loops thought to be responsible for the existence of alternative equilibria in shallow lake ecosystems. The qualitative effect of each route in the diagram can be determined by multiplying the signs along the way. In this way it can be seen that both the vegetated and the turbid state are self-reinforcing. The qualitative effect of management measures discussed in this paper can be checked in the same way if a 'manager' box with positive or negative arrows pointing to either of the shaded parts of the system is added.*

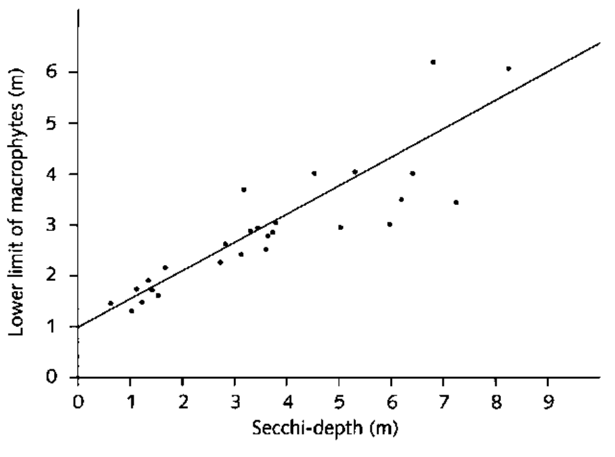


Figure 2.2: *Relation between transparency ('secchi-depth') and the lower limit of vegetation in 27 Finnish lakes (Wetzel, 1975).*

effect of vegetation on water transparency in freshwater lakes. Lakes with a high cover of submerged macrophytes tend to have a higher transparency than lakes with the same nutrient status in which vegetation is sparse or absent (Figure 2.3).

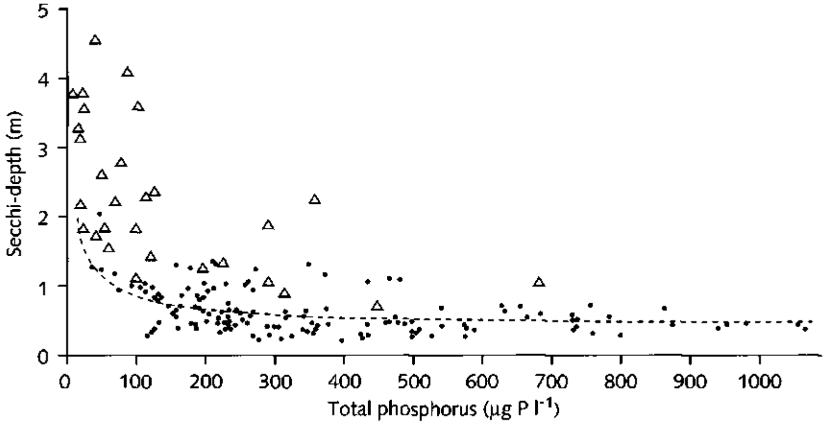


Figure 2.3: *Summer mean transparency ('secchi-depth') in relation to lake water total-P for shallow Danish lakes with high cover of submerged vegetation (triangles) and lacking such vegetation (small dots).*

THEORY OF ALTERNATIVE LAKE EQUILIBRIA

The question whether these ecological mechanisms may indeed be expected to cause alternative stable states has been explored extensively with the use of minimal models (Scheffer, 1989, 1990). The basic idea, however, can already be clarified from a simple graphical approach (Figure 2.4). Vegetation can stabilize a clear water state in shallow lakes up to relatively high nutrient loadings, but once the system has switched to a turbid state, it takes a strong nutrient reduction to enable recolonization by plants. This graphical analysis is based on some rather crude simplifications like the assumption that submerged vegetation disappears abruptly at a critical turbidity, but models employing more realistic assumptions (Scheffer, 1990) produce similar results (An example is given in box 1).
The stability properties of such systems can be visualized by means of 'marble-in-a-cup' pictures (Figure 2.5). The equilibrium line with 'catastrophe fold' shown at the bottom of the figure is computed from the vegetation-algae model explained in box 1. The valleys in the stability landscapes correspond to stable parts of the fold curve and the hill tops to the dashed breakpoint part that marks the separation between the basins of attraction. Each picture in the series shows the stability properties at a different nutrient status. The front landscape represents a hypertrophic situation in which just one equilibrium exists, a turbid one. The rear picture represents the pristine state of a lake, a low nutrient situation in which a clear water equilibrium is the only possible stable

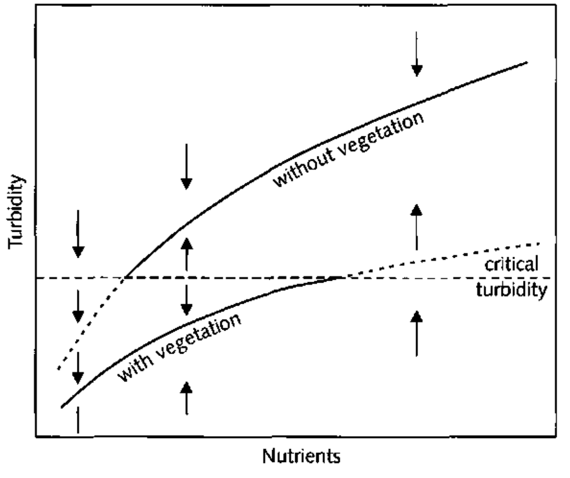


Figure 2.4: *Alternative equilibrium turbidities caused by the presence and absence of aquatic vegetation. Equilibrium turbidity increases with the nutrient level, but because vegetation reduces turbidity, two different relations apply depending on whether vegetation is present or not. Vegetation presence itself, however, is also dependent on turbidity. Light limitation prevents growth below a (turbidity dependent) depth, and since shallow lakes are often rather homogeneous in depth, the response of the vegetated area to turbidity tends to be discontinuous. Here we assume the extreme case of this were vegetation totally disappears from the lake when the turbidity exceeds a threshold value at which the critical light level for vegetation growth at this depth is reached. Consequently, the 'with vegetation' line applies below the critical turbidity and the 'without vegetation' line above this level. Hence, the dashed parts of the two equilibrium lines do not represent stable states. The emerging picture shows that at low nutrient levels only the vegetated clear equilibrium exists and at high nutrient levels only the turbid vegetationless one. However, over a range of intermediate nutrient concentrations two alternative stable states are possible. Here, the critical turbidity represents the breakpoint of the system separating the attraction areas of these alternative states. Arrows indicate the direction of change in turbidity when the system is out of equilibrium.*

state. Between these two extremes there is a range of nutrient levels over which two alternative equilibria exist.

The response of a lake with these stability properties to eutrophication and subsequent restoration efforts can be derived from this representation. Starting from the pristine state, a moderate increase in nutrient level gives rise to an alternative turbid equilibrium, but if no large perturbations occur, the system will stay in the clear state. Continuing enrichment, however, gradually causes the stability of the clear state to shrink to nil, making it more and more vulnerable to perturbations that can bring it within the basin of attraction around the turbid equilibrium. Even in the absence of perturbations the hysteresis period in which the lake hardly responded to nutrient loading will finally end with a catastrophic transition into a turbid state at the inflection point of the catastrophe fold where the clear water equilibrium disappears.

Obviously, restoration of such a lake by reduction of the nutrient level may often have little effect, since the system can show hysteresis again, staying in its current turbid state. However, in this situation a change to the alternative clear water equilibrium can be achieved in other ways. One way to force a switch is by 'pushing the ball over the hill top', bringing it within the attraction basin of the clear state. More specifically, this requires a temporary reduction in the turbidity of the lake, sufficient to allow recolonization by submerged vegetation. The other obvious possibility from the theoretical point of view is to 'move the hill top temporarily to the other side of the ball'. The hill top is situated at the critical turbidity for recolonization by submerged vegetation (Figure 2.5). Since it is water depth in combination with turbidity that determines whether the underwater light level for vegetation development is met, the hill top can be moved by changing water level. Lowering the water level causes an increase in critical turbidity and it can be seen from figure 2.5 that this may bring a system from a formerly stable turbid state on the upper equilibrium line into the attraction area of the vegetated state.

It should be noted that a high potential impact of vegetation on the system and a sigmoidal decrease of vegetation with turbidity are important in the proposed mechanisms (Figure 2.4 and box 1). Therefore, the phenomenon of alternative clear and turbid stable states is expected to be restricted

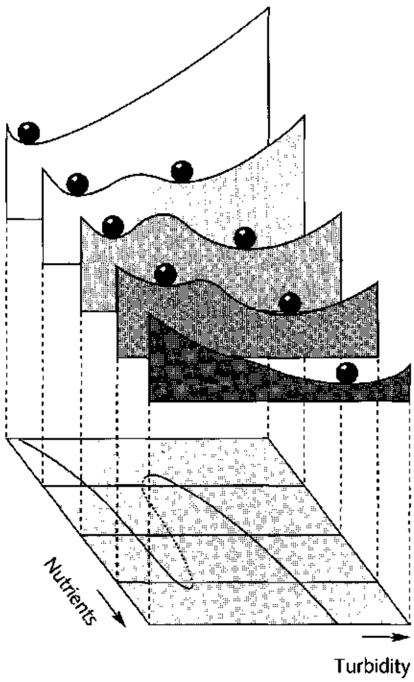


Figure 2.5: *Stability properties of a shallow lake system at different nutrient levels, as derived from model analyses (Scheffer, 1990).*

to shallow lakes of homogeneous depth where a major part of the water body can be occupied by plants and small changes in turbidity or water level can have a relatively high impact on vegetation when the light climate is just critical for plant growth at the average lake depth.

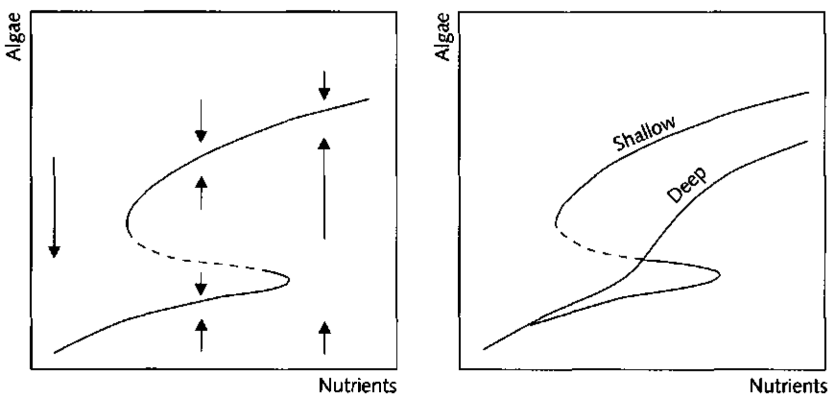
BOX 1. A VEGETATION-ALGAE MODEL

A simple model (Scheffer, 1990) for the interaction between the growth of planktonic algae (A) and the abundance of vegetation (V) illustrates the potential for alternative equilibria in shallow lakes:

$$\frac{dA}{dt} = rA\left(\frac{N}{N+h_n}\right)\left(\frac{h_v}{V+h_v}\right) - cA^2$$

$$V = \frac{h_A}{A^p + h_A^p}$$

Algal growth is basically logistic with a maximum intrinsic growth rate (r) and a competition coefficient (c) as parameters. In addition, growth increases in a Monod fashion with the nutrient level and decreases in a similar way with vegetation abundance (h_N and h_V being the half-saturation constants). Vegetation abundance is a negative sigmoidal function of algal biomass (h A being a half-saturation constant again). The value of the power (p) shapes this relation. A high value of p causes it to approach a step function representing the disappearance of vegetation from a shallow lake of homogeneous depth around a critical algal biomass where turbidity makes the average depth of the lake unsuitable for plant growth. If the equilibrium density of phytoplankton (dA/dt = 0) is plotted against the nutrient level for the shallow lake case, a catastrophe fold arises which is a smooth edged version of the representation derived graphically in figure 2.4. The response of vegetation to increased turbidity will be less discontinuous in deeper lakes with gradually declining slopes (Scheffer, 1990). When we mimic



this by decreasing the value of p, the range of nutrient values over which alternative equilibria exist becomes smaller until the alternative equilibria disappear and the response of phytoplankton equilibrium density to nutrient level becomes continuous. Obviously, each depth profile will actually have its own specific vegetation-turbidity response, but the result suggests that alternative equilibria arising from the modelled interaction are limited to shallow lakes. Another reason to expect this is that the effect of vegetation on turbidity will be strongest in shallow water where vegetation structure can fill the whole water column. High vegetation impact can be represented in the model by decreasing the h_V. It appears that such an increase of vegetation impact does indeed increase the tendency of the model to generate alternative stable states.

EVIDENCE FROM THE FIELD

The theoretical results supply a search image of the symptoms to look for in the real world. For instance, one would expect some sets of shallow lakes to show a bimodality of states, being clear or turbid depending on history rather than physical and chemical conditions. Also, relatively swift transitions from a vegetated clear state to a turbid vegetationless situation and vice versa should incidentally occur as a response to disturbances or changes in external factors other than nutrients. The current literature on shallow lakes does indeed provide several observations of these phenomena.
A good example of a set of shallow lakes showing bimodality of state is the Great Linford sand and gravel pit complex in England. The site has 14 lakes excavated over the past 40 years. Some were dry-dug, others wet-dug. The digging method appears to have a pronounced effect on turbidity. Dry digging results in clear lakes, while wet digging results in turbid ones because of a high loading of fine silt. Remarkably, after some decades the wet-dug lakes are still turbid and devoid of vegetation, whereas the dry-dug ones remained clear and richly vegetated (Giles, 1986). In 1987, part of the fish stock was removed from one of the turbid lakes. This led to a reduction of turbidity, and large weed beds quickly developed in the 25-year-old lake, which had no such growth previously (Giles, 1988; Wright & Phillips, 1982). The lake has, so far, remained in this state, supporting the view that clear and turbid states are indeed alternative stable equilibria.

Another way to trace bimodality of states is to analyze the history of one lake rather than the current situation in a set of lakes. Some lakes are known to have switched back and forth between a clear vegetated state and a distinct turbid situation repeatedly in the past. Although, the information about such switches is often anecdotic, there are some relatively well documented cases also.
A good example of a switching lake is Tomahawk Lagoon in New Zealand (Mitchell *et al.*, 1988; Mitchell. 1989). Since 1963, phytoplankton and aquatic vegetation each have predominated in turn in this shallow lake for periods of 1-5 years. In the clear vegetation-dominated years phytoplankton production can be reduced by as much as two orders of magnitude. The

mechanism inducing the switches is not yet clear, but the strong contrast between the two states suggests that they are separate equilibria.
A similar situation is found in Lake Takern and Lake Krankesjön, two shallow lakes in the south of Sweden (Blindow, 1992). Periods with clear water and abundant submerged vegetation have alternated with periods of turbid water and sparse submerged vegetation over the past 40-50 years without considerable change in the external nutrient loading. Although, reconstruction of the mechanism of change is difficult, there are indications that changes in the water level affecting the performance of submerged macrophytes may have been an important trigger of switches in these lakes. The best information is available for Lake Krankesjön (Bindow, 1982; Andersson *et al.*, 1990) which showed a marked change from clear to turbid in the early seventies after an increase in water level. A period of low water level during 1985 and 1986 seems to have been the onset for a pronounced switch back to a clear state with abundant vegetation growth and waterfowl.
Obviously, the fact that these observations fit the theory is by no means a proof of its validity. Alternative explanations may be possible in any specific case, and it is, in fact, questionable whether experimental determination of the unique responsible mechanism is feasible at all in ecosystems Quinn & Dunham, 1983; Roughgarden, 1983; Scheffer & Beets, 1993). Nonetheless, the case for the alternative stable state idea appears strong enough to persuade lake managers to aim at forcing turbid shallow lakes into a clear equilibrium with a single perturbation (Hosper & Jagtman, 1990).

APPLICATION TO THE MANAGEMENT OF SHALLOW LAKES

The restoration of eutrophied turbid shallow lakes is notoriously difficult. Reduction of the nutrient loading rarely leads to a satisfactory recovery of the clear state in shallow lakes. This can in part be explained from the release of buffered phosphorus from the sediment delaying the response of the actual nutrient level of the water to reduction of the external loading (Cullen & Forsberg, 1988; Sas, 1989; Jeppesen *et al.*, 1991; Van der Molen & Boers, 1994). However, the current theory of bistability suggests an additional explanation. Even if the nutrient level is considerably reduced, this will often be insufficient to restore the clear water state in bi-stable shallow lakes, as the turbid equilibrium can be (locally) stable down to low nutrient levels (Figs. 2.4 and 2.5). In such cases restoration requires an additional 'shock therapy' to bring the ecosystem within the basin of attraction of the alternative clear water equilibrium.
Recently, reduction of the fish stock ('biomanipulation' (Gulati *et al.*, 1990) has been successfully applied to several turbid shallow lakes to enforce this switch (Chapter 4; Van Donk *et al.*, 1990; Sondergaard *et al.*, 1990). Two mechanisms seem to be predominantly responsible for the initial increase of clarity after the fish stock reduction in shallow lakes (Figure 2.1). In the first place, the strongly debated (DeMelo *et al.*, 1992; Carpenter & Kitchell, 1992) trophic cascade effect is observed (Van Donk *et al.*, 1990: Sondergaard *et al.*, 1990). Reduction of the predation pressure from planktivorous fish allows populations of large-bodied zooplankters to peak and graze down the algal biomass causing clear water in spring (Carpenter, 1988; Scheffer, 1992). At least as important as the trophic cascade, however, is the effect of reduced sediment resuspension in

many shallow lakes (Chapter 4; Breukelaar *et al.*, 1994). When the fish community is dominated by species that feed in the bottom like carp (*Cyprinus carpio*) or bream (*Abramis brama*) resuspended bottom material is often the main cause of turbidity, and consequently removal of fish leads to an almost instantaneous increase of transparency.

The increase of transparency after biomanipulation is typically followed in shallow lakes by a strong development of submerged vegetation in the following years (Chapter 4; Van Donk *et al.*, 1990; Sondergaard *et al.*, 1990). Recruitment of the remaining fish is generally good under the new conditions, giving rise to large numbers of young fish in the subsequent years. Such small fish are mainly planktivorous and can potentially exert a huge predation pressure on zooplankton. Nonetheless, the lakes stay clear, presumably because of the manifold stabilizing effect of vegetation on the clear water situation (Chapter 6). An analysis of the long-term response of four particularly well-studied cases (Chapter 6) shows that these lakes have remained in the obtained clear water state for at least 4-5 years (Figure 2.6; Chapter 6). Although changes are still occurring in the lakes and it is unsure whether they will all stay clear in the future, the current results support the alternative stable state hypothesis.

As argued, lowering the water level should be another possibility for inducing the switch to a vegetated clear state. The fact that the pronounced changes in the Swedish lakes Krankesjön and Takern (Blindow, 1992; Andersson *et al.*, 1990) are presumably induced by natural fluctuations in water level, supports this idea. We are not aware of cases in which the water level has been manipulated with the explicit purpose of changing the ecosystem state, but it is known that the effect of such manipulation on the community of shallow lakes can be dramatic. A well documented example is the case of Lake Tämnaren, another Swedish lake (Wallstein & Forsgren, 1989). The construction of a dam increased the water level in this shallow (< 2 m) lake by 0.5 m. This caused a decrease in vegetated area from 80% to 14% of the lake bed. The large numbers of birds that used to forage in the vegetated lake disappeared, and the water that had been clear enough to see the bottom through the vegetation became turbid because of wind resuspension of

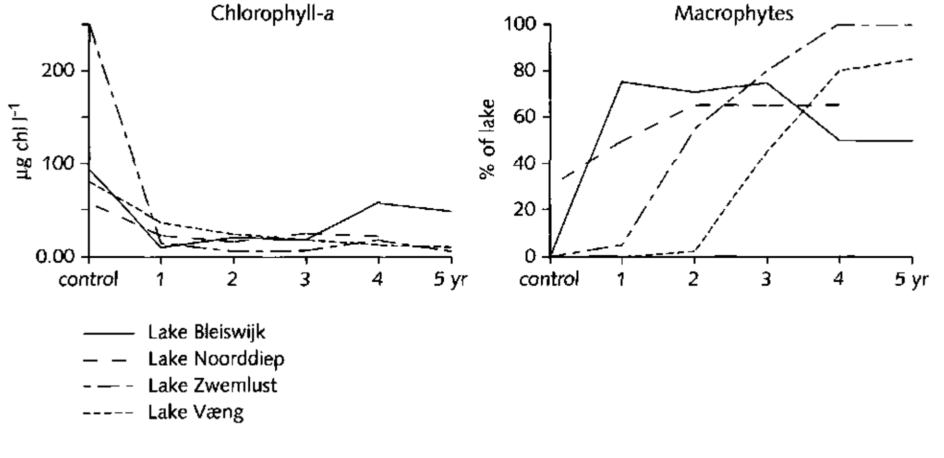


Figure 2.6: *Sustained effects of biomanipulation in four shallow lakes (Chapter 6).*

the unconsolidated sediment and increased algal growth. A subsequent lowering of the water level would be necessary to check whether the clear and the turbid state are indeed alternative equilibria in this specific case, but the response of the lake illustrates the potential of water level manipulation as a tool for managing the ecosystem state of shallow eutrophic lakes.

Obviously, many of the mechanisms governing the dynamics of shallow lake communities are still poorly understood, and it remains difficult to determine whether an alternative clear equilibrium may be expected in any specific case. Nonetheless, the current experiences are encouraging from a management point of view, since they suggest that shallow lakes which stay turbid despite reduction of the nutrient loading may be permanently restored by a single perturbation, provided that the nutrient status has been brought down to a low enough level to allow the existence of an alternative clear equilibrium.

CHAPTER 3

IMPACT OF CYPRINIDS ON ZOOPLANKTON AND ALGAE IN TEN DRAINABLE PONDS

M-L. Meijer, E.H.R.R. Lammens, A.J.P. Raat, M.P. Grimm & S.H. Hosper, 1990

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IMPACT OF CYPRINIDS ON ZOOPLANKTON AND ALGAE IN TEN DRAINABLE PONDS

ABSTRACT

To study the impact of cyprinids on algae, zooplankton and the physical and chemical water quality, ten drainable ponds of 0.1 ha (depth 1.3 m) were each divided into two equal parts. One half of each pond was stocked with 0+ cyprinids (bream, carp and roach of 10-15 mm), the other was free of fish. The average biomass of the 0+ fish at draining of the ponds was 466 kg ha^{-1}, to which carp contributed about 80 %. The fish and non-fish compartments showed significant differences. In the non-fish compartments the density of *Daphnia hyalina* was 10-30 ind l^{-1} and that of *Daphnia magna* 2-4 ind l^{-1}, whereas in the fish compartments densities were 1 ind l^{-1}. Cyclopoid copepods and *Bosmina longirostris,* however, showed higher densities in the fish compartments. The composition of algae in the two compartments differed only slightly, but the densities were lower in the non-fish compartments. The significant difference in turbidity was probably caused by resuspension of the sediment by carp. No significant difference in nutrient concentration between the compartments was found.

INTRODUCTION

In the last 30 years the turbidity of the water of most lakes in the Netherlands has increased due to eutrophication. Increased nutrient loading has resulted in large phytoplankton biomasses and the decline in submerged vegetation. This situation led to the disappearance of the predatory fish pike *Esox lucius* in many waters (Grimm, 1981b). Consequently highly enriched waters contain large biomasses of planktivorous and benthivorous fish, mainly bream (*Abramis brama*) (Lammens, 1986). Reduction of nutrient-loading is the main policy for eutrophication control. However, the present fish stock seems to hamper the recovery of the lakes. Biomanipulation, involving reduction of the bream biomass, may speed up the recovery process (Shapiro, 1980; Hosper, 1989).
In recent years much attention has been paid to the role of planktivorous fish in the freshwater system. Planktivorous fish feed on large zooplankton species and within one species the larger individuals are preferred (Hrbáček *et al.*, 1961; Brooks & Dodson, 1965). Large zooplankters are the most efficient predators on algae. In lakes containing a large biomass of planktivorous fish, grazing on algae by zooplankton may be too low to control algal biomass. Beside zooplankton some fish also feed on benthic fauna (such as chironomids), causing resuspension of the sediment which leads to

a higher turbidity and an increased release of nutrients from the bottom. Furthermore fish may prevent young macrophytes from settling (Ten Winkel & Meulemans,1984).
Enclosure experiments have shown the effects of fish on the mean individual length of the zooplankton and on the turbidity of the water (Anderson *et al.*, 1978). In small lakes also, removal of fish has resulted in a shift to large zooplankton species, lower turbidity and lower algal concentrations (De Bernardi & Guissani, 1978; Reinertsen & Olsen, 1984; Shapiro & Wright, 1984; Lazarro, 1987).
Most of the biomanipulation experiments up to now have been done in deep waters. In the shallow Dutch lakes there will be also an impact of resuspension of the bottom.
In order to obtain a better insight into the impact of the removal of planktivorous fish from shallow waters, a number of experiments has been carried out in drainable fishponds.
The results of the experiments are reported in this paper.

METHODS

The experiments took place at the experimental station of the Organisation for the Improvement of the Inland Fisheries in Beesd in the period May-November 1986. Ten drainable ponds of 0.1 ha (40 x 25 m, 1.3 m depth) were divided into two compartments by screens (plastic foil/gauzy material). One compartment of each pond was stocked with fish (Table 3.1): roach (*Rutilus rutilus*), bream (*Abramis brama*) and common carp (*Cyprinus carpio*). The other compartment was not stocked with fish.

Table 3.1: *Fish stocking with 0+ individuals in the ponds.*

Species	Date	Size (mm)	Number
Roach	3-06-1986	10	3150
Bream	3-06-1986	8	6300
Carp	3-07-1986	19	3000

The ponds were inundated by pumping in water from an adjacent polder through a net (2 mm) that excluded fish but allowed algae and zooplankton to enter the ponds. Nitrogen (urea) and phosphate (superphosphate) were added four times to eliminate problems due to nutrient depletion. In total 3.35 g N m^{-2} and 0.5 g P m^{-2} were added to the water during the experimental period.

Oxygen concentration, pH and Secchi transparency were measured in situ. Water samples were taken with a transparant tube of 1.5 m length and 5 cm diameter, which sampled the entire water-column. For each compartment samples taken in 25 places were mixed. In the samples nutrient concentrations (silicon, nitrate, nitrite, ammonium, total nitrogen, orthophosphate and total phosphate), chlorophyll-*a* concentrations and species and numbers of algae and zooplankton were determined. Methods employed were according to Dutch Standard Methods with occasional minor modifications. Generally, Dutch Standard Methods (NEN) are in compliance with International Standards (ISO). The nutrients were determined by automated colorimetric methods. For chlorophyll-*a* an ethanol extraction was used. To determine zooplankton 25 litres of water was filtered over 120 μm filter. The samples were immediately fixed in 4 % formaline. In general subsamples of 1:10 were taken with a Kott-subsampler.

To determine phytoplankton 1 litre water was fixed with Lugol solution. The samples were concentrated from 1 litre to 10 ml by sedimentation.

At biweekly intervals fish samples were taken in all ponds with a lift net (1.5 x 1.5 m). The fork- and total length were measured. On average 5-20 individuals were caught in each compartment. In four ponds the gut content of the fish was examined. The gut content was fixed by 4 % formaline. Individuals of zooplankton, insect larvae and snails were counted; the biomass of the vegetation was estimated. Monthly, the composition and degree of cover of the submerged vegetation was monitored in each compartment.

In the first week of November the ponds were drained and the fish was removed and weighed.

RESULTS

The results are illustrated by the time-series of the average of all fish and non-fish compartments. A sign test (Sokal & Rohlf, 1981) was used to quantify the significance of the differences between the compartments for the average of all ponds and for the individual ponds.

Fish

Growth of stocked 0+ cyprinids took place in the first three months of the experiment. At draining of the ponds their total weight (± standard deviation) was 466 ± 74 kg ha^{-1}. Two length classes of common carp were distinguished by length frequency analyses. Carp constituted 84.3 % of the total fish biomass (large carp, 8-14 cm: 92 ± 32 kg ha^{-1}; small carp, 5.5-8 cm: 304 ± 74 kg ha^{-1}). The biomass of roach (7.4 ± 0.4 cm) at draining was 22 ± 6 kg ha^{-1}, the biomass of bream (6.2 ± 0.4 cm) was 52 ± 26 kg ha^{-1}. Mortality among the stocked bream and roach was high (87 % and 95 % respectively), but 83 % of the stocked common carp survived till the end of the experiment.

Zooplankton

Zooplankton densities were much alike in all ponds. Figure 3.1 shows the development of the average densities of the main zooplankton species over the 10 ponds. In the fish compartments the densities of large zooplankton species like *Daphnia hyalina* and *Daphnia magna* are significantly lower (Table 3.2) than in those without fish. In June high densities of the large Cladocera (65 ind l^{-1}) were found in both compartments. From July on the density of *Daphnia hyalina* rose to 10-30 ind l^{-1} in the non-fish compartments and that of *Daphnia magna* to 2-4 ind l^{-1}, whereas in the fish compartments densities were 1 ind l^{-1}. However, smaller species like *Bosmina longirostris* and the cyclopoid copepods reached significantly higher numbers (20-30 and 30-80 ind l^{-1} respectively) in the fish compartments than in those without fish (Table 3.2). In the non-fish compartments the density of the copepods was 5-20 ind l^{-1}, that of *Bosmina* about 15 ind l^{-1}.

Table 3.2: *Significance of differences between fish and non-fish compartments from 10th July to 30th October (sign test Sokal & Rohlf. 1981, + = higher in fish compartments, - = lower in fish compartments).*

Ponds	1	2	3	4	5	6	7	8	9	10	avg.
Zooplankton											
D. magna	0	-	---	--	0	--	---	0	-	0	---
D. hyalina	--	---	---	---	---	---	---	---	--	---	--
Bosmina sp.	0	0	+++	++	++	0	++	++	++	0	+
Cyclopoid copepods	++	++	+++	++	++	0	++	+++	+++	++	+++
Nauplii	+++	+	+++	+	+	+	+++	+++	+++	+++	++
Phytoplankton											
Chlorophyll-*a*	+++	+++	+++	++	0	0	+	+++	+	++	+++
Tot. number	++	+	++	+	+	0	++	++	+++	+++	++
Tot. Diatoms	++	0	++	++	-	0	++	+	+++	++	+++
Tot. Chrysophyceae	++	++	+++	0	++	+++	0	+++	+++	+	++
Tot. Cryptophyceae	--	0	0	0	+	0	0	0	0	+	0
Tot. Chlorococcales	++	++	++	+++	++	0	+++	++	+++	++	+++
Tot. Cyanophyceae	-	0	0	0	0	0	--	0	++	0	0
% Diatoms	0	0	0	0	0	--	0	0	0	0	0
% Chrysophyceae	+++	0	+	+	0	++	0	+	+	0	+++
% Cryptophyceae	---	0	--	0	-	0	0	-	0	0	-
% Chlorococcales	++	++	+	0	--	+	++	+	++	+++	++
% Cyanophyceae	---	0	--	---	0	0	---	---	0	--	--
Turbidity	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++
Nutrients											
Ortho-P	0	0	--	0	--	0	0	0	0	0	0
Total P	0	0	0	0	0	0	0	0	0	0	0
Soluble N	++	+	++	0	0	0	-	0	0	0	0
Total N	0	0	0	0	0	0	0	0	0	0	0

+++ --- $p \leq 0.005$; ++ -- $p \leq 0.01$; + - $p \leq 0.05$; 0 = no significant difference

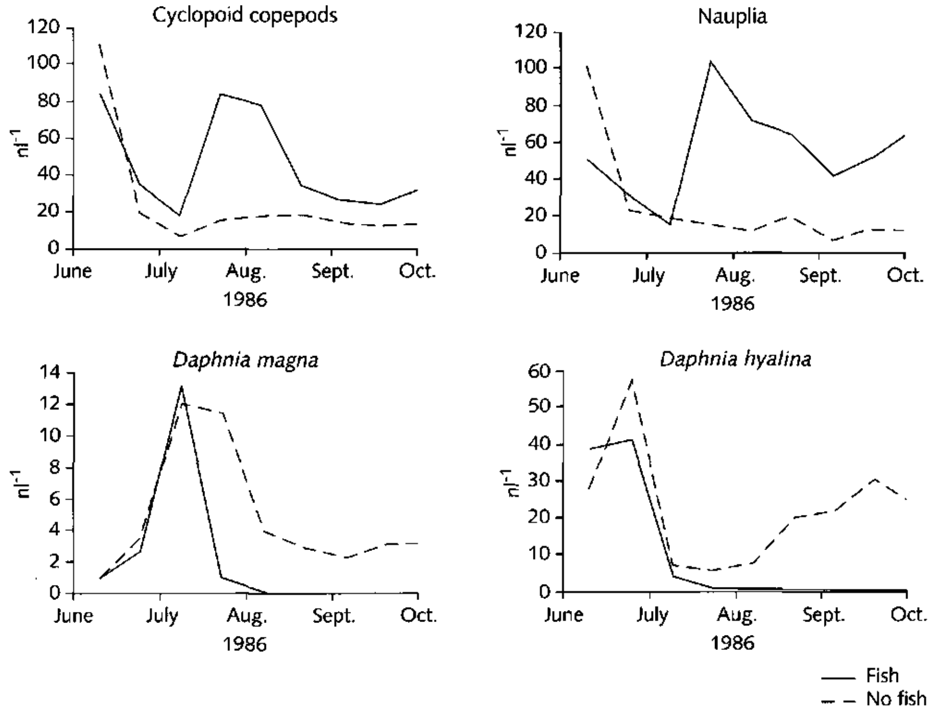

Figure 3.1: *Density (ind l^{-1}) of large Cladocera Daphnia magna and Daphnia hyalina, cyclopoid copepods and Nauplia in fish and non-fish compartments throughout the experiments. Average values of ten ponds.*

Phytoplankton

In most ponds chlorophyll-a concentrations were significantly higher in the fish compartments than in those without fish (Figure 3.2, Table 3.2). However, the difference is small. The chlorophyll-a concentrations were generally low in both compartments (5-15 mg m^{-3}).

Figure 3.4 shows the development of the different groups of algae in the ponds. In June the phytoplankton consisted mainly of Cryptophyceae (50 %), in July and August diatoms became dominant (40-70 % abundance), whereas in the final months mainly Cryptophyceae, Chlorococcales and diatoms were present. The diversity of the phytoplankton is high in both compartments: as many as 70 different species were found. The relative abundance of the groups differed slightly from pond to pond. In general the same groups were dominant in all ponds but not at the same time. The difference in the total numbers of algal cells is mainly attributed to diatoms, Chrysophyceae and Chlorococcales (Table 3.2). The differences in Chrysophyceae are caused by the growth of *Dinobryon divergens* and *D. sertularia*. Several *Navicula*, *Gomphonema* and *Nitzschia* species contributed to the difference in total number of diatoms. *Monoraphidium* was the main species of the Chlorococcales during the whole period. No difference between the two compartments was

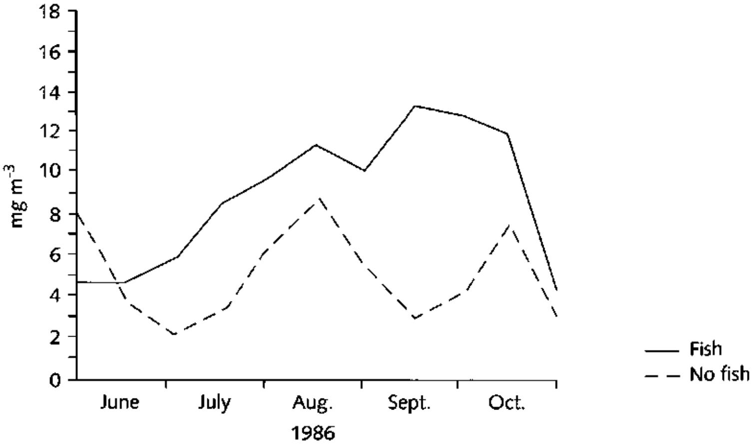

Figure 3.2: *Chlorophyll-a concentration (mg m^{-3}) throughout the experiments. Average values of ten ponds.*

found in the total number of Cryptophyceae (Table 3.2). This is probably due to the equal presence in the compartments of the abundant species *Rhodomonas minuta* and *Cryptomonas erosa*. Cyanophyceae show no consistent response on the presence of fish in the ponds (Table 3.2).
It appears that in these experiments the proportion of different algal groups in the total cell numbers was hardly influenced by the presence of fish. The abundance of the most important algae groups was similar in both compartments (Table 3.2). Only the relative abundance of the Cyanophyceae, Chrysophyceae and the Chlorococcales differed slightly between the compartments.

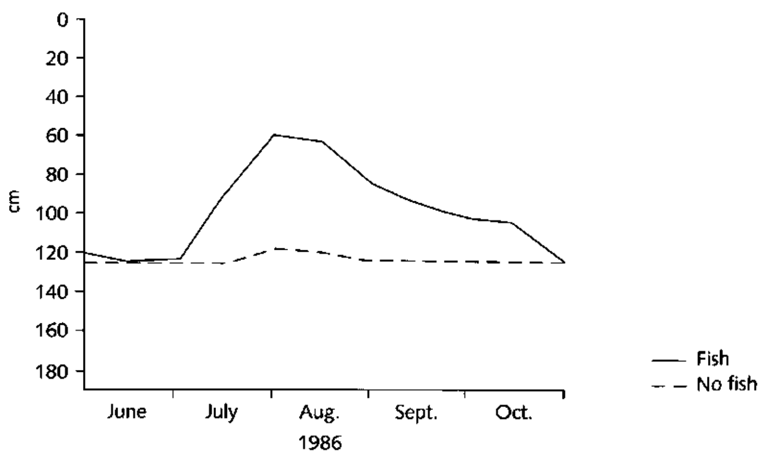

Figure 3.3: *Secchi-disc transparency (cm). Average values of ten ponds.*

Turbidity

After the first month the turbidity of the water was lower in the non-fish compartments than in those with fish. In the non-fish compartments Secchi transparency reached the bottom (Figure 3.3). In the fish-compartments the Secchi depth varied from 60 to 80 cm.

This turbidity pattern was found in all ponds (Table 3.2). The small differences in chlorophyll-*a* concentrations would hardly contribute to this difference in turbidity. The brown-grey colour of the water in the fish compartments suggests that its turbidity was mainly caused by suspended sediment particles. Some observations indicate that in these experiments carp was mainly responsible for the turbidity caused by resuspension of the sediment. In August two non-fish compartments suddenly turned turbid. Carp were discovered in both compartments. After their removal the compartments cleared within 2 days.

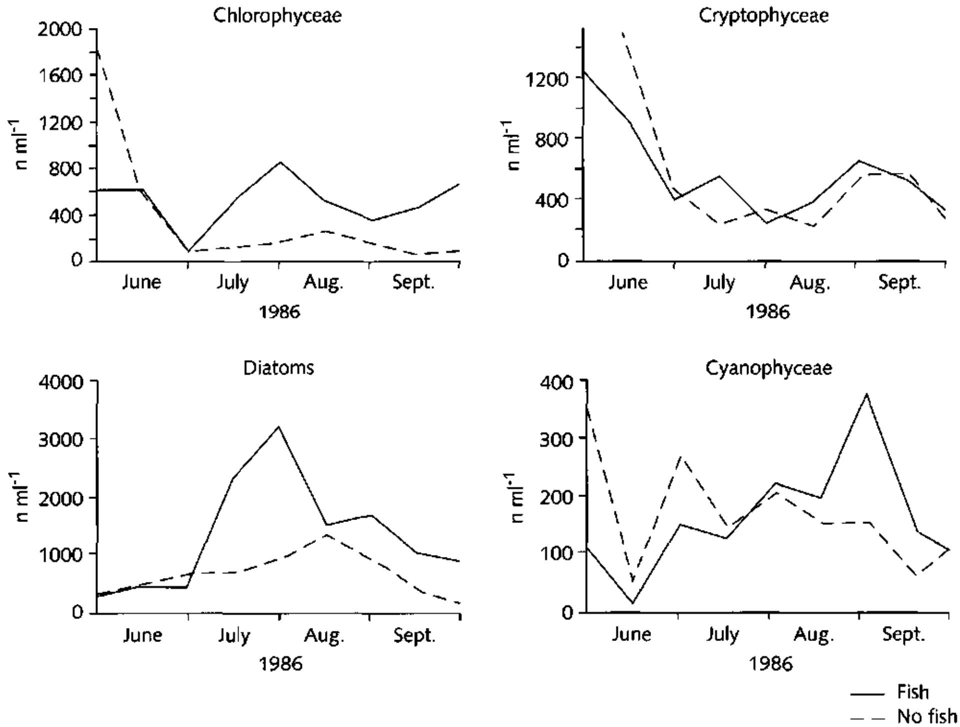

Figure 3.4: *Density (n ml^{-1}) of the main phytoplankton groups throughout the experiments. Average values of ten ponds.*

Nutrients

Nutrient concentrations in the fish and non-fish compartments did not show significant differences (Table 3.2). In spite of the addition of fertilizer to the ponds nutrient levels stayed fairly low. No apparent rise in nutrient concentrations after fertilisation could be observed. The total phosphate concentration was about 0.08 mg P l^{-1}, total nitrogen concentration was in average 1.2 mg N l^{-1}. The concentrations of soluble nutrients were low, the soluble nitrogen concentration was generally about 0.02-0.08 mg N l^{-1}, orthophosphate was 0.005-0.015 mg P l^{-1}.

Macrophytes

In all ponds dense stands of submerged vegetation established themselves. *Chara* was the main genus in all ponds from July to September. In one pond *Potamogeton pectinatus* was dominant. The degree of cover seemed higher in the non-fish compartments. The significance of these differences can not be tested because of lack of exact data in the fish compartments due to high turbidity.

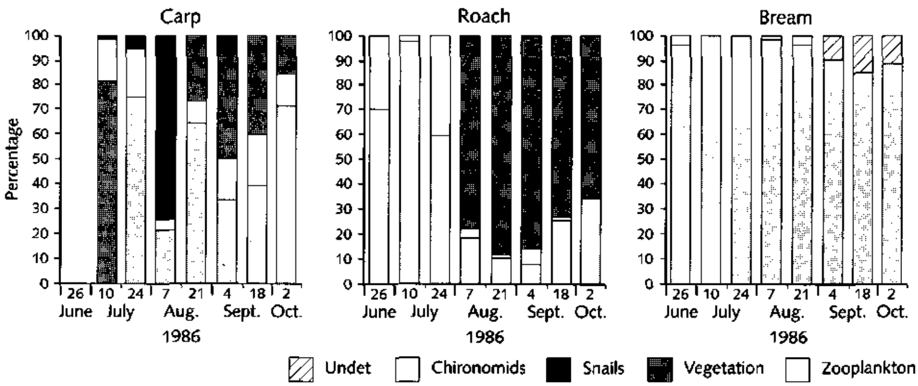

Figure 3.5: *Relative contribution of different food organisms (%) in the gut of 0+ bream, roach and carp.*

Gutcontents

Figure 3.5 shows the diet of the fish in four ponds investigated. Bream mainly ate zooplankton during the whole period. Roach fed on zooplankton until the end of July and then switched to macrophytes. Carp ate zooplankton, chironomids, snails and macrophytes. Approximately 25 % of the biomass of the diet of carp consisted of zooplankton.

An indication of the selectivity of fish when feeding on zooplankton is presented in Figure 3.6. Nauplii are strongly negatively selected by all species. *Bosmina* on the other hand is consumed in disproportionally high quantities by bream and roach. It is striking that *Daphnia* seems to be negatively selected by all three fish species, although the time-series presented in Figure 3.1 shows that population densities of *Daphnia* are suppressed by the presence of fish.

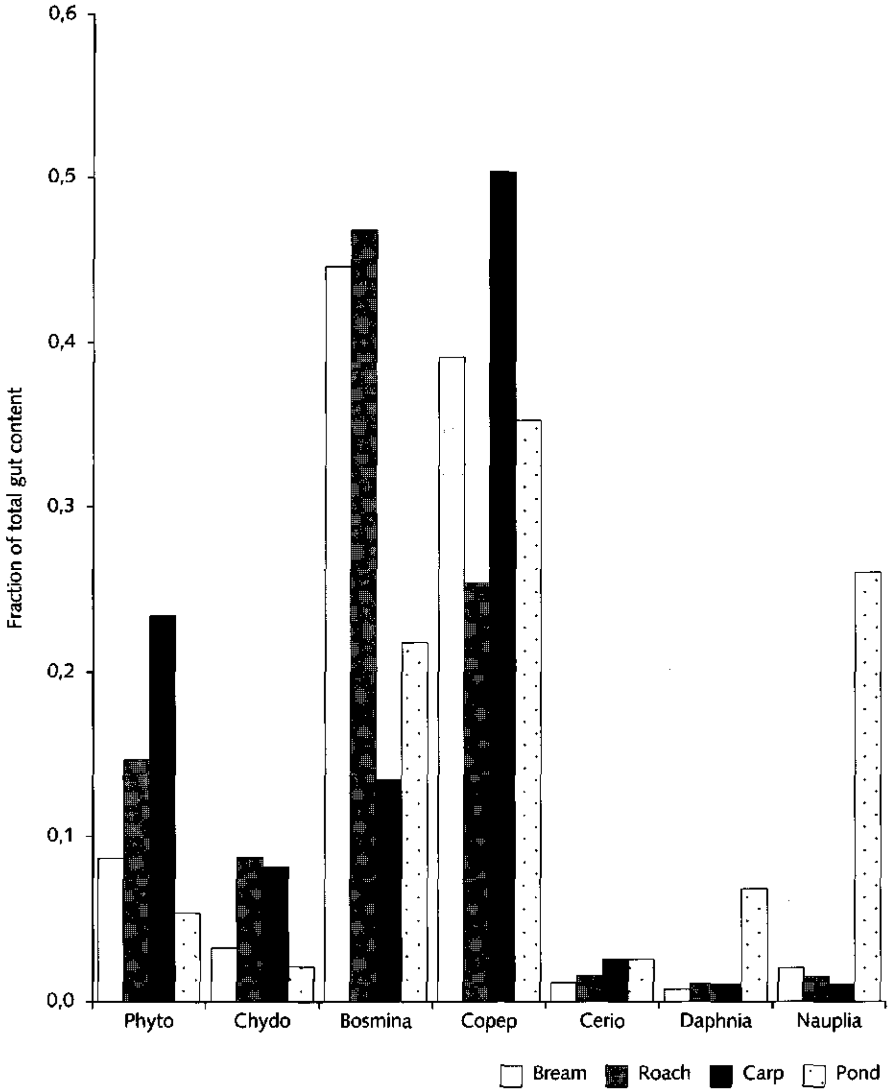

Figure 3.6: *Selection of zooplankton species by 0+ bream, roach and carp. Percentages of the most important species or groups of the total number of zooplankton are given for the gut contents of these fishes and for the ponds. (Phyto = zooplankton associated with plants, Chydo = Chydorus sp., Copep = copepods, Cerio = Ceriodaphnia).*

DISCUSSION

The average figures for the ten ponds give a representative picture for each one of them. The observed pattern is generally alike for all ponds, but the periodicity is not the same. In accordance with the findings of several authors (De Bernardi & Guissani,1982; Andersson *et al.*, 1978; Reinertsen & Olsen, 1984; Benndorf *et al.*, 1984) the largest zooplankton species are found in the absence of fish. The high densities of small zooplankton species found in the fish compartments are probably due to reduced competition from the larger species (Brooks & Dodson, 1965).
The negative preference for *Daphnia* found in the analysis of the gut content of the fish is not in accordance with the suppression of *Daphnia* by fish. This discrepancy may be caused by differences between the time of the fish sampling and the time that *Daphnia* is eaten. Another explanation may lie in a lower growth rate of *Daphnia* compared to the smaller zooplankton species or a repressed growth of *Daphnia* by the resuspended particles.
The effect of fish on the algal biomass (chlorophyll-a) is significant. Hardly any effect of the presence of fish on the phytoplankton composition is found. This is in accordance with findings of Post & McQueen (1987) and Leah *et al.* (1980). However, Reinertsen & Olsen (1984); Lynch & Shapiro (1981) and Benndorff *et al.* (1984) found no decrease of the phytoplankton biomass, but a shift to other algae species in the absence of fish.
The density of *Cryptomonas* sp. and *Rhodomonas* sp. is not influenced by the presence of fish. The equal density of these small flagellates in situations with and without fish was also found by Shapiro & Wright (1984), Benndorf *et al.* (1984) and Andersson *et al.* (1978). The lack of impact of zooplankton on the abundance of these species is probably not due to a negative preference of the zooplankton. Several authors showed that zooplankton grazes on these algae (Lynch & Shapiro, 1981; Porter, 1977). It is more likely that the high growth rate of these algae prevents substantial reduction of their density by zooplankton (Fott, 1975; Reynolds *et al.*, 1982).
Contrary to the results of other authors (Tatrai & Istvánovics, 1986; Andersson *et al.*, 1978; Henrikson *et al.*, 1980) the fish did not influence the total nutrient concentrations in the ponds. No significant difference between the compartments is found in total nitrogen and phosphorus concentrations.
In spite of repeated fertilisation, the nutrient concentrations were too low to be sure that no nutrient depletion of the algal growth has occurred. Probably nutrient depletion has occurred in August. No reason was found for the fairly low chlorophyll-a concentrations in the fish compartments in the other months. Added nutrients were quickly buffered by the system. Probably the growth of macrophytes contributed to this.
According to several models (McQueen *et al.*, 1986; Scheffer, 1989) fish removal will be more successful at relatively low nutrient levels. A comparative study of several biomanipulation experiments also led to the conclusion that at high nutrient loadings no improvement of water quality can be found (Benndorf *et al.*, 1987).
To investigate the possibilities of biomanipulation as a restoration method in eutrophic waters in the Netherlands, experiments have been started in small natural lakes. Fish have largely been removed and then predatory fish have been introduced. The first results of these experiments show that in these shallow eutrophic lakes fish stock management can lead to low algal biomass and clear water (Van Donk *et al.*, 1990c; Chapter 4). The experiments will be continued for at least four years

to study whether the obtained situation is a stable one. Until now long-term success of biomanipulation is only documented for an oligotrophic lake (Henrikson *et al.*, 1980).
To conclude, the results reported here indicate that in shallow mesotrophic waters removal of planktivorous and benthivorous 0+ fish may have a pronounced effect on turbidity. Resuspension of sediment by fish is an important factor for the increases of turbidity in the experiments. In addition, the density of large zooplankton species is reduced. A slightly higher chlorophyll-*a* content of the water was observed in the presence of fish.

ACKNOWLEDGEMENTS

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CHAPTER 4

RESTORATION BY BIOMANIPULATION OF LAKE BLEISWIJKSE ZOOM

(THE NETHERLANDS)

M.-L. Meijer, A.J.P. Raat, & R.W. Doef, 1989
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RESTORATION BY BIOMANIPULATION OF LAKE BLEISWIJKSE ZOOM

(THE NETHERLANDS)

ABSTRACT

In 1987, the Bleiswijkse Zoom, a small, shallow lake in The Netherlands, was divided into two compartments to investigate the possible use of biomanipulation as a tool for restoring the water quality of hypertrophic lakes. The biomass of the fish stock before restoration was about 650 kg ha^{-1}, composed mainly of bream, white bream and carp. Pike-perch was the main fish predator in the lake. In April 1987, in one compartment (Galgje) all planktivorous bream and white bream and 85 % of the benthivorous bream and carp were removed. Advanced pike-perch fry were introduced as predator during the transient period. The other compartment (Zeeltje) was used as a reference. Removal of the fish in Galgje resulted in low concentrations of chlorophyll-*a*, total phosphorus, nitrogen and suspended solids. The absence of bottom-stirring activity by benthivorous fish and the low chlorophyll-*a* concentrations led to an increase in the Secchi disk transparency from 20 to 110 cm. Within two months after removal of the fish, macrophytes, mainly Characeae, became abundant. Until July the high density of large zooplankton species caused low algal biomass. From June onwards, the zooplankton densities decreased, but the algal concentrations remained low. This is probably because of nutrient limitation or depression of algal growth by macrophytes or both. Compared with the non-treated compartment the number of fish species in the treated compartment was higher. Perch, rudd and roach, i.e. the species associated with aquatic vegetation, were found in the samples. The survival of the 0+ pike-perch was poor. The pike-perch could not prevent the growth of young cyprinids. Within two months after the removal of the fish a habitat for northern pike was created.

INTRODUCTION

The eutrophication of Dutch lakes resulted during the past forty years in large increases of algal biomass and water turbidity and a decline in submerged vegetation. This led in many waters to the disappearance of the northern pike, *Esox lucius*, (Grimm, 1981a, 1983, 1989; De Nie, 1987), a common fish predator in the northern temperate lakes (Raat, 1988). Such lakes contain, therefore, large biomasses of planktivorous and benthivorous fish, mainly bream, *Abramis brama* (Lammens, 1986) with pike-perch, *Stizostedion lucioperca*, as fish predator.

The main policy for eutrophication control so far has been to reduce the nutrient loading. However, the presence in the lakes of high fish stocks seems to hamper the recovery of the lakes (Hosper, 1989). Biomanipulation, i.e. reduction of the biomass of planktivorous and benthivorous fish, may speed up the recovery process (Shapiro *et al.*, 1975; Shapiro, 1980; Benndorf, 1988; Hosper, 1989; Lazarro, 1987).

Bream has a negative effect on water quality, because it feeds on large zooplankters and benthic fauna (Lammens, 1986). First, in absence of large zooplankters, grazing on algae is low and high algal biomasses can be reached; secondly, the benthivorous activity of the bream causes resuspension of the sediment, which leads to a higher turbidity and an increased nutrient release from the bottom. Both the high algal biomass and the resuspension of sediment cause deterioration of the light climate in the water. In several small lakes a complete removal of benthivorous and planktivorous fish has resulted in a dominance of large zooplankters, a decrease in algal concentrations and an increase in water transparency (De Bernardi & Guissani, 1978; Reinertsen & Olsen, 1984; Shapiro & Wright, 1984; Stenson *et al.*, 1978).

Most of the biomanipulation experiments up to now have been done in oligo-mesotrophic waters, mostly deep. At low nutrient concentrations fish removal is expected to be more successful because of the lower growth rate of algae caused by nutrient depletion and the lower production of planktivorous and benthivorous fish. Furthermore in deep waters the impact of resuspension of the bottom is small. The results of the above experiments may not apply to the Dutch situation, because most Dutch lakes are eutrophic and shallow. In an experiment in shallow ponds the presence of carp (*Cyprinus carpio*) and bream led to an increase in water turbidity (Chapter 3), mainly because of the sediment resuspension.

In 1987 two experiments were started in The Netherlands to investigate the effect of fish stock management on the water quality in eutrophic lakes. In Lake Zwemlust all the fish were first removed and thereafter pike (*Esox lucius*) and macrophytes were introduced (Van Donk *et al.*, 1989, 1990a). However, in most lakes it is not possible to remove all fish. In the shallow and eutrophic lake Bleiswijkse Zoom an experiment was started to investigate the effect of intense fishery and introduction of predatory fish. In 1987, the lake was divided into two compartments. In one compartment 85 % of the fish stock was removed and pike-perch was introduced, the other compartment served as a reference.

The study will be continued for at least four years during which effects of the biomanipulation measures will be monitored.

EXPERIMENTAL AREA

Lake Bleiswijkse Zoom is a narrow lake (length 2 km; area 14.4 ha) in the west of The Netherlands (Figure 4.1). The lake consists of two small interconnected lakes. It was constructed in 1972 for recreational purposes. The average depth of the lake is about 1.1 m. The sediment of the lake contains mainly clay. A water inlet connects the lake with the eutrophic river Rotte, though in 1987 no water was let in. The loss of water by evaporation is compensated by precipitation and by some seepage from the river Rotte. During 1980-1987 the lake was characterised by high phosphorus concentrations (0.4 mg P l^{-1}), resulting in summer average chlorophyll-*a* concentrations of 80-200 µg l^{-1} and a Secchi-disc value of 0.2 m. Macrophytes were absent and densities of both bream and carp were high.

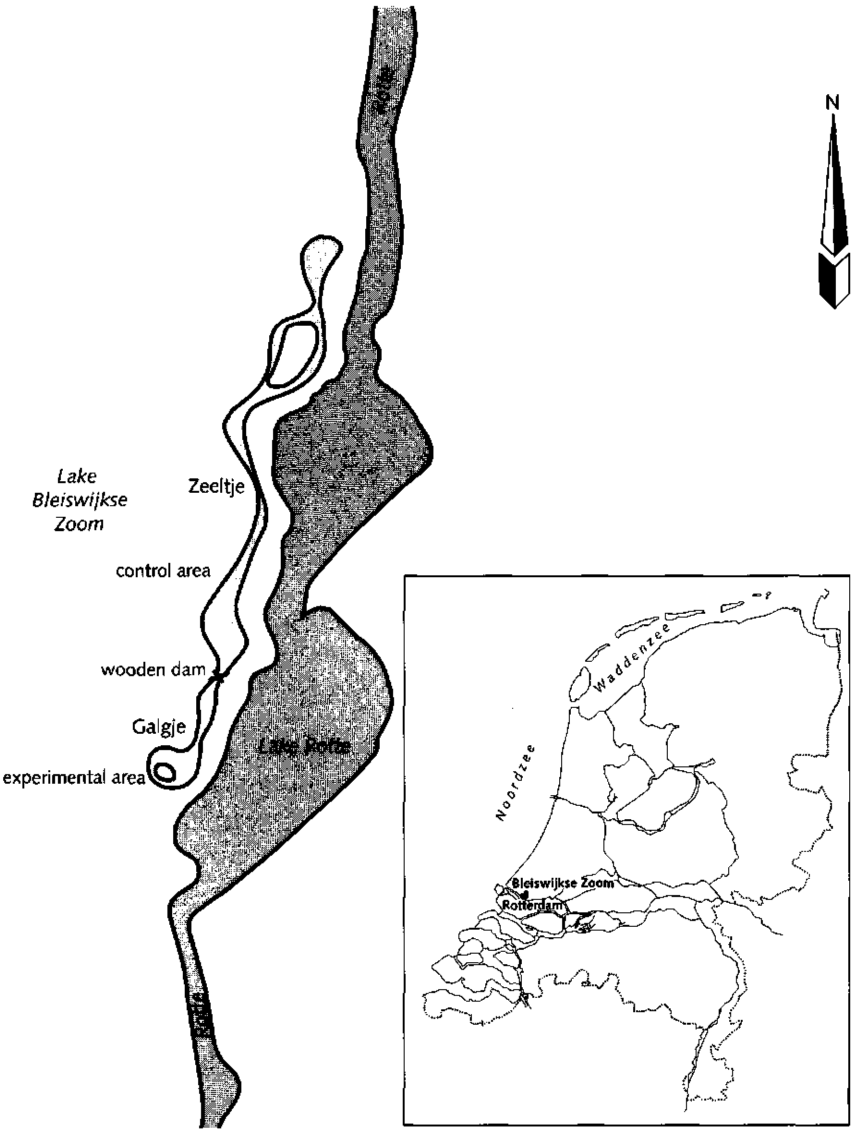

Figure 4.1: *Morphology of the Bleiswijkse Zoom.*

FISH STOCK

During 1973-1987 management measures were undertaken to create a good fish stock for carp angling. During 1973-1974 and 1980-1982 carp was stocked. Initially aquatic macrophytes were abundant, but disappeared probably because of the activity of the large stock of benthivorous carp. Bream and carp have been removed several times from the lake to improve the individual growth of the cyprinids. Removal of 170 kg ha^{-1} carp and 210 kg ha^{-1} bream in 1981 and 290 kg ha^{-1} bream in 1982 did not lead to an improvement of the water transparency or to the return of aquatic macrophytes.
In the fall of 1986 the fish stock in the lake was estimated with the adjusted Petersen method by marking and recapturing the fish (Ricker, 1975). The fish stock was mainly composed of large carp (250 kg ha^{-1}), bream/white bream (*Blicca bjoerkna*) (150 kg ha^{-1} 8-16 cm, and 200 kg ha^{-1} > 16 cm) and pike-perch (50 kg ha^{-1}).

BIOMANIPULATION MEASURES

In March 1987, the lake was divided into two compartments, the Galgje (3.1 ha, experimental area) and the Zeeltje (11.3 ha, control area) by a wooden dam with an opening of 10 x 20 cm, provided with a gauze (mesh diameter of 0.4 cm), allowing exchange of water, but not fish, between the two compartments.
In April 1987 2,000 kg fish were removed from the Galgje by seine- and electro-fishing. This included most bream/white bream (1,200 kg), carp (550 kg) and pike-perch (230 kg) (Table 4.1). Part of the removed carp (380 kg = 33 kg ha^{-1}) and pike-perch (120 kg = 10 kg ha^{-1}) were stocked in The Zeeltje. The composition of the fish stock in the Zeeltje was not essentially changed by these stockings. Thus, the Zeeltje will be referred to as the control compartment.
After removal of the fish at least 45 kg ha^{-1} of bream/white bream (44 kg ha^{-1} > 16 cm) and 59 kg ha^{-1} carp were left in the Galgje compartment. Thus, almost all the planktivorous fish and about 77 % of the benthivorous fish were removed. Two specimens of northern pike (33 and 36 cm) were left in the compartment. In May and July small pike-perch (in total 800 individuals of 3.0 cm) were introduced in the Galgje (experimental compartment) to control the 0+ bream and carp. The rational for this measure is that during the transient period, i.e. the time between removal of the fish and colonisation of the macrophytes, a fish predator adapted to turbid water should be present (Van Densen & Grimm, 1988).

Table 4.1: *Removed fish from Galgje (April 1987).*

Species	Forklength cm	Number	Biomass kg	Biomass kg ha^{-1}
Pike-perch	< 12	200	0.4	
	12-22	11	0.7	
	22-37	205	55.3	
	37-46	101	73.4	
	> 46	45	96.9	
Total			226.7	73
Bream/White bream	8-16	33,521	636.5	
	16-24	398	41.3	
	24-29	158	45.1	
	29-34	219	110.8	
	> 34	455	353.8	
Total			1187.5	383
Common carp		108	550.0	
Pike		5	16.3	
Perch		7	0.8	
Roach		63	1.4	
Crucian carp (Carassius)		3	1.5	
Eel (Anguilla)		62	15.8	
Total			585.8	189
Total fish removed			2000.0	645

SAMPLING AND ANALYSIS

The water temperature, pH, oxygen concentration and the Secchi depth of the water were measured fortnightly. Water was sampled with a perspex tube, 1.5 m long and 5 cm in diameter. In each compartment samples were taken at 25 stations and mixed. These composite samples were used to analyse the concentrations of total phosphorus, ortho-phosphate, total nitrogen and dissolved nitrogen, dissolved silica, both total and inorganic suspended matter and chlorophyll-*a*. The species composition and density of the zooplankton and phytoplankton were determined, as described in chapter 3.

In June, July and August the densities and species composition of benthic fauna, sampled with an Eckmann sampler and sieved over 0.5 mm, were investigated in both the lake compartments. In July and August the presence of macrophytes was documented.

0+ fish were caught monthly with a seine net and fork length and total length were measured. In the winter of 1987/1988 the fish stock in both the compartments was estimated with the adjusted Petersen method (Ricker, 1975).

RESULTS

Transparency

After removal of the fish the Secchi disk transparency in the Galgje increased within two weeks to 1.1 m, i.e. the lake bottom (Figure 4.2). In the control compartment the Secchi value was 0.25 m, i.e. it remained at the same level as before the biomanipulation. In the southern part of the experimental compartment the Secchi value was from August onwards lower than in the rest of this compartment, most likely because of sediment resuspension by carp. In the winter of 1987/1988 the transparency increased in the control compartment because of low algal biomass and low activity of the fish. This was also reflected in the concentrations of chlorophyll-*a* (Figure 4.3) and inorganic suspended solids (Figure 4.7).

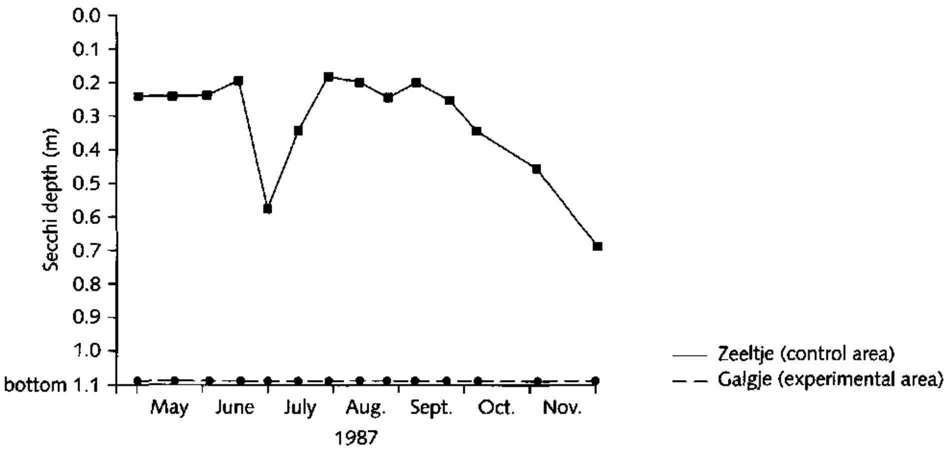

Figure 4.2: *Transparency depth (in m) in the Bleiswijkse Zoom following fish-stock management in April 1987.*

Phytoplankton

Treatment led to a decrease of the chlorophyll-*a* concentration to 5-10 µg/l, but in the control compartment the chlorophyll-*a* concentration varied between 50-120 µg/l (Figure 4.3). The lower chlorophyll-*a* concentrations were also reflected in the lower abundance of algae in the experimental compartment. The algal population consisted mainly of green algae *Ankistrodesmus falcatus* and *Scenedesmus* sp. The flagellate *Cryptomonas* sp. was found incidentally.
Also in the control compartment *Ankistrodesmus falcatus* en *Scenedesmus* sp. were found. The abundance of *Cryptomonas* was relatively higher than in the treated part. In September a diatom bloom of *Stephanodiscus hantzschii* and *Nitschia* sp. occurred.

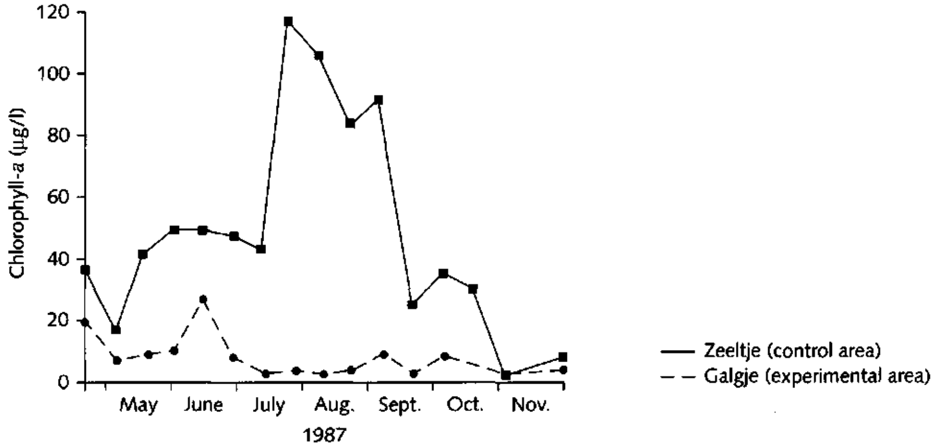

Figure 4.3: *Chlorophyll-a (in µg/l) in the Bleiswijkse Zoom following fish-stock management in April 1987.*

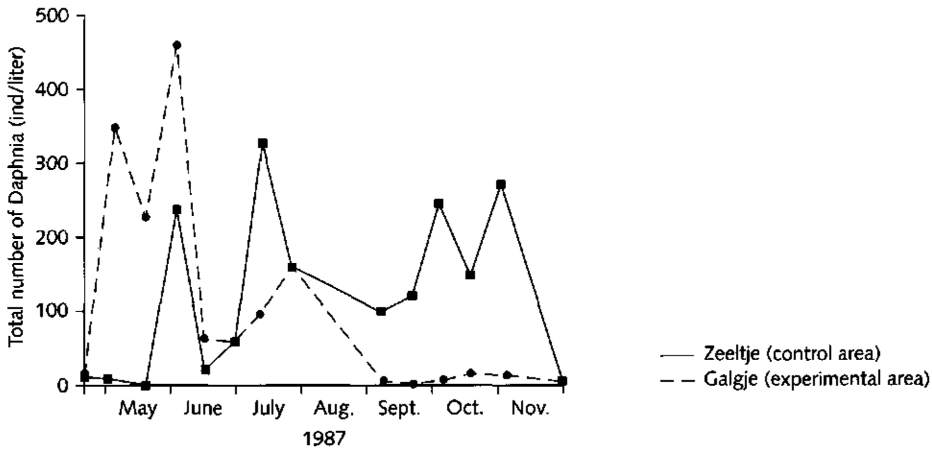

Figure 4.4: *Total number of* Daphnia *in the Bleiswijkse Zoom following fish-stock management in April 1987.*

Zooplankton

Up to July the numbers of large zooplankters, mainly *Daphnia hyalina* (mean length 0.9 mm) were high (220-470 ind l^{-1}) in the experimental compartment (Figure 4.4). Thereafter, the density of the zooplankton became higher in the control compartment. From August onwards *Daphnia* sp. almost disappeared in the experimental part, while in the control part the numbers remained about 150 ind l^{-1}. The mean length of the Daphnids was approximately the same in both the compartments.

The densities of small-sized zooplankters like copepods (Figure 4.5) were in general higher in the non-treated compartment.

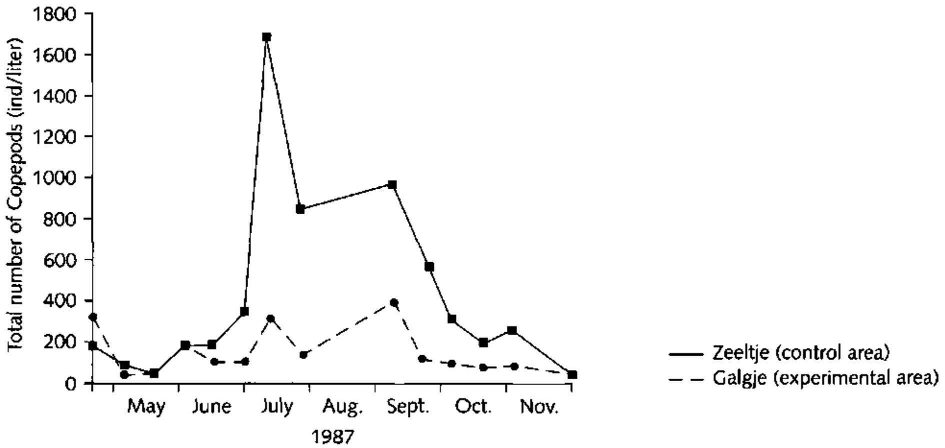

Figure 4.5: *Density of copepods in the Bleiswijkse Zoom.*

Fish

In the winter of 1987/1988 the fish biomass was estimated at 220 kg ha^{-1} in the experimental compartment, and 650 kg ha^{-1} (carp 320 kg ha^{-1}, bream/white bream at least 300 kg ha^{-1} and pike-perch 33 kg ha^{-1}) in the control compartment. In the experimental compartment not only the biomass, but also the composition of the fish stock differed from the pre-treatment situation and from the situation in the reference part. In the experimental compartment about 165 kg ha^{-1} was formed by bream/white bream (> 10 cm, 105 kg ha^{-1}) and carp (58 kg ha^{-1}). At least 36 carp were still present, probably causing the local turbidity in the southern part of the compartment. Besides carp and bream/white bream, rudd *Scardinius erythrophtalmus*) and northern pike were found in the samples (Table 4.2). Both these last named species prefer clear water with aquatic macrophytes (De Nie, 1987). The estimated 18 northern pike specimens showed excellent growth; their length varied between 32 and 41 cm, compared with 56 and 61 cm for their parents. The density of the 0+ pike-perch population was estimated to vary between 20 and 90 individuals (14-26 cm); 30 % of the pike-perch originated from the stocked fish.

The total 0+ population in the experimental compartment was estimated at 40 kg ha^{-1}. Yearlings amounted to 25 kg ha^{-1} for bream and white bream, 2 kg ha^{-1} for rudd, 3 kg ha^{-1} for roach (*Rutilus rutilus*) and 12 kg ha^{-1} for perch (*Perca fluviatilis*).

In the reference compartment 0+ bream/white bream was virtually absent, probably because of predation by pike-perch. No species related to macrophytes were found.

Table 4.2: *Estimates of the fish stock in the Galgje in the winter of 1987/88; + = all fish (0+ and > 0+); * = Gymnocephalus cernua; ** = Gasterosteus aculeatus; s.d. in parentheses.*

Species	number		> 0+ biomass (kg)	0+ biomass (kg)
Roach	> 58		5.8	9.8
Bream/White bream	805	(527)	327.8	68.6
Common carp	> 36		180.0	-
Rudd (> 16 cm)	> 22		5.1	7.0
Perch (> 15 cm)	> 3		0.5	39.7
Ruffe *				0.9
Stickleback **				0.1
Pike-perch (14-26 cm)	47	(41)	4.4+	-
(> 26 cm)	12	(7)	11.8	
Northern pike	> 20		10.7+	
Total (kg)			548	126.1
Total (kg ha^{-1})			177	40

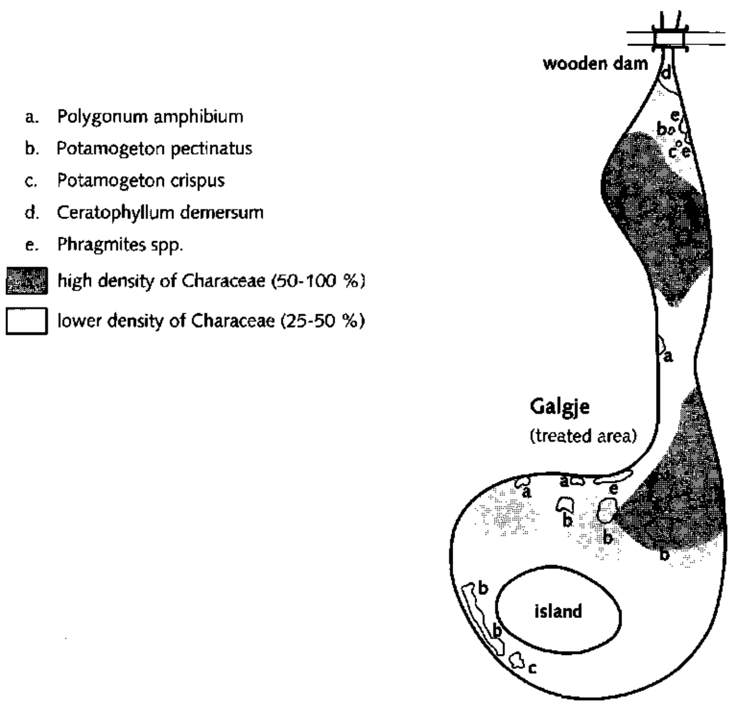

Figure 4.6: *Presence of macrophytes in the experimental compartment Galgje on 10 August 1987.*

Bottom fauna

In the treated part the number of oligochaetes, chironomids, snails and mussels were higher than in the control compartment. The number of species in the different groups also increased after treatment.

Macrophytes

A rapid colonisation of aquatic macrophytes took place within 5 weeks after treatment. In the northern part of the treated compartment the abundance of the macrophytes (*Chara vulgaris var. longibracteata*) was 50-100 % (Figure 4.6). In the southern part, behind the island, other macrophytes such as *Potamogeton pectinatus* and *Ceratophyllum demersum* were present (Figure 4.5). In the control compartment some emerged macrophytes were encountered, restricted to the shore.

Chemical analyses

Up to July the pH was almost identical (8.0-8.6) in both parts, but from August on it was higher (9.0-9.5) in the experimental part. The oxygen concentrations were higher in the experimental compartment, except in July. The concentration of inorganic suspended solids (Figure 4.7) was much higher in the control compartment (15-40 mg l^{-1}) when compared with the treated part (5-10 mg l^{-1}). This was caused by a significant resuspension of the bottom material by fish.
In accord with the lower concentrations of chlorophyll-*a* and inorganic suspended solids the concentrations of total nitrogen and total phosphorus became lower after treatment. The total nitrogen concentrations were 2.0- 2.5 mg N l^{-1} in the control compartment and 1.0-1.5 mg N l^{-1} in the experimental part. The total phosphorus concentrations were 0.20 -0.36 mg P l^{-1} and 0.14-0.18 mg P l^{-1} in the reference and the experimental compartment respectively (Figure 8). The ortho-phosphate were < 0.01 mg P l^{-1} in both the compartments until July, but from August on they were slightly higher, resp. 0.05 and 0.03 mg P l^{-1} in the experimental and the control compartment respectively (Figure 4.9). The higher concentration in the experimental compartment is probably caused by the high pH, resulting form the high productivity of the macrophytes. From July on the ammonium concentrations (Figure 4.10) were low in the experimental compartment (< 0.05 mg N l^{-1}). In general the concentrations were higher in the control part (0.06-0.4 mg N l^{-1}). Nitrate and nitrite were almost absent in both compartments.

DISCUSSION

The experimental part of Lake Bleiswijkse Zoom developed in general in line with the expectations. The biomanipulation measures have resulted in low algal biomass and in an increase of the water

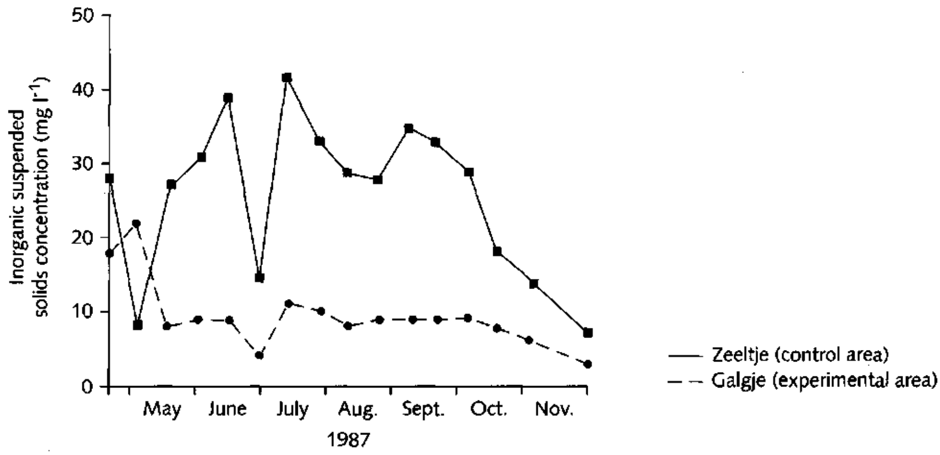

Figure 4.7: *Inorganic suspended solids concentration (mg l^{-1}) in the Bleiswijkse Zoom following fish-stock management in April 1987.*

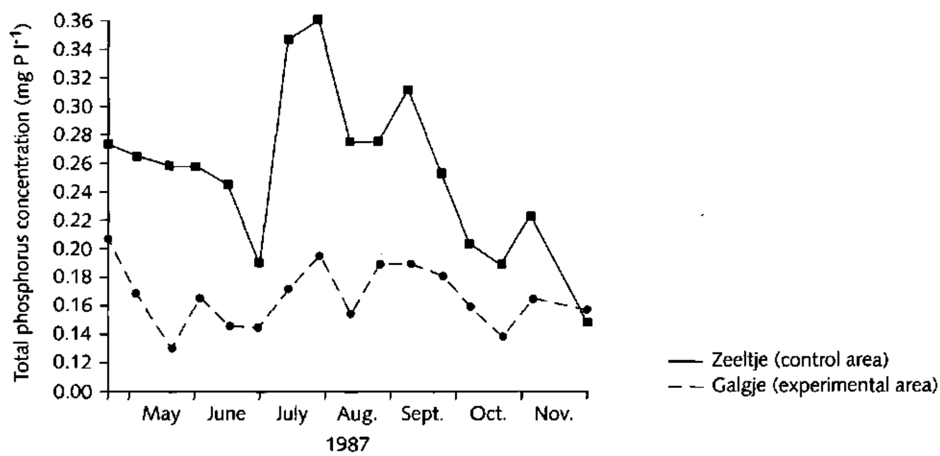

Figure 4.8: *Total phosphorus concentration (mg l^{-1}) in the Bleiswijkse Zoom.*

transparency. Removal of the large, benthivorous fish led to a decrease in the sediment resuspension, reflected in the decrease of the inorganic suspended material. This is in accordance with the laboratory experiments of Lammens (1989) who found that bream larger than 25 cm feed deep in the sediment, causing an increase in turbidity of the water by sediment particles.

During the first three months after the biomanipulation measures a high density of larger zooplankton species apparently controlled the algal biomass. This is similar to the observations of

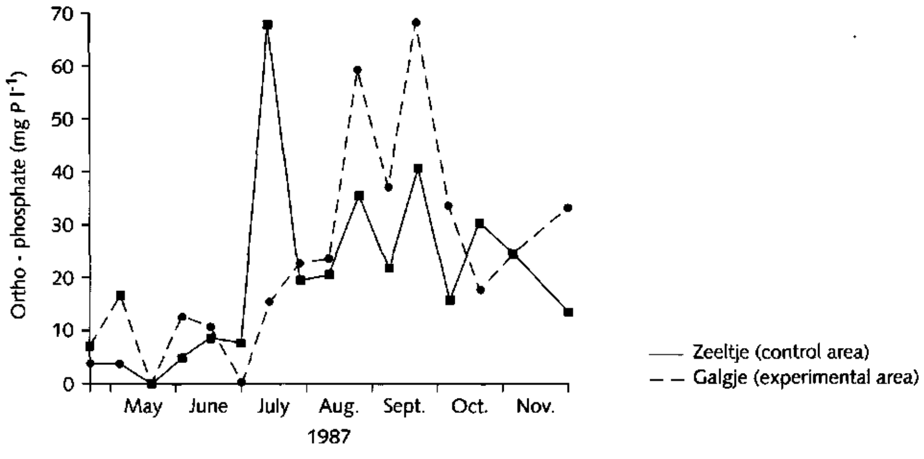

Figure 4.9: *Ortho-phosphate concentration (mg l^{-1}) in the Bleiswijkse Zoom following fish-stock management in April 1987.*

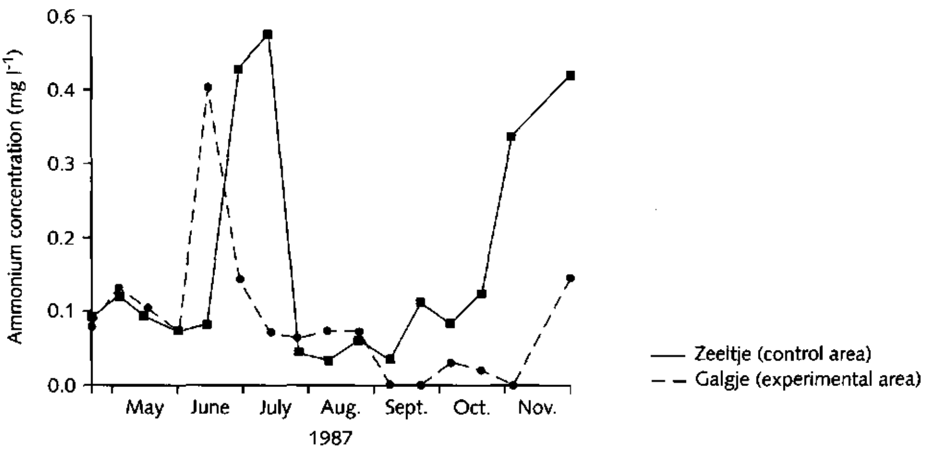

Figure 4.10: *Ammonium concentration (mg l^{-1}) in the Bleiswijkse Zoom following fish-stock management in April 1987.*

other workers (De Bernardi & Guissani, 1978; Shapiro & Wright, 1984; Reinertsen & Olsen, 1984; Van Donk *et al.*, 1990c; Gulati, 1989).

From July to November other factors than zooplankton grazing were responsible for the high transparency of the water. It is plausible that this was related to the high abundance of macrophytes (*Chara* sp.), which have a high uptake of nitrogen (Wetzel, 1975). The ammonium concentrations became very low (Figure 4.10) and algal growth in the experimental part was possibly limited by nitrogen. In October 1987, a bioassay experiment showed some increase of algal biomass after addition of nitrogen and a large increase after addition of phosphorus and nitrogen, as well as some expected decrease by zooplankton grazing (unpubl. results). There may be another explanation for the limitation of the algal growth by macrophytes. Laboratory studies indicated that some *Chara* species limit algal growth by means of allelopathy (Wium-Anderson *et al.*, 1982; Anthoni *et al.*, 1980). Therefore Characeae have probably been very important for this study. These macrophytes were present in the lake only during the first four years of its existence, until 1976. The development of the macrophytes declined probably because of resuspension of the bottom materials by fish. This bioturbation prevented the settling of macrophytes as well as adversely affected the light climate. However, after the biomanipulation in 1987 Characeae appeared within five weeks. Therefore, spores of these plants apparently remained present and were vital for their re-occurrence after 11 years. This is borne out by enclosure experiments in Lake Maarsseveen, in which fish was excluded, and *Chara* already appeared after two weeks (Ten Winkel & Meulemans, 1984).

The low density of zooplankton from July onwards in the experimental compartment is possibly caused by food limitation because of the algal growth limitation. However, the 0+ cyprinids (40 kg ha^{-1}) could also have contributed to the decrease of *Daphnia* in the treated compartment. Furthermore, the zooplankton density may be underestimated because of non-representative sampling between the macrophytes (Timms & Moss, 1984), where zooplankton may concentrate during daytime, being the time of sampling. In the control part grazing of the zooplankton could not prevent high algal biomasses, although the biomasses of large zooplankters were quite high, probably caused by the low biomass of 0+ cyprinids in this compartment.

The very low biomass of 0+ cyprinids in the control compartment was probably due to predation by pike-perch on the larvae in early June. Nevertheless, the survival of the 0+ pike-perch (7-11 cm) in the reference compartment was low, probably because of the low food availability for piscivorous pike-perch from June on and because of the predatory interactions within the pike-perch population. The high transparency and the abundance of macrophytes in the experimental compartment probably created adverse conditions for the survival of the 0+ pike-perch (Barthelmes, 1988), although food was available for growth. The stocked pike-perch fry (3.0 cm) have not affected a change in the fish fauna or an enhancement of the pike-perch stock. The fish stock, which increased form 104 kg ha^{-1} to 220 kg ha^{-1} in the treated part, included minimally 40 kg ha^{-1} 0+ fish, caused by the low predation by pike-perch. The carp did not increase in biomass; the > 0+ bream/white bream produced about 60 kg ha^{-1}. Although a habitat for pike was created about two months after restoration, the pike was not yet able to develop a high predation pressure on the 0+ cyprinids. In 1988 pike were introduced to increase the predation pressure on the cyprinids.

CONCLUDING REMARKS

The experiment in Lake Bleiswijkse Zoom showed that a rigorous removal of planktivorous and benthivorous fish was necessary to improve the quality of the water. Removing of about 50 % of the benthivorous carp and bream population a few years before the here presented experiment did not result in an improved water quality.

Removal of 85 % of the benthivorous fish stock was sufficient to lower the concentrations of resuspended material and with that the turbidity of the water. The first results showed that already within five weeks after the removal of the planktivorous and benthivorous fish, aquatic macrophytes developed and the chemical and physical conditions of the water improved.

Models (Scheffer, 1989) and comparative research studies (e.g. Benndorf, 1987; McQueen *et al.*, 1986) indicated that biomanipulation will be successful only at low nutrient concentrations. Apparently, at higher nutrient levels only short-term success is possible. Until now long-term success has been documented only for an oligothrophic water (Henrikson *et al.*, 1980). Benndorf (1987) and Benndorf *et al.* (1988) found that at higher nutrient levels more negative aspects can be expected, namely growth of blue-green algae. However, recolonisation of the macrophytes created an important element for a stable, clear water ecosystem (Moss, 1989). The macrophytes are likely to stabilise the system by the uptake of nutrients and allelopathy. Also, macrophytes offer a shelter against fish predation to zooplankton, which can therefore be stimulated (Timms & Moss, 1984). Moreover, pike will have better survival conditions (Grimm,1981a; Raat, 1988); as a consequence planktivorous and benthivorous fish will be controlled. However, it is possible that in eutrophic lakes measures involving fish stock management need to be repeated. Therefore, the research in Lake Bleiswijkse Zoom will be continued for at least four years to determine if the newly created situation is a stable one and if supplementary measures are needed. The stocked and naturally produced pike-perch did not regulate the 0+ cyprinid production, probably because of the low turbidity and the abundance of macrophytes. In this situation introduction of 0+ pike could have been more effective. In large water bodies, in which it is more difficult to remove most (85 %) of the fish stock and where a longer period between removal of fish and appearance of macrophytes can be expected, enhancement of fish predation by stocking advanced 0+ pike-perch may be more successful, but this has so far not been attempted.

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CHAPTER 5

IS REDUCTION OF THE BENTHIVOROUS FISH AN IMPORTANT CAUSE OF HIGH TRANSPARENCY FOLLOWING BIOMANIPULATION IN SHALLOW LAKES

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Hydrobiologia 200/201: 301-315

IS REDUCTION OF THE BENTHIVOROUS FISH AN IMPORTANT CAUSE OF HIGH TRANSPARENCY FOLLOWING BIOMANIPULATION IN SHALLOW LAKES

ABSTRACT

Experimental reduction of the fish stock in two shallow lakes in The Netherlands shows that biomanipulation can lead to a substantial increase in transparency, which is caused not only by a decrease in algal biomass, but also by a decrease in resuspended sediment and detritus. A model was developed to describe transparency in relation to chlorophyll-*a* and inorganic, suspended solids (resuspended sediment). With the use of this model it is shown that more than 50 % of the turbidity in these shallow lakes before biomanipulation was determined by the sediment resuspension, mainly caused by benthivorous fish.

Another analysis reveals that the concentration of inorganic suspended solids and the biomass of benthivorous fish are positively correlated, and that even in the absence of algae a benthivorous fish biomass of 600 kg ha^{-1} can reduce the Secchi depth to 0.4 m in shallow lakes. In addition, it is argued that algal biomass is also indirectly reduced by removal of benthivorous fish. Reduction of benthivorous fish is necessary to get macrophytes and macrophytes seem to be necessary to keep the algal biomass low in nutrient-rich shallow lakes. It is concluded that the impact of benthivorous fish on the turbidity can be large, especially in shallow lakes.

INTRODUCTION

In the past two decades or so biomanipulation has been studied as an additional tool in water management in deep lakes (Shapiro *et al.*, 1975; Hosper, 1989). Reducing the planktivorous fish stock has led to a higher density of zooplankton grazers (De Bernardi & Guissani, 1978), a lower algal biomass and an increase in transparency (Shapiro & Wright, 1984; De Bernardi & Guissani, 1978; Henrikson *et al.*, 1980; Reinertsen & Olsen, 1984; Van Donk *et al.*, 1989). However, in shallow lakes not only phytoplankton is responsible for the high turbidity of the water, but also sediment resuspended by wind and benthivorous fish (Chapter 4; Painter *et al.*, 1988). The resuspension of sediments by wind is particulary important in large lakes (Gons *et al.*, 1986; Hanson & Butler, 1990), whereas fish may be more important in small lakes (Chapter 4).

Enclosure experiments have demonstrated that benthivorous fish may have an indirect impact on the turbidity (Andersson *et al.*, 1978; Tatrai & Istvanovics, 1986; Horpilla & Kairesalo, 1990) by a stimulated algal production due to nutrient release from the bottom, but also a direct effect by resuspension of bottom particles (Threinen & Helm, 1954; McGrimmon, 1968). In some shallow Dutch lakes the fish biomass is usually composed mainly of large bream, *Abramis brama*, and carp, *Cyprinus carpio* (Grimm, 1989). In these lakes the role of benthivorous fish might be important for water quality since its biomass can be very high due to high productivity and stocking by anglers.
The main purpose of this paper is to demonstrate that in small, shallow lakes with a high benthivorous fish stock (500-700 kg ha^{-1}) the turbidity is caused not only by algae but also by resuspension of the sediment by fish. For this purpose we removed between 70 and 85 % of the total fish stock in two shallow lakes and monitored the changes in water quality and fish populations. We discuss the mechanisms causing the lower algal biomass and inorganic suspended solids concentration, leading to the higher transparency following fish reduction. The relationship between the presence of benthivorous fish, resuspended sediment and the turbidity of the water has been quantified.

STUDY AREA

Lake Bleiswijkse Zoom is narrow (length 2 km; width 50-200 m; surface area 14.4 ha; mean depth 1.0 m) and is divided into two parts. In 1987 2000 kg fish (mainly bream and carp) were removed from one part (3.1 ha). Pike-perch (1000 0+*Stizostedion lucioperca*) were stocked in 1987 and pike (3500 0+and 90 1+*Esox lucius*) in 1988. The other part (11.3 ha) served as a control. The lake is surrounded by trees and, therefore, wind-protected. The sediment contains mainly clay. A more extensive description of the lake is given in chapter 4.
Lake Noorddiep, a former branch of the river IJssel, is long and narrow (total surface area 31 ha), divided into 3 parts by roads. In winter 1987-1988 2630 kg fish (mainly bream and carp) were removed from one part (4,5 ha; depth varying from 0.8-2.4 m; mean depth 1.5 m). No predatory fish was stocked because 30 kg ha^{-1} pike still remained. One of the two other parts (16 ha; mean depth of 1,5 m) served as a control. The lake is small, on one side surrounded by trees and, therefore, wind protected. The sediment contains mainly clay.
To analyse the relationship between suspended solids and benthivorous fish also data from ponds in lake Wolderwijd were used. The experiments were carried out in two ponds (surface area 1.0 ha; depth 1.5 m), one without fish and one with 215 kg ha^{-1} large bream in 1987 and 320 kg ha^{-1} carp, 70 kg ha^{-1} bream and 145 kg ha^{-1} roach (*Rutilus rutilus*) in 1988. The sediment of the ponds contained mainly sand.

MATERIALS AND METHODS

Fish

The fish were removed by seine- and electro-fishing during February-April. Each winter (November-February) the fish biomass was estimated with the adjusted Petersen mark-recapture method (Ricker, 1975). The fish stock was divided into: benthivores (all carp; bream and roach larger than 20 cm) planktivores (all 0+fish except the predatory species and carp), predators (all pike, pike-perch and perch *Perca fluviatilis*) and rest (mainly rudd, *Scardinius erythrophtalmus*, tench *Tinca Tinca*, and bream and roach smaller than 20 cm).
Because the large fish were partly planktivorous in early summer when the *Daphnia* densities were high, only the results from July to September were used.

Field work

Fortnightly Secchi depth transparency was measured and water was sampled with a tube sampler (perpex tube: length 1.5 m; diameter 5 cm). In each lake samples were taken at 25 sites and lumped (25-50 liter).
Concentrations of silica, nitrogen (nitrate, nitrite, ammonium, total-N) and phosphorus (orthophosphate, total-P) were measured according to Dutch standard methods (NEN) which comply with international Standards (ISO); also chlorophyll-*a* (ethanol extraction) algae and zooplankton were determined on routine basis. Suspended solids were measured by first filtering the sample over a dried and pre-weighed membrane filter (45 μm) of cellulose-acetate; the samples were dried for 2 h at 105 °C and weighed again. Inorganic suspended solids were measured as residue remaining on igniting the dried filter for 45 minutes at 600 °C. To determine the crustacean zooplankton density 25 l water was filtered over 120 μm and the zooplankton on the filter was removed by back washing and fixed in 4 % formalin. To determine phytoplankton 1 liter of water was fixed with Lugol solution. Every month the presence, species composition and density of macrophytes were determined.

Bioassays

Nutrient limitation of the phytoplankton was studied in bioassays, *in vitro*, at the prevalent water temperatures (16-20 °C) and light conditions using white fluorescent tubes (light intensity in flasks of about 150 $\mu E.m^{-2}.s^{-1}$, L/D according to field situation). Six one-litre flasks were filled with lake water filtered over 100 μm gauze to remove large crustacean zooplankton. Two flasks were filled with unfiltered lake water to analyse the effect of the zooplankton grazing. Four incubations were used in two replicates each, viz. Control (no addition); +Phosphate (PO_4 = 0.35 mg P l^{-1}); +Nitrogen (NO_3 = 0.62 mg N l^{-1} and NH_4 = 0.33 mg N l^{-1}); +Phosphate and Nitrogen (PO_4, NO_3, and NH_4). Samples were taken daily during 6 days and phytoplankton density (Coulter Counter 70 μm orifice tube) was measured. Mean growth rates (μ) were calculated according to Van Donk *et al.* (1988) by least squares linear regression analysis of log-transformed data (Sokal & Rohlf, 1969).

A model to determine the Secchi depth from suspended solids

A model was developed to determine the relationship of suspended solids to the Secchi depth. A multiple regression analysis with measured Secchi depths as a dependent variable, and the concentrations of the chlorophyll-*a*, detritus and inorganic suspended solids, did not give high computed Secchi depth values as expected, because of a lack of lakes with low background extinction. Therefore, the Secchi depth was calculated using the diffuse attenuation coefficient based on optical properties of water and substances in water (Preisendorfer, 1986):

$$Sd = C/(c+K)$$

Sd is Secchi disk depth (m)
c is beam attenuation coefficient (m^{-1})
K is diffuse attenuation coefficient (m^{-1})
C is constant, calibrated on 7.4

The diffuse attenuation coefficient is determined by absorption and scattering and is calculated according to Kirk (1983). The absorption and scattering coefficients are the sum of the absorption and scattering coefficients of water and of yellow substance, chlorophyll-*a*, detritus and inorganic suspended matter in the water. The beam attenuation coefficient (c) is the sum of the absorption and scattering coefficients.

The Secchi depth equation is optimised using the constant C. The data from Secchi disc measurements in four lakes (Wolderwijd, Veluwe, Bleiswijkse Zoom and Noorddiep) were used. Low Secchi depth values are predicted better than the high values. For small lakes (Bleiswijkse Zoom and Noorddiep) Secchi disk depths seem to be slightly underestimated if transparency is high (Figure 5.1).

Based on this model a simple equation for the Secchi disk depth is determined using a multiple regression analysis of the reciprocal Secchi depth (calculated with the model) and the concentrations of chlorophyll-*a*, detritus and inorganic suspended solids.

$$1/SD = 0.234+0.064*In+0.013*Chl+0.061*Det$$

In = Inorganic suspended solids (mg l^{-1})
Chl = Chlorophyll-*a* (mg l^{-1})
Det = Detritus (mg DW l^{-1})

Detritus is calculated as the difference between total suspended solids and inorganic suspended solids plus dry weight of algae. The dry weight of algae (mg l^{-1}) is calculated as 0.1*chl-*a* in $\mu g\ l^{-1}$ (Bakema, 1988). Only data from July to September are used to determine this relationship.

For Figure 5.8b a correction for the detritus was made: we assumed that 0.75*algal dry weight is detritus formed in the water column (pers. comm. H. Los). The remaining detritus is resuspended from the bottom.

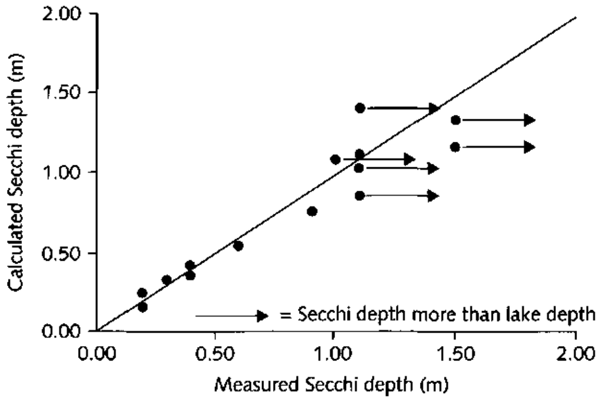

Figure 5.1: *Validation of Secchi depth model using data from Lake Bleiswijkse Zoom and Lake Noorddiep. A regression line between estimated Secchi depths and measured Secchi depths. Arrows indicate that the measured Secchi depth is underestimated because of the bottom of the lake.*

RESULTS

Fish stock

In Lake Bleiswijkse Zoom the standing crop of fish was c. 750 kg ha^{-1}, which after the biomanipulation was reduced to about 120 kg ha^{-1}. However the fish stock gradually increased after treatment to 220 kg ha^{-1} in one year and reached 350 kg ha^{-1} two years after its reduction. In Lake Noorddiep about 650 kg ha^{-1} of fish biomass present before the measure was reduced to 145 kg ha^{-1}, but it increased to 300 kg ha^{-1} in one year. Before the fish reduction the fish biomass in both lakes was composed largely of benthivores (bream and carp) (Figure 5.2). In Lake Bleiswijkse Zoom the benthivorous fish stock formed 90 % of the total fish stock, in Lake Noorddiep 80 %. In Lake Bleiswijkse Zoom between 45 and 55 % of the biomass and 5 and 10 % of the total number of benthivorous fish stock were formed by carp; in lake Noorddiep these percentages were 60-75 % and 10-30 % respectively. In Lake Bleiswijkse Zoom in the two years following the reduction the planktivorous, piscivorous and rest fraction increased to 7, 18 and 30 % respectively. A year after the fish reduction in Noorddiep the rest fraction (rudd, roach and tench) had increased to 40 %, while the predatory, planktivorous and benthivorous fish formed 20, 7 and 33 % respectively.

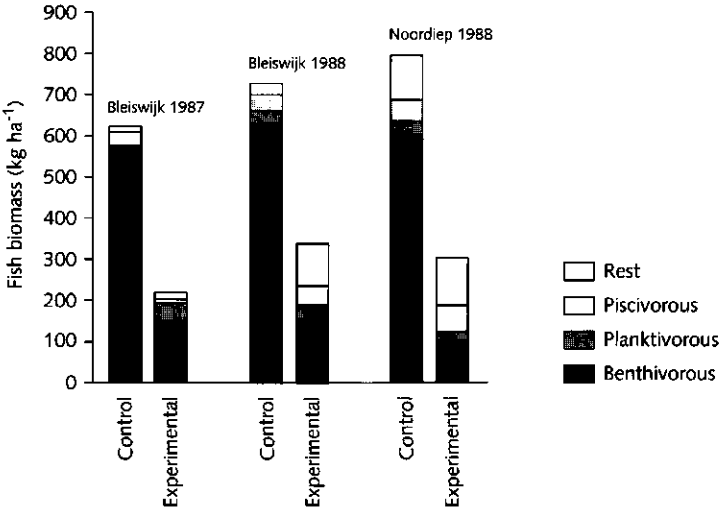

Figure 5.2: *Composition of the total fish stock in Lake Bleiswijkze Zoom and Lake Noorddiep in the experimental and the control parts. The fish stock is divided according to their preferred food habitats.*

Secchi depth

In the control compartments of both lakes the Secchi depth values varied between 20 and 30 cm (Figure 5.3a). After fish reduction the Secchi depth increased and the bottom was mostly visible. In Lake Bleiswijkse Zoom this was true for all sampling dates in 1987, and for two-thirds of the dates (April-June, September) in 1988. In Lake Noorddiep on three-quarters of the dates (June-September) the lake bottom was visible. Therefore, the Secchi depth was underestimated on these dates. Occasionally the Secchi depth decreased because of algae blooms (April-May in Noorddiep) or because turbid water was let in (Bleiswijkse Zoom in June-July 1988). In both lakes the Secchi depth has become significantly higher after the fish reduction ($p < 0.05$). In winter the Secchi depth increased in the control compartments of Lake Bleiswijkse Zoom to 45-75 cm and in Lake Noorddiep to 45-90 cm.

Plankton

The average chlorophyll-*a* concentrations in the two lakes significantly decreased from 60-100 $\mu g\ l^{-1}$ to 5-20 $\mu g\ l^{-1}$ (Figure 5.3b). In 1988 the chlorophyll-*a* concentrations were higher in Lake Bleiswijkse Zoom than in 1987 because of an inlet of water rich in algae and nutrients (Meijer, unpubl. results). In winter the concentrations decreased in the control parts to 40-50 $\mu g\ l^{-1}$ in Lake Noorddiep and 20-80 $\mu g\ l^{-1}$ in Lake Bleiswijkse Zoom.

Only in Lake Bleiswijkse Zoom was the average density of *Daphnia hyalina* higher in the experimental part than in the control part (Figure 5.3c). However, the density of *Daphnia* was also rather high in the control part. In Lake Noorddiep the density of *Daphnia* during summer was higher in the control part than in the experimental part. However, in both lakes the differences were not significant.

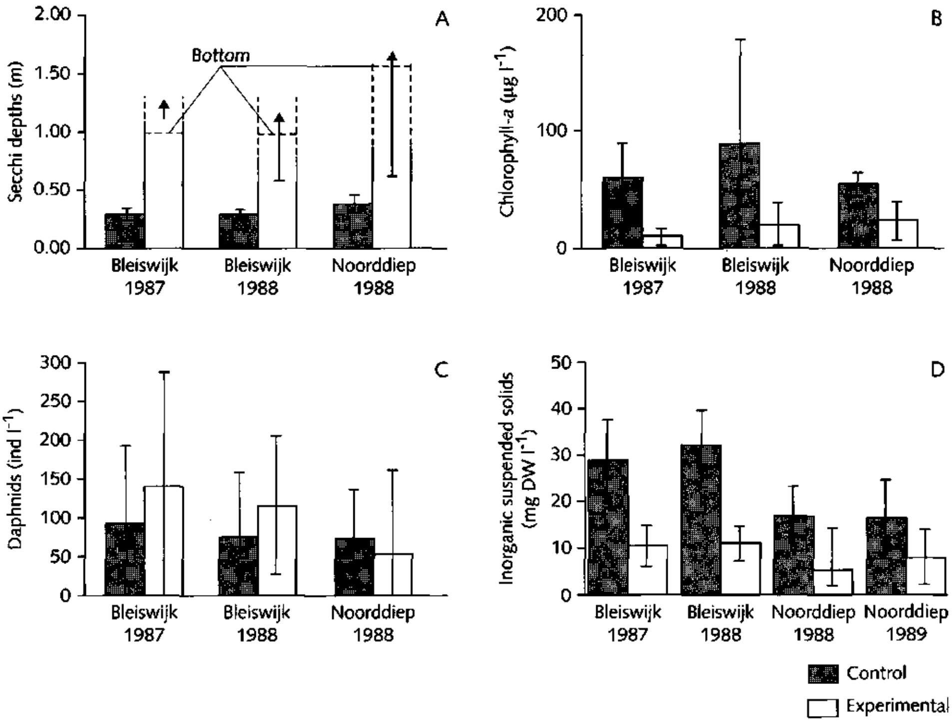

Figure 5.3: *Summer (April-September) average concentrations with standard deviation (n=13) of Secchi depths* (a), *chlorophyll-*a (b), *Daphnia hyalina* (c) *and inorganic suspended solids* (d) *in Lake Bleiswijkse Zoom and Lake Noorddiep in the exerimental and the control parts.*

Nutrients

The summer averages of the dissolved-N did not differ significantly between the experimental and the control parts (Table 5.1). The total-N concentrations were, however, significantly higher ($p < 0.05$) in the control parts. In Lake Noorddiep, and in 1988 also in Lake Bleiswijkse Zoom the ortho-P concentrations were significantly higher ($p < 0.05$) in the experimental parts than in the control parts. In 1987 the total-P concentration was significantly higher in the control part of Lake Bleiswijkse Zoom ($p < 0.05$).

The bioassays show a significant increase of the algal growth rate after addition of N and N+P in the experimental parts (Table 5.2). In the control part of Lake Noorddiep no increase in growth rate was found after N addition. No data from the control part of Lake Bleiswijkse Zoom are available.

Table 5.1: *Average nutrient concentrations with standard deviation in Lake Bleiswijkse Zoom and Lake Noorddiep (in mg l^{-1}) during summer (April-September).*

Site/nutrient	NH_4	NO_3+NO_2	Kj-N	Ortho-P	Total-P
Lake Bleiswijkse Zoom					
1987 Exp	0.07 (0.45)	0.09 (0.07)	1.63 (0.30)	0.02 (0.02)	0.10 (0.03)
C	0.12 (0.02)	0.07 (0.06)	2.62 (0.05)	0.02 (0.02)	0.23 (0.07)
1988 Exp	0.05 (0.01)	0.06 (0.04)	1.88 (0.37)	0.12 (0.12)	0.27 (0.14)
C	0.07 (0.02)	0.08 (0.06)	3.52 (0.40)	0.02 (0.01)	0.27 (0.10)
Lake Noorddiep					
1988 Exp	0.12 (0.02)	0.04 (0.06)	1.70 (0.23)	0.20 (0.15)	0.34 (0.13)
C	0.11 (0.02)	0.03 (0.01)	2.05 (0.31)	0.02 (0.01)	0.18 (0.05)

Exp = Experimental part
C = Control part

Table 5.2: *The mean net growth rates ($\bar{\mu}$, d^{-1}) of the phytoplankton community, in bioassays for different combinations of nutrients. Control;+N (NO_3, 0.62 mg N l^{-1} and NH_4, 0.33 mg N l^{-1});+P (PO_4, 0.35 mg P l^{-1}), +N+P (NO_3, NH, and PO_4).+Zoo (zooplankton not removed, no nutrient addition). The standard deviations are given between parentheses.*

		Lake Noorddiep Control	Experimental	Lake Bleiswijkse Zoom Experimental
May	Control	0.065 (0.007)	0.126 (0.014)	0.040 (0.040)
	+N	0.045 (0.008)	0.257 (0.069)	0.552 (0.050)
	+P	0.078 (0.004)	0.123 (0.028)	0.098 (0.050)
	+N+P	0.133 (0.009)	0.151 (0.042)	0.548 (0.072)
	+Zoo	0.082 (0.047)	0.110 (0.004)	0.630 (0.048)
July	Control	0.038 (0.007)	0.041 (0.019)	0.040
	+N	0.055 (0.018)	0.082 (0.030)	0.075
	+P	0.045 (0.012)	0.049 (0.030)	0.029
	+N+P	-	0.113 (0.040)	0.036
	+Zoo	0.040 (0.008)	0.017 (0.020)	0.006

Inorganic suspended solids

In the control parts the concentration of inorganic suspended solids varied in summer between 15 and 30 mg l^{-1}, and in the experimental parts between 7 and 12 mg l^{-1} (Figure 5.3d). In both lakes the concentrations were significantly lower after the reduction of the fish stock ($p < 0.005$). In winter the concentration decreased in the control parts to between 8 and 20 mg l^{-1} (Figure 5.4), while in the experimental part the concentration remained low throughout the year. At most sites from 40 to 70 % of the total suspended solids were composed of inorganic material (Figure 5.5). Algae formed only 20-30 % of the total suspended matter, detritus about 10-30 %.

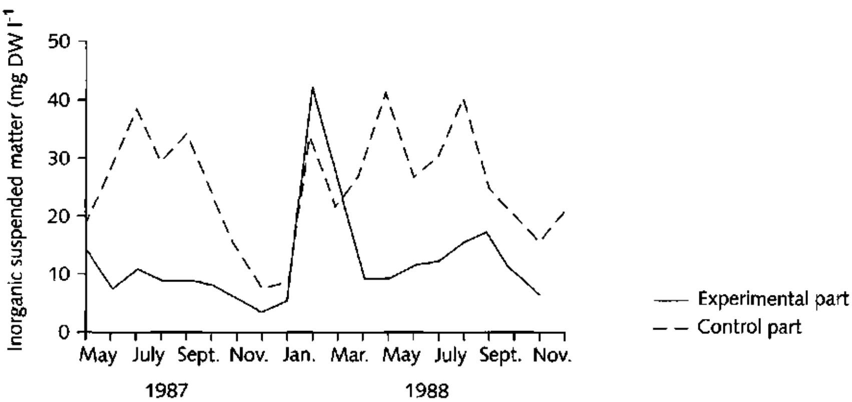

Figure 5.4: *Inorganic suspended solid concentration in Lake Bleiswijkse Zoom in the experimental and the control part (in mg DW l^{-1}); continuous line experimental part, broken line control part.*

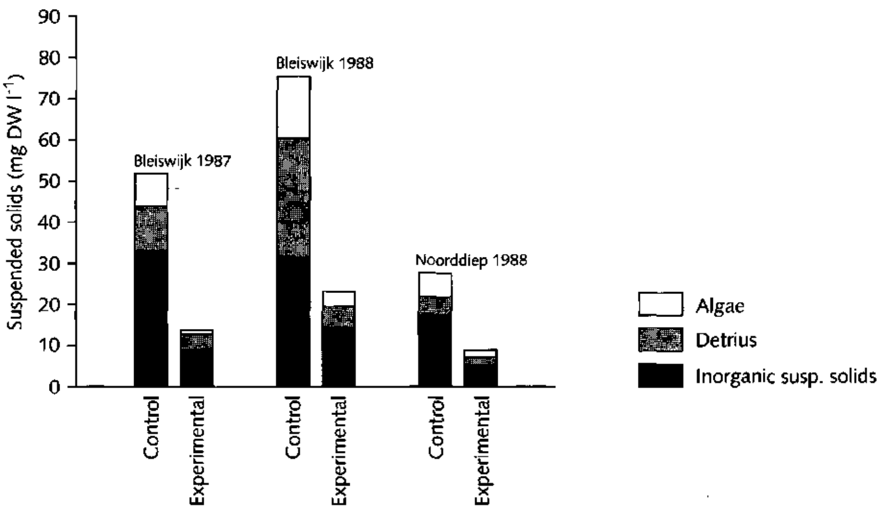

Figure 5.5: *Composition of the suspended solids concentrations in lake Bleiswijkse Zoom and Lake Noorddiep in the experimental and the control part. Averages July-September.*

Macrophytes

After the fish reduction macrophytes rapidly increased especially in Lake Bleiswijkse Zoom (Figure 5.6). At the beginning of June 1987, i.e. two months after the fish removal, Characeae became abundant and remained present throughout the winter. They disappeared in March after turbid water was let in and were replaced in May 1988 by a massive growth of *Potamogeton pectinatus* (Figure 5.6). In Lake Noorddiep emergent macrophytes (*Nuphar lutea*) were present before fish reduction; the submerged macrophytes increased after fish was reduced. In Lake Bleiswijkse Zoom this increase was more pronounced. In both lakes filamentous macro algae (*Spyrogyra*) increased. The species diversity of macrophytes was higher in Lake Noorddiep (*Utricularia globularis, Chara globularis, Elodea nutallii*).

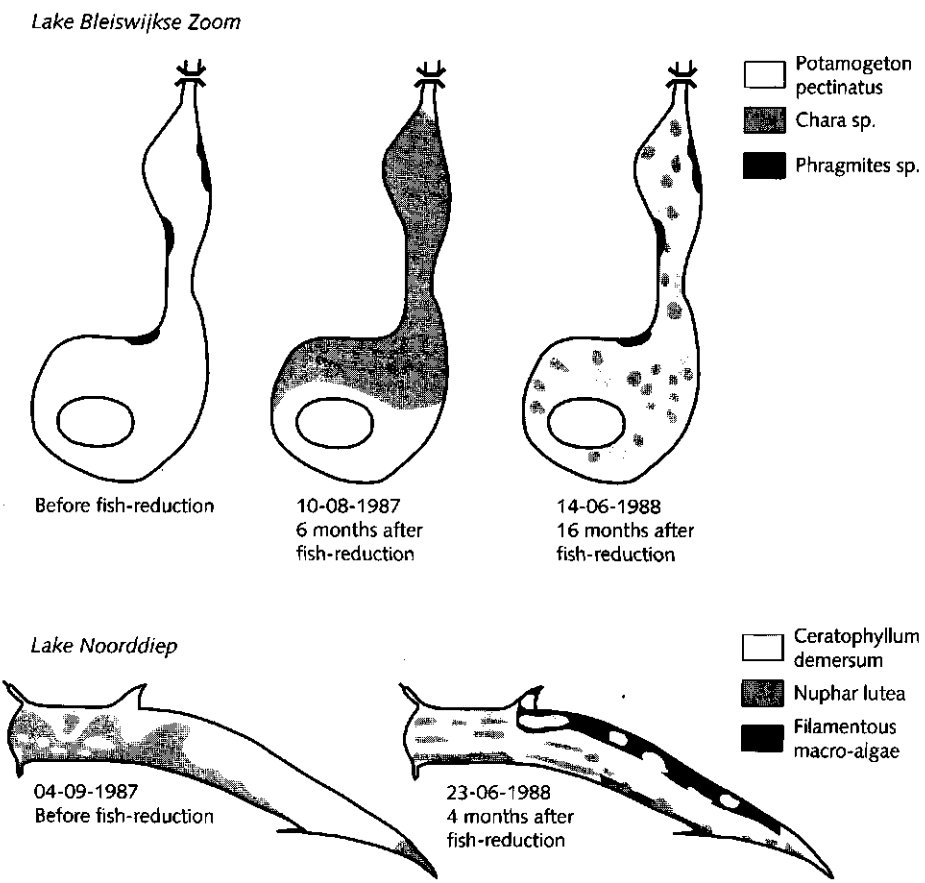

Figure 5.6: *The abundance of macrophytes in Lake Bleiswijkse Zoom and in Lake Noorddiep before and after fish stock reduction.*

The relation between benthivorous fish and inorganic suspended solids

With the use of the model the contribution of algae, detritus and inorganic suspended solids to the turbidity before and after the fish reduction can be estimated (Figure 5.7). The algae caused 10-45 % of the light extinction, detritus 10-30 % and inorganic suspended solids 20-45 %. A significant positive correlation ($r = 0.90$; $n = 16$; $p < 0.005$) was found between the benthivorous fish (per unit of volume) and the concentrations of inorganic suspended matter (Figure 5.8a). Also the sum of detritus and inorganic suspended solids was positively correlated to the fish stock ($r = 0.92$; $n = 16$; $p < 0.005$).

Combining the Secchi depth model with the regression between benthivorous fish and the sum of inorganic suspended solids and a small fraction (0.25) of the detritus, a model for assessing the direct impact of fish on the turbidity can be constructed (Figure 5.8b). According to that model benthivorous fish having a biomass of 600 kg ha^{-1} is able to reduce the Secchi depth to 0.4 m (in absence of algae and at a depth of 1.0 m). In absence of algae and detritus a Secchi depth of 0.5 m will be obtained.

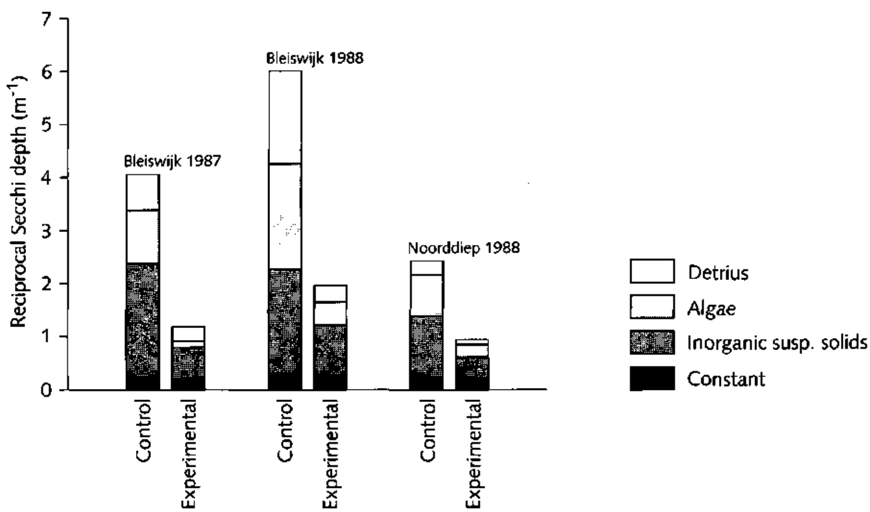

Figure 5.7: *Contribution of chlorophyll-a, detritus and inorganic suspended solids to the reciprocal Secchi depths in Lake Bleiswijkse Zoom and Lake Noorddiep. Results of the Secchi depth model.*

DISCUSSION

The results show that in the lakes the suspended matter is not only composed of algae, but also to a large extent of inorganic suspended solids. As in deeper lakes and lakes with mainly planktivorous

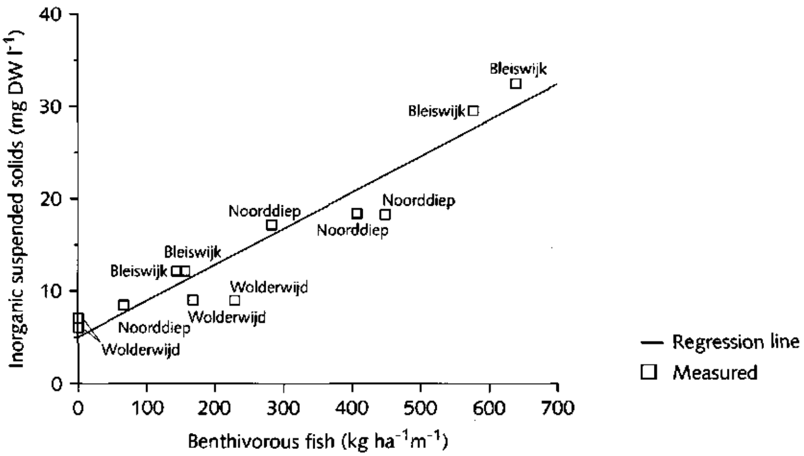

Figure 5.8a: *Regression between the biomass of benthivorous fish and inorganic suspended solids in Lake Bleiswijkse Zoom, Lake Noorddiep and the ponds in Lake Wolderwijd.*

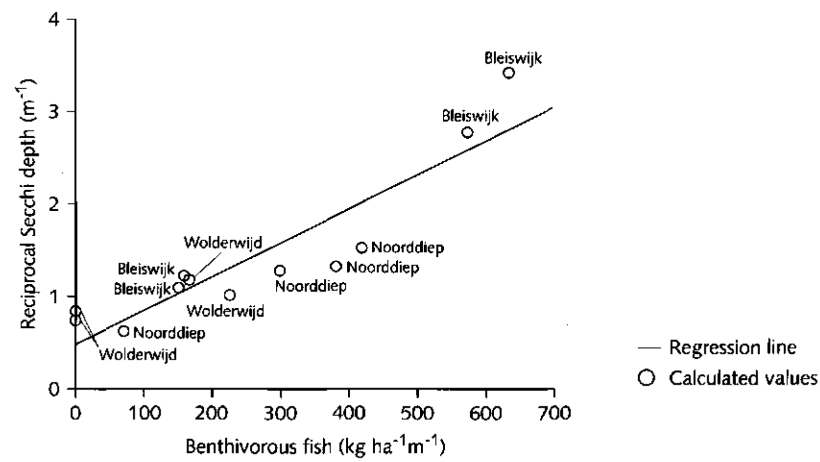

Figure 5.8b: *Regression between the biomass of benthivorous fish and the reciprocal Secchi depth in Lake Bleiswijkse Zoom, Lake Noorddiep and the ponds in Lake Wolderwijd.*

fish the reduction of the fish stock has led to a decrease in algal biomass. However, contrary to the biomanipulation cases in deep waters (Shapiro *et al.*, 1975), only 30-38 % of the measured increase in transparency can be explained by algal biomass alone. The decrease in the inorganic material contributed also to the improved light climate. We will discuss the role of benthivorous fish in causing both the low algal biomass and the low concentration of inorganic suspended solids.

Algal biomass

In Lake Bleiswijkse Zoom the decline in algal biomass can be partly explained by a higher grazing pressure by *Daphnia hyalina*, especially in spring (Gulati, 1990). In Lake Noorddiep the density of *Daphnia* was higher in the control part. However, in both lakes a clear water phase occurred when the *Daphnia* density was high (April-May). From June onwards the algal biomass increased in the control part despite the high *Daphnia* density, while in the experimental parts the algal biomass remained low at low *Daphnia* densities (Chapter 3, unpubl. results Meijer; unpubl. results Van Berkum).

The low algal biomass can, therefore, not only be due to mortality by zooplankton grazers. In the experimental parts of both lakes N limited the algal growth while in the control parts no nutrient limitation of the algal growth was formed. However the dissolved-N concentrations were not significantly lower in the experimental parts. In Lake Bleiswijkse Zoom the dissolved-N concentrations were lower in the experimental part than in the control part in some periods. This decrease in dissolved N is probably caused by the presence of the macrophytes, as demonstrated in Lake Zwemlust (Ozimek *et al.*, 1990; Van Donk *et al.*, 1989). The macrophytes are able to take up nutrients from the water. In addition, the presence of the filamentous macro-algae and the macrophytes probably create a situation with alternating aerobic and anaerobic zones where denitrification can occur very easily. The lower algal biomass might also be influenced by allelopathy (Wium-Andersen *et al.*, 1982). In 1988 laboratory experiments (carried out at non-limiting nutrient concentrations) showed a lower algal growth in water from the experimental parts with macrophytes, than in water from the control parts without macrophytes (pers. comm. Hootsmans & Breukelaar). This might be the effect of allelopathy on the growth of the algae. Furthermore, Moss (1990) and Jeppesen *et al.* (1990b) suggest that the filter feeders such as mussels and zooplankton, associated with macrophytes, can increase the grazing pressure. Therefore, macrophytes seem to control the algal growth in several ways.

The high impact of macrophytes on algal biomass is probably specific to shallow lakes, since only in shallow lakes macrophytes can develop abundantly. It seems likely that the abundance of submerged vegetation is largely facilitated by the reduction of the benthivorous fish stock. Not only do benthivorous fish affect the under water light climate (as discussed below), they also directly influence the presence of macrophytes (Robel, 1961; Roberts, 1969; Crivelli, 1983; Ten Winkel & Meulemans, 1984). By disturbing the sediments fish prevent macrophytes from settling and taking root. Robel (1961) and Crivelli (1983) found a negative correlation between the biomass of carp and the biomass of macrophytes. According to Robel (1961) 75 % cover of *Potamogeton pectinatus* persisted at carp densities of 450 kg ha^{-1} and 60 % at 670 kg ha^{-1}. Crivelli (1983) found that 68 % of the vegetation (mainly *P. pectinatus*) persisted at carp densities of 450 kg ha^{-1}. Ten Winkel & Meulemans (1984) found complete removal of *Chara* sp. at a much lower density of benthivorous bream (50 kg ha^{-1}). Resuming, it can be inferred that the decrease in algal biomass observed after fish removal in those shallow lakes is probably partly due to increased grazing by zooplankton, but that abundant development of macrophytes is likely to have also contributed to the decrease in chlorophyll-*a*. Reduction of benthivorous fish, as in our lakes from 600-700 kg ha^{-1} to 120-145 kg ha^{-1}, is essential to achieve such vegetation development.

Inorganic suspended solids

In addition to the lower algal biomass, the decrease in the inorganic material contributed to the improved light climate. Because hardly any diatoms were present, the contribution of algae to the inorganic material was neglectible. Assuming that specific sedimentation rates are similar in all lakes the high concentration of inorganic suspended matter indicates the extent of resuspension of the sediment and lake depth. Therefore, either benthivorous fish or wind, or both, should be held responsible for the higher concentrations in the control parts. The higher concentration of inorganic suspended solids in summer than in winter in the control parts, is an indication that fish is the major factor, since fish activity is highest in summer, whereas in general wind-induced resuspension is much lower in summer than in winter.

In principle, the decrease in inorganic suspended solids after biomanipulation could also be an effect of vegetation development, since macrophytes are able to reduce the waves, and, therefore, to lower the sediment resuspension (Moss, 1990; Vermaat *et al.*, 1990; Jeppesen *et al.*, 1990b). However, in our manipulated lakes the macrophytes are probably not the main cause of the decrease in the inorganic suspended matter concentration, because in both lakes the decline in concentration was measured after fish reduction but 4-8 weeks before the macrophytes appeared.

Hence, our work indicates a pronounced effect of benthivorous fish on turbidity. Several other authors come to globally the same conclusion, although contradicting results have been observed too. According to Threinen & Helm (1954) and McGrimmon (1968) carp increase turbidity, but Crivelli (1983) and Fletcher *et al.* (1985) found no impact of carp on the transparency. Also, different mechanisms are suggested for explaining the impact of benthivorous fish on turbidity. Several authors (Tatrai & Istvanovics, 1986; Horpilla & Kairesalo, 1990; Andersson *et al.*, 1988) relate the impact of benthivorous fish on the turbidity to an increase in the algal productivity caused by a release of phosphate from the sediments. In the present study the lower P-concentration in the control parts does not indicate nutrient release caused by benthivorous fish, but the higher inorganic suspended solids concentrations in summer as well as the relationship between benthivorous fish and suspended solids do indicate that fish are responsible for sediment resuspension.

Quantitative differences in outcome can often be attributed to differences in sediment type or water depth (Fletcher *et al.*, 1985; Painter *et al.*, 1988). Most authors relate turbidity to the fish biomass per unit of area (kg ha^{-1}). We divided the fish biomass also by the depth, because the depth has a significant effect on the concentration of suspended solids. In the ponds in Lake Wolderwijd the concentration of inorganic suspended solids was relatively low (Figure 5.8a), probably because the bottom sediment is sandy, while in case of Lake Noorddiep and Lake Bleiswijkse Zoom the sediment is formed by clay. In 1988 the biomass of carp was high (320 kg ha^{-1}, 80 % of the benthivorous fish stock) in the pond in Lake Wolderwijd. We found, however, no higher concentrations of suspended matter in the pond in Lake Wolderwijd than in the other lakes, probably because of a rapid sedimentation of sand due to its high specific sedimentation rate. Robel (1961) found no impact of carp on the turbidity at a density of 670 kg ha^{-1} (at a depth of 0.75 m), but a higher density (2244 kg ha^{-1}) caused a dramatic decrease in the transparency. These densities are extremely high, but Robel states that the sandy soil type is fairly resistant to resuspension, which is consistent with our results.

In addition to water depth and sediment type, differences in fish species may explain discrepancies in the outcome of studies. One would expect that carp has a higher impact on resuspension than bream, because of its higher preference for benthos. This is supported by experiments (Breukelaar, *et al.*, 1994). Furthermore, experiments performed in artificial ponds (Meijer *et al.*, 1990a) have shown that a low density of small carp (length 10-15 cm) could reduce the Secchi depth from > 1 m to 0.4 m. The chlorophyll-*a* concentrations, being extremely low ($< 10\ \mu g\ l^{-1}$), played no role in the decreased transparency in this experiment. In view of these results, the predictions of our statistical model relating benthivorous fish to suspended solids and Secchi depth should be interpreted carefully.
Furthermore, it is likely that a specific biomass of benthivorous fish has a higher impact in large lakes than in smaller lakes, because on a larger scale the fish will increase the resuspension by wind.

CONCLUSIONS

It can be concluded that in shallow lakes several processes cause the higher transparency after biomanipulation. As in some deep lakes, the reduction of planktivorous fish and thus the increase in zooplankton grazers has led to a decline of the algal biomass. In our lakes the reduction of planktivorous fish was important to induce this decline. The continuation of the low algal biomass is most likely also caused by the presence of macrophytes by means of nutrient limitation, allelopathic effects and because the macrophytes create a refuge for zooplankton (Figure 5.9). For the development of macrophytes the reduction of benthivorous fish seems essential. In presence of benthivorous fish the resuspension of the bottom sediment causes a substantial reduction in transparency, and macrophytes are not able to colonise. Other authors relate benthivorous fish also to higher nutrients, and therefore higher algal biomass. Figure 5.9 illustrates that in several ways benthivorous fish create turbid water. The importance of macrophytes for clear water is shown. In large lakes turbidity can also be caused by wind-induced resuspension, which is stimulated bv benthivorous fish, because the fish keep the sediment loose, while macrophytes reduce the resuspension. This study is a first attempt to quantify the direct impact of benthivorous fish on water quality and has to be improved with more specific, experimental data. It appears that the impact of benthivorous fish on the turbidity should not be neglected in restoration studies in shallow lakes involving biomanipulation.

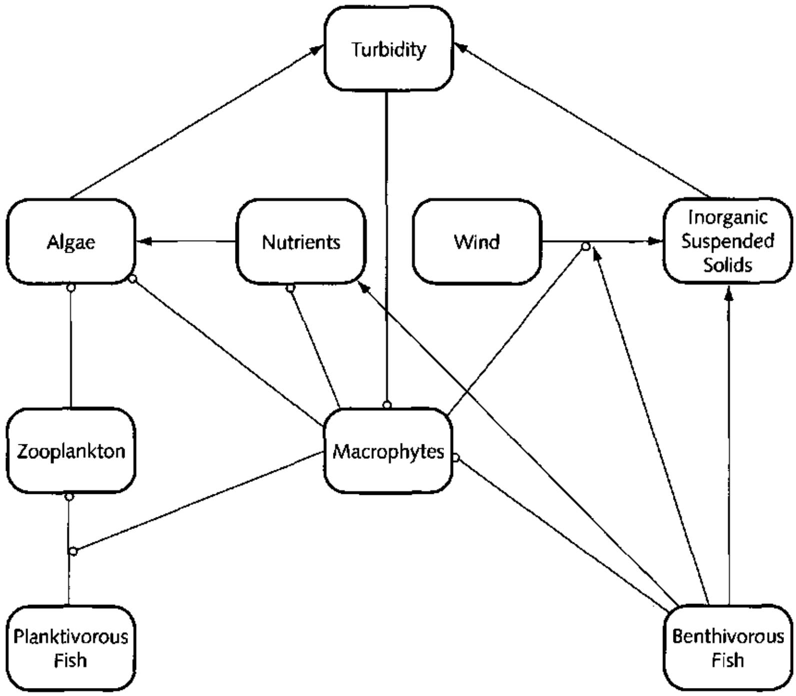

Figure 5.9: *Factors leading to turbidity in shallow lakes.*
→ *stimulation;* —∘ *reduction.*

Acknowledgements
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CHAPTER 6

LONG-TERM RESPONSES TO FISH-STOCK REDUCTION IN SMALL SHALLOW LAKES: INTERPRETATION OF FIVE-YEAR RESULTS OF FOUR BIOMANIPULATION CASES IN THE NETHERLANDS AND DENMARK

M.-L. Meijer, E. Jeppesen, E. van Donk, B. Moss, M. Scheffer, E. Lammens,
E. van Nes, J.A. van Berkum, G.J. de Jong, B.A. Faafeng, & J.P. Jensen, 1994
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LONG-TERM RESPONSES TO FISH-STOCK REDUCTION IN SMALL SHALLOW LAKES: INTERPRETATION OF FIVE-YEAR RESULTS OF FOUR BIOMANIPULATION CASES IN THE NETHERLANDS AND DENMARK

ABSTRACT

The effects of fish stock reduction have been studied in three Dutch lakes (Lake Zwemlust, Lake Bleiswijkse Zoom and Lake Noorddiep) and one Danish lake (Lake Væng) during 4-5 years. A general response is described. The fish stock reduction led in general to a low fish stock, low chlorophyll-*a*, high Secchi-disk transparency and high abundance of macrophytes. Large *Daphnia* became abundant, but their density decreased, due to food limitation and predation by fish. The total nitrogen concentration became low due to N-uptake by macrophytes and enhanced denitrification. In Lake Bleiswijkse Zoom the water transparency deteriorated and the clear water state was not stable. The fish stock increased and the production of young fish in summer was high. Clear water occurred only in spring. Large daphnids were absent in summer and the macrophytes decreased.

In Lake Zwemlust, Lake Væng and Lake Noorddiep the water remained clear during the first five years. In summer of the sixth year (1992) transparency decreased in Lake Zwemlust (with high P-concentration of 1.0 mg P l^{-1}). Also in Lake Væng (with a low nutrient concentration of 0.15 mg P l^{-1}) a short-term turbid stage (1.5 month) occurred in summer 1992 after a sudden collapse of the macrophytes. Deterioration of the water quality seems to start in summer and seems related to a collapse in macrophytes. At a low planktivorous fishstock (e.g. Lake Væng) the duration of the turbid state is shorter than in presence of a high planktivorous fish biomass (e.g. Lake Zwemlust, and later years of Lake Bleiswijkse Zoom).

INTRODUCTION

Fish stock reduction may cause a shift from turbid water to clear water (Reinertsen & Olsen, 1984; Van Donk *et al.*, 1990a). Reduction of planktivorous fish may lead to an increase of large daphnids (Shapiro *et al.*, 1975), while reduction of benthivorous fish causes a decrease in resuspension of the sediment (Chapter 5) and a reduction in P-release of the sediment (Andersson *et al.*, 1978). Although many experiments have clearly demonstrated these short-term effects, there is still much controversy on the long-term stability of the clear water state. The stability is likely to be related to the nutrient concentrations; the highest stability is expected at low nutrient levels (Bendorff, 1987; Scheffer, 1990: Jeppesen *et al.*, 1990a, 1990b; Sarnelle, 1992).

Data from 300 shallow Danish lakes showed that at P-levels < 0.10 mg P l^{-1} and in small lakes (< 3 ha) at < 0.35 mg P l^{-1} clear water states occur frequently (Jeppesen *et al.*, 1990a, 1990b, 1991): the share of piscivorous fish is often higher, leading to a better control of planktivorous fish and also the abundance of macrophytes is often high. However, Scheffer (1990) showed that theoretically a clear water state obtained by biomanipulation will always be vulnerable to perturbations. The mere fact that the manipulated lake was turbid under the same external conditions before manipulation implies that the obtained clear state is not the only equilibrium of the ecosystem. Therefore, a sufficient perturbation should always be able to cause a shift back to the turbid state.

This paper is a result of an international workshop on long-term stability of manipulated lakes held in April 1992 in Lelystad, The Netherlands. We have studied three small lakes in The Netherlands and one lake in Denmark during 5 years after reducing the fish biomass. A general pattern will be discussed in this paper and a hypothesis for the mechanisms causing a return to the turbid water state is presented.

STUDY AREAS

All four lakes are small and shallow, but their phosphorus levels differ from 0.15 mg P l^{-1} (Lake Væng) to 1.0 mg P l^{-1} (Lake Zwemlust) (Figure 6.1g). In the three Dutch lakes the fish stock was drastically reduced during one winter (80-100 %), in Lake Væng the fish stock reduction was 50 % in 1.5 year. In Lake Væng and Lake Zwemlust no additional fish removal has occurred, in Lake Noorddiep and Lake Bleiswijkse Zoom two and three years after the fish reduction a small additional fishery has been carried out on behalf of the anglers (maximum 3-10 % of the original fish stock). In Lake Zwemlust and Lake Bleiswijkse Zoom almost every year young pike were introduced to increase the predation pressure on young-of-the-year cyprinids.

Table 6.1: *Main characteristics of the studied lakes.*

Lake	Surface area (ha)	Mean depth (m)	Max. depth (m)	Fish reduction (%)
Væng	15.0	1.2	2.0	50
Noorddiep	4.5	1.5	2.5	80
Bleiswijkse Zoom	3.5	1.1	1.5	85
Zwemlust	1.5	1.5	2.5	100

METHODS

The summer averages (Denmark: May-October; The Netherlands: April-September) of *Daphnia* (> 0.8 mm), Chlorophyll-*a* concentration, Secchi-disk transparency, % macrophytes cover, total N-, total P-concentration and the estimates of the fish stock at the end of the summer are compared with the previous reference state. In Lake Væng, Lake Zwemlust and Lake Noorddiep, data for the year before the fish reduction are used as reference, in Lake Bleiswijkse Zoom the data of the lake part without a fish reduction are used as a reference.
Concentrations of nitrogen, phosphorus and chlorophyll-*a* (ethanol extraction) were measured according to International standards (ISO). *Daphnia* biomass was calculated using a L-DW relationship from Bottrell *et al.* (1976). In the Dutch lakes and in 1986 in Lake Væng the fish biomass was estimated with the adjusted Petersen mark-recapture method (Ricker, 1975). In Lake Væng a standardised test fishing was undertaken in August each year using multiple gillnets with 14 different mesh-sizes. Results are expressed in Catch per unit effort (CPUE, kg net^{-1}). For details about method and results see Meijer *et al.*, 1990; Van Donk *et al.*, 1990; Søndergaard *et al.*, 1990; Jeppesen *et al.*, 1990a, 1990b, 1991.

GENERAL RESPONSES

A general pattern can be found based on the results of the four lakes. In all lakes the fish stock has drastically been reduced (Figure 6.1a). In two lakes (Lake Væng and Lake Zwemlust) the *Daphnia* biomass was high in the first year after the fish reduction, and afterwards the biomass decreased due to food limitation and predation by fish (Figure 6.1b). In the two other lakes, the *Daphnia* biomass was already high before the fish reduction. The Secchi-depth increased to maximum values (to the bottom) and the chlorophyll-*a* concentrations became very low (Figures 6.1c and 6.1d). As a consequence the lake surface became covered with submerged macrophytes (Figure 6.1e). In all lakes the total nitrogen concentration started decreasing not in the year that the fish reduction took place, but in the year that macrophytes covered more than 50 % of the lake surface area (Figures 6.1e and 6.1f), indicating that macrophytes caused this decrease. The total nitrogen concentration remained low due to uptake by macrophytes and enhanced denitrification (Ozimek *et al.*, 1990; Van Donk *et al.*, 1993; Moss, 1990). Total phosphorus concentration did not show a general pattern (Figure 6.1g).

DIFFERENCES BETWEEN THE LAKES

Lake Væng

In Lake Væng the relative fish stock reduction was less drastic than in the Dutch lakes. This might explain why most responses were more gradual in Lake Væng than in the other lakes. In Lake Væng

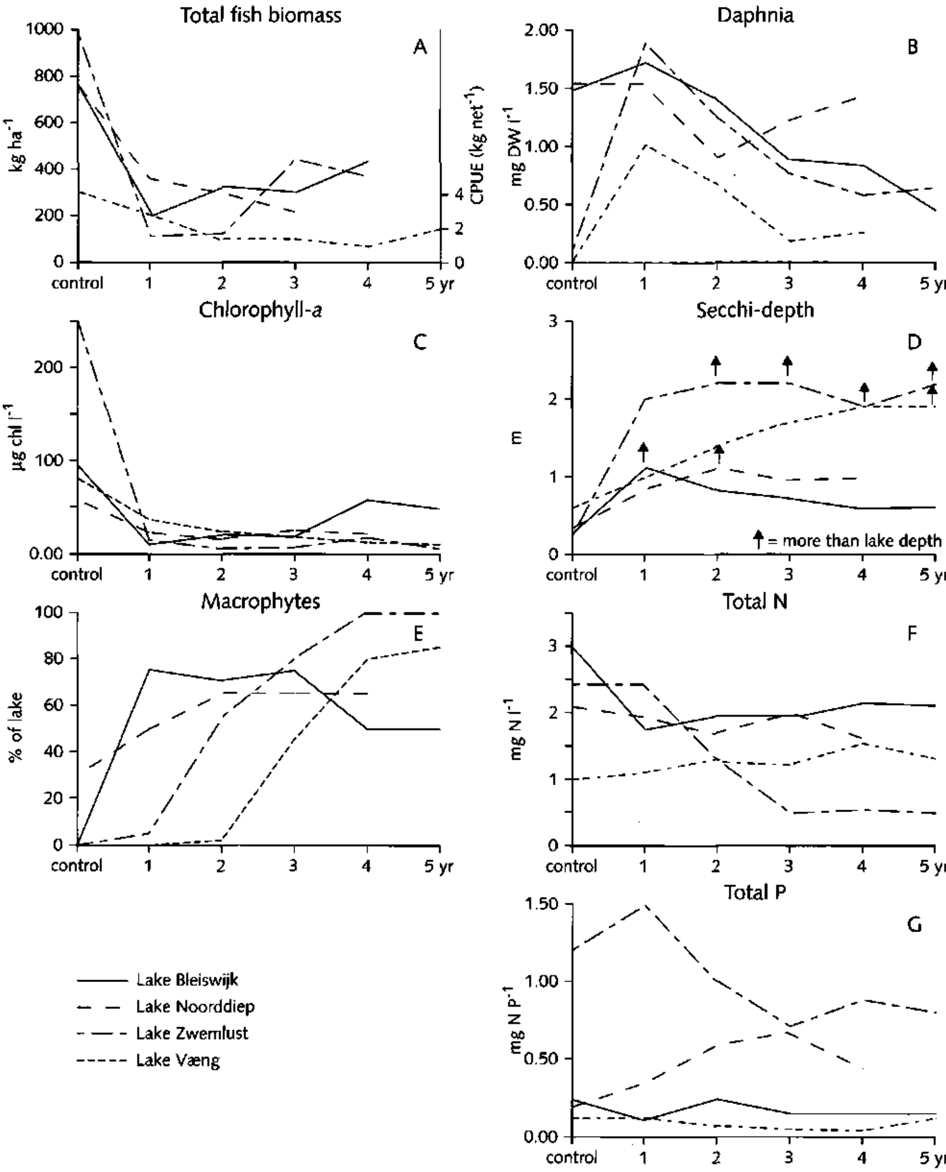

Figure 6.1: *Fish biomass in kg ha^{-1} in Lake Bleiswijkse Zoom, Lake Zwemlust and Lake Noorddiep, in Lake Væng fish stock is expressed as both fish biomass (mark-recapture) and CPUE (kg net^{-1}) in 1986 and only as CPUE in 1987-1991 (a). Summer averages (Denmark May-October; The Netherlands April-September) of* Daphnia *biomass (b), chlorophyll-*a *(c), Secchi-depth (d), estimation of areal coverage of macrophytes (e), total nitrogen (f), total phosphorus (g) in Lake Væng, Bleiswijkse Zoom, Zwemlust and Noorddiep. As control data variables in the year before fish reduction or in a reference part of the lake without drastic fish reduction (Bleiswijkse Zoom) are used.*

the increase of the Secchi-depth to the bottom took 3 years, while in the Dutch lakes this was reached in the first year after the fish reduction. Also the decrease of chlorophyll-*a*, total P and the increase in macrophytes progressed more slowly. The delay in recovery of the macrophytes in Lake Væng was probably caused by the slower increase in Secchi transparency and macrophyte grazing by water fowl (Lauridsen *et al.*, 1994). A drastic decrease in total N was found in the third year when the macrophytes became abundant. The decrease in *Daphnia* biomass was mainly caused by a decrease in *Daphnia* length. The amount of fish caught in the test fishing (CPUE) did not increase in the course of the years, possibly due to the lower nutrient concentration and the high percentage of piscivorous fish (Figure 6.4). The water remained continuously clear during these five years.

Lake Zwemlust

The response of Lake Zwemlust was very similar to the general pattern as described above. A strong response in Secchi-depth, chlorophyll-*a* and *Daphnia* biomass was found in the first year after the very drastic fish stock reduction. The *Daphnia* biomass decreased in the following years, due to a shift to small *Daphnia* species. A strong increase in macrophytes occurred in the second year, followed by a decrease in nitrogen concentration. The water continuously remained clear during the five years. Incidentally large colonies and cyanobacteria were found for short periods (Van Donk *et al.*, 1990c). A small decrease of the coverage of the macrophytes was found, starting in 1990, probably caused by the increased herbivory by birds and rudd (Van Donk *et al.*, 1994). The fish stock gradually increased, combined with an increase in planktivorous fish and a decrease in percentage of piscivores (Figure 6.4).

Lake Noorddiep

Unlike the response in the other lakes, in Lake Noorddiep the total P-concentration significantly increased after the fish removal. This might be caused by the fact that in Lake Noorddiep more than in the other lakes filamentous macroalgae were present at the bottom, leading to P-release in anaerobic zones. As in Lake Bleiswijkse Zoom, large *Daphnia* were already abundant before fish reduction, because the fish stock was mainly composed of benthivorous fish (e.g. large bream *Abramis brama* and carp *Cyprinus carpio*). In Lake Bleiswijkse Zoom and Lake Noorddiep gut analysis showed that the large bream and carp almost exclusively ate chironomids.

In Lake Noorddiep the fish biomass rapidly increased in the first year after the fish reduction, from 145 kg ha^{-1} to 300 kg ha^{-1} in October of the first year, but afterwards the fish stock gradually decreased. The Secchi-depth remained high in all four studied years.

Lake Bleiswijkse Zoom

Lake Bleiswijkse Zoom is the only lake in which a deterioration can be found during the five years. In the first year Lake Bleiswijkse Zoom was in a clear water state, thereafter a deterioration was found, probably triggered by a repeated inlet with turbid water. The fish stock increased, chlorophyll-*a* concentration increased, Secchi-depth decreased and the macrophytes became less abundant. Detailed observations showed that in Lake Bleiswijkse Zoom the water became turbid only in summer; in spring the water was often clear, due to abundance of large *Daphnia* (Figure 6.2).

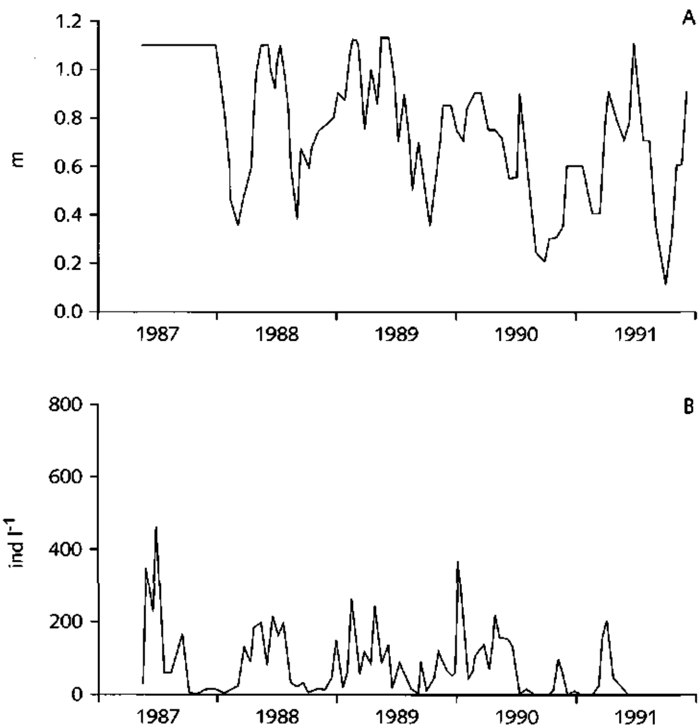

Figure 6.2: *Individual data on Secchi-depth (a) and* Daphnia *density (b) in Lake Bleiswijkse Zoom. In March 1987 the fish stock was drastically reduced. In March and June 1988 and in June 1989 inflow of turbid water (rich in algae and suspended sediment) occurred.*

HYPOTHESIS ON THE CHANGE IN SEASONAL CYCLE

Results from Lake Bleiswijkse Zoom show that the seasonal cycle is important. We formulate a hypothesis on the change in the seasonal cycle in the years after the fish stock reduction. A stable clear water state is compared with a system going back to the turbid state, with emphasis on differences in spring and summer. Deterioration of the light climate starts in summer. The summer differs from spring in many aspects: we pay mainly attention here to the higher predation pressure of young-of-the-year fish on *Daphnia* and the presence of macrophytes, which may cover a substantial part of the lake area.

First two years

In the first two years all systems respond approximately alike. In early spring an algal bloom may occur. In April-June (May-June in Denmark) large *Daphnia* is able to develop exponentially and control algal biomass, because fish predation on zooplankton is low. Due to the reduction in benthivorous fish also the concentration of resuspended bottom material is low and the water becomes clear. Reduction of mainly benthivorous fish may reduce the phosphorus concentration (Havens, 1993), as also can be seen in Lake Bleiswijkse Zoom. However, Lake Noorddiep did not show this pattern. Macrophytes start to develop. *Daphnia* decreases in early summer due to food limitation (Gliwicz & Pijanowska, 1989), but recovers in summer when the predation by planktivorous fish remains low. Algal biomass remains low in summer due to grazing by large daphnids. If macrophytes are already abundant in those years, also limitation of the algal growth by macrophytes and associated filterfeeders can be expected (see below).

Later years

Around the third year after the fish reduction differences start to develop between lakes establishing a stable clear water state, and lakes that are returning to the turbid state (Figure 6.3).

To a stable clear water state

Only slight changes occur in the course of the years. The fish stock hardly increases, probably due to a high impact of piscivorous fish. In summer some 0+ planktivorous fish might occur. An early spring algal bloom might occur. In May-June large *Daphnia* reduces the algal biomass. Then the *Daphnia* density decreases due to food limitation as can be seen from fecundity data. In summer *Daphnia* might become abundant again, when the predation by planktivorous fish remains low. In summer the algal biomass is kept low by grazing by large daphnids and the impact of the macrophytes. Macrophytes cause a decrease of the nitrogen concentration directly by uptake and indirectly by creating alternately aerobic and anaerobic zones in the sediment, enhancing denitrification. Because algal productivity under N-limited conditions is low in the summer the grazing pressure needed to control the algal biomass is not high, so a relatively low density of *Daphnia* is able to control the algal biomass. N_2 fixing cyanobacteria which could have compensated for the low nitrogen levels, are not important in these macrophyte rich lakes (Søndergaard *et al.*, 1990; Van Donk *et al.*, 1990a). The presence of a dense cover of macrophytes stabilise the clear water state. Short term destabilisation may occur along with macrophyte succession due to die-back of a monoculture of e.g. *Elodea* (Lauridsen *et al.*, 1994), fish entrance, or water level alterations (Blindow, 1992). However the percentage piscivorous fish remains high and a return to a clear water stage occurs within months (Lake Væng, unpubl.) to years (Perrow *et al.*, 1994).

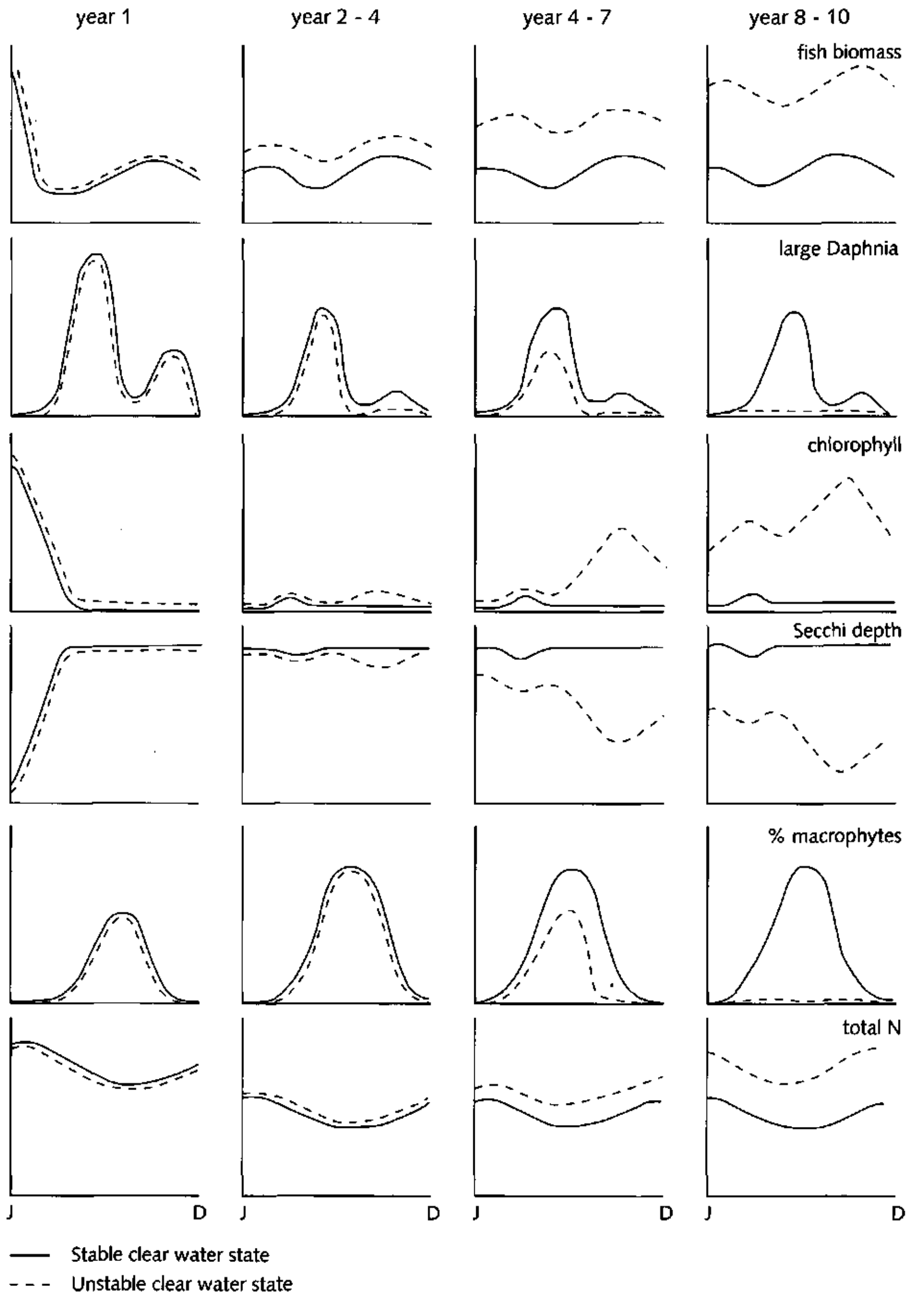

Figure 6.3: *Hypothesised generalisation of developments of fish,* Daphnia, *chlorophyll-*a, *Secchi-depth, macrophytes and nitrogen in the long term in stable and unstable clear water states.*

Return to a turbid state

In spring of the first year or two large *Daphnia* is still able to develop exponentially and control the algal biomass, because the fish predation on zooplankton is relatively low until the end of June. From then onwards the young-of-the-year fish start feeding on large *Daphnia.*
In summer the production of 0+ fish can reach such high levels that the planktivorous fish stock exceeds a threshold level and large *Daphnia* might disappear in summer (e.g. Lake Bleiswijkse Zoom, Figure 6.2). In the first years macrophytes compete with phytoplankton for nitrogen and thus keep the algal biomass low and the transparency high. In later years the Secchi-depth gradually decreases during this period. Eventually macrophytes may disappear due to e.g. periphytic growth (Phillips *et al.*, 1978), abrupt die-back of a monoculture of macrophytes (Lauridsen *et al.*, 1994) or external disturbances such as water inlet (Meijer *et al.*, 1990b) or increased herbivory (Van Donk *et al.*, 1994) and the water becomes turbid. The first years with turbid water in summer, are still followed by clear water in spring (e.g. Bleiswijkse Zoom, Figures 6.2 and 6.3). But at some point due to a low percentage of piscivorous fish the planktivorous fish stock will become so high that large *Daphnia* can not reach high densities in spring anymore and the water may remain turbid throughout the year. Also the biomass of benthivorous fish increases, causing higher resuspension of the sediment. Some lakes may alternate between the turbid and clear water stage over decades (Jeppesen *et al.*, 1990a, 1990b; Perrow *et al.*, 1994). The mechanisms behind the alterations at those lakes are not yet clear.

SIGNALS OF DETERIORATING STABILITY

None of the cases studied has really returned to the permanently turbid state yet, but deterioration in summer and other signs of instability are observed in Lake Bleiswijkse Zoom, and in Lake Zwemlust, such as:

- increase of total fish stock, decrease of percentage of predatory fish and an increase of 0+ fish (Figure 6.4);
- decrease of mean length of *Daphnia* in August (Lake Bleiswijkse Zoom and Lake Zwemlust, Gulati, 1990);
- increase of periphyton on macrophytes and decrease of areal coverage of macrophytes (Lake Bleiswijkse Zoom, pers. comm. R.W. Doef; Zwemlust, Van Donk *et al.*, 1994).

In Lake Væng and Lake Noorddiep less signs of instability are present (Table 6.2). According to the Danish data which show that clear water can occur at P-levels of ca. 0.10 mg P l^{-1} (Jeppesen *et al.*, 1990a, 1990b) only Lake Væng (Figure 6.1) seems suitable for a stable clear water state. Indeed in Lake Væng none of the above mentioned indications for a deterioration are observed in first 5 years. However in 1992 also in Væng the water became turbid (Table 6.2) after the macrophytes almost disappeared in spring, probably reflecting a sudden die-back of a monoculture of *Elodea* sp. (Lauridsen *et al.*, 1994). However this return was only temporary (1.5 month) and the percentage of piscivorous fish remained high, both in numbers and biomass. In Lake Noorddiep and Lake

Bleiswijkse Zoom the surface area and P-levels are close to the range in which stable clear water might be expected (lakes < 3 ha at P-levels of 0.35 mg P l^{-1}). However, the latter lake is deteriorating, probably triggered by a repeated inlet of turbid water.

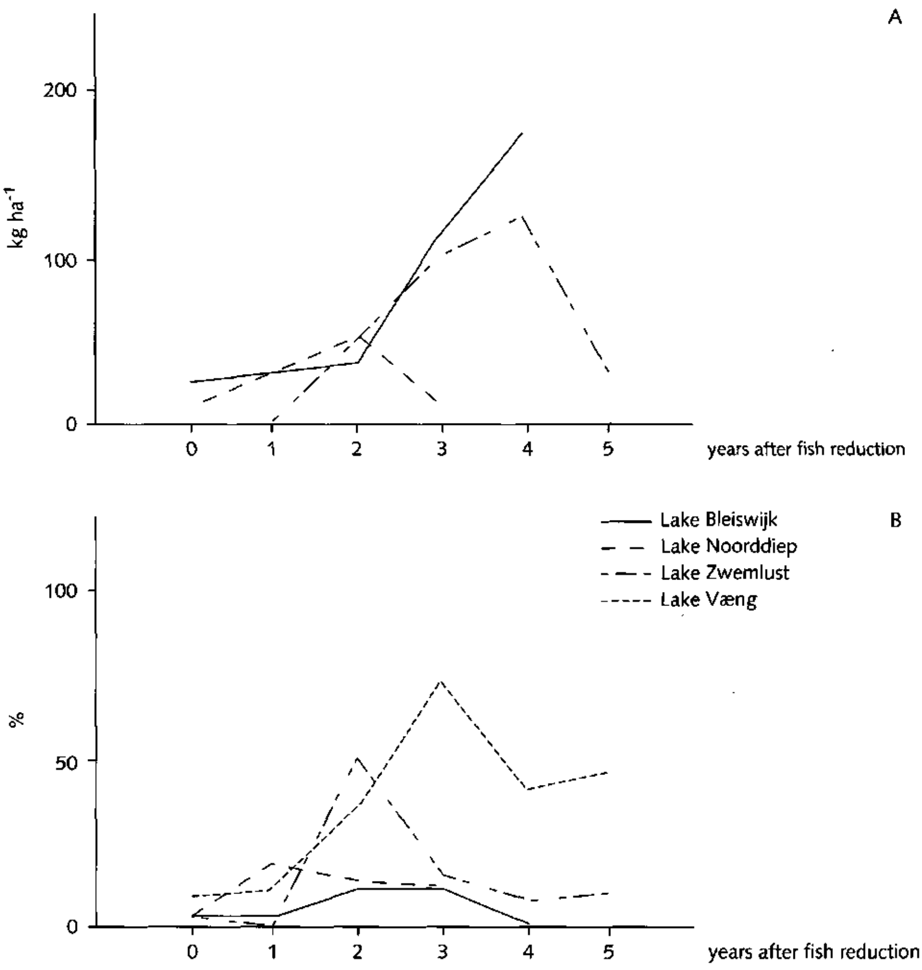

Figure 6.4: *Total biomass of 0+ planktivorous fish (a) and percentage of piscivores (b) in Lake Væng, Zwemlust, Bleiswijkse Zoom and Noorddiep.*

However, in 1990 hardly any and in 1991 no water inlet had taken place, but still the water became turbid in summer due to a decrease of macrophytes and an increase in algal biomass. The production of 0+ fish was very high and large cladocerans were absent in summer (Figures 6.2 and 6.4). Each spring the water became clear. In Lake Noorddiep with the same morphology and

nutrient level as in Lake Bleiswijkse Zoom, the increase of the fish stock was much lower. It is not exactly known why in Lake Noorddiep the fish stock is not increasing. The total P-concentrations even increased after the measure, probably due to P-release from the sediment under a dense cover of filamentous macroalgae, and the total nitrogen concentration did not decrease much. Possibly the natural pike population (composed of small individuals) was better able to control planktivorous 0+ recruitment. The nutrient levels, especially P, in Lake Zwemlust were so high that no stable clear water state was expected. Nevertheless the water remained clear for over five years (Van Donk *et al.*, 1993). One reason for the remarkably long period of high transparency might be that in Lake Zwemlust all fish were removed and the lake was stocked with piscivorous fish and some rudd. In addition young pike were added throughout the investigation period. The increasing fish stock and the absence of large *Daphnia* in summer are indications that the clear water situation might not continue, although the results show that the water can stay clear with those high planktivorous fish densities. As in Lake Væng the water became turbid in summer 1992 (Table 6.2). In Lake Zwemlust the turbid period lasted longer (still turbid in October 1992) than in Lake Væng, possibly because of the higher biomass of planktivores due to a lower % of piscivorous fish. Especially in Lake Zwemlust and Lake Bleiswijkse Zoom the amount of small planktivorous fish is increasing (Figure 6.4), despite the repeated introduction of 0+ pike in the lakes. In Lake Væng and Lake Noorddiep where the development of planktivorous fish has been less explosive, pike was already present before the fish reduction. In these two lakes the conditions were already favourable for pike. It seems that a natural pike population is better able to control 0+ fish than a population of stocked 0+ pikes. One explanation for the limited success of introduced pike may be that pike needs a high abundance of emergent vegetation (Grimm & Backx, 1990) and apparently this vegetation does not develop automatically after a fish reduction measure.
An abrupt return to the turbid state, as can be seen in summer in Lake Væng, Lake Zwemlust and Lake Bleiswijkse Zoom seems more related to a decrease in macrophytes than to a high predation by planktivorous fish. However, a high percentage of piscivores associated with a low density of planktivorous fish, makes it more likely that the turbid stage will not last long. An increase in planktivorous fish causing the disappearance of large *Daphnia*, makes the system more vulnerable to sudden changes in macrophyte populations and can lead to a gradual decrease in transparency. Although in Lake Bleiswijkse Zoom, the water becomes clear again in each spring, the transparency in later years was lower than in the first year after the fish removal.

Table 6.2: *Presence of signs of stability in the summer 4-5 years after the fish stock reduction in Lake Væng, Noorddiep, Bleiswijkse Zoom and Zwemlust. + = yes; - = no.*

Lake	Secchi 4-5 years high	Fish stock decreases	Few 0+ fish	High % pisc. fish	Daphnia length stays high	Secchi-depth summer 1992 stays high
Væng	+	+	+	+	+	-
Noorddiep	+	+	±	-	±	+
Bleiswijkse Zoom	-	-	-	-	-	-
Zwemlust	+	-	-	-	-	-

CONCLUSIONS

- In small shallow lakes from which fish stocks have been reduced, the water can remain clear irrespective of the nutrient levels for at least five years.
- In Lake Bleiswijkse Zoom the water quality deteriorated from the second year onwards, probably triggered by a perturbation (e.g. inlet of turbid water). In Lake Væng a short term (1.5 month) turbid stage was found in summer 1992 (sixth year). Also in Lake Zwemlust the water became turbid in July 1992, but here the water was still turbid in October 1992.
- The return to the turbid water state starts in summer. At first, the water becomes clear again in next spring. At a low biomass of planktivorous fish the recovery of the system goes faster than in presence of a high biomass of planktivores.
- None of the lakes has yet returned to the turbid water state the whole year around, so we do not know how much time it will take for a system to return to the turbid state permanently. The more fish is removed, the longer the expected longevity of the clear situation.
- Based on the four cases there are some indications that the clear water state is most likely more stable at low nutrient levels. However, more information is needed on the factors that determine the succession in macrophytes and the reasons for a sudden collapse of the macrophyte population. Possibly also the conditions for an efficient predator (pike) population are important.
- The results indicate that macrophytes play a key-role in keeping the water clear in the lakes included in the present analysis. All studied lakes are small and shallow and therefore suitable for abundant growth of submerged macrophytes. Vegetation cannot develop to the same extent in deeper and larger lakes. We, therefore, expect the long-term effects of fish stock reduction described here are only valid for small and shallow lakes.

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CHAPTER 7

DEVELOPMENT OF FISH COMMUNITIES IN LAKES AFTER BIOMANIPULATION

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(*Cyprinus carpio*) hamper the recovery of a lake, by eating large zooplankton and by resuspending the sediment (Hosper, 1989).

Therefore, biomanipulation can act as an additional method for restoring lakes (Hosper & Jagtman, 1990; Gulati *et al.*, 1990). Biomanipulation was originally defined as the "deliberate exploitation of the interactions between the components of the aquatic ecosystem in order to reduce the algal biomass" (Shapiro *et al.*, 1982).

In the Netherlands, the most common biomanipulation measure is the removal of > 75 % of the total fish stock and if absent the addition of young-of-the-year (Y-O-Y) northern pike (*Esox lucius*) (Chapter 6). Reducing the planktivorous fish stock will lead to a higher density of zooplankton grazers and a lower algal biomass (Van Donk *et al.*, 1990a, chapter 6). Reduction of benthivorous fish will decrease the resuspension of sediments (Chapter 5) and also the nutrient concentration might decrease (Breukelaar *et al.*, 1994). The low algal biomass and lower concentrations of resuspended sediments will result in a high transparency of the water. These conditions will initiate the growth of macrophytes and create an alternative stable condition (Scheffer, 1990; Scheffer *et al.*, 1993).

In clear overgrown water the living conditions for fish will be different from the old turbid state. The macrophytes will create better conditions for pike (Grimm, 1981b; 1989), perch *Perca fluviatilis* (Winfield, 1986; Persson, 1988, 1991) and rudd *Scardinius erythrophtalmus* (Diehl, 1988). A large effect of pike predation on the Y-O-Y cyprinids is expected (Hosper, 1989; Grimm, 1989). Pike predation in eutrophic systems should prevent the development of planktivorous 0+ cyprinids > 20 kg ha $^{-1}$ (De la Haye & Meijer, 1991). However, experiments in ponds showed, that the theoretically expected effects of northern pike on 0+ cyprinids were not found in practice (Raat, 1990).

In 1987 and 1988 biomanipulation experiments have started in three small shallow lakes (Noorddiep, Bleiswijkse Zoom and Zwemlust). The fish stock reduction has led to a decrease of the algal growth, a high transparency and abundant vegetation. These results have already been reported (Van Donk *et al.*, 1990a; Chapter 5 and 6).

We will evaluate the effect of the measures on the development of fish communities testing the following hypotheses:

- pike will be able to keep the biomass of Y-O-Y low
- after biomanipulation the species diversity of the fish stock will increase.

STUDY AREA AND METHODS

All studied lakes (Noorddiep, Bleiswijkse Zoom, Zwemlust) are small shallow lakes with high nutrient concentrations (Table 7.1). In all lakes before the measures the Secchi-disk transparency of the water was low (0.2-0.3 m) and the algal biomass was high. For the experiment Noorddiep and Bleiswijkse Zoom were divided into two parts. From one part the fish was removed, the other part served as a reference. Exchange of water was possible between the parts, but no exchange of fish. In Noorddiep ca. 80 % of the total fish stock was removed, but no pike was added as already a pike population was present (Table 7.2, Chapter 6). In Bleiswijkse Zoom a similar measure was performed, but in spring fingerlings of pike-perch (1987) and pike (later years) were added, because the existing pike population was almost nil (Table 7.2, Chapter 5). In Zwemlust the whole fish

population was removed and replaced by pike and rudd (Table 7.2; Van Donk *et al.*, 1989, 1990). In all lakes after the biomanipulation the biomass and composition of the fish community were monitored during at least five years. The density of fish was estimated with the adjusted Petersen mark-recapture method (Ricker, 1975). The sample size for the mark-recapture fisheries was usually aimed at estimates with 10 % of the true population within the 95 % confidence. Therefore, sample size in terms of mark (m) and capture (c) was determined using graphs from Robson and Regier (1964). The density was converted to biomass by applying the length-weight relations to the length-frequency distributions. The Y-O-Y cyprinids could not be marked. Their estimated biomass is based on the seine catches and forms a minimum estimate of the Y-O-Y biomass. All estimates represent the biomass of the fish stock at the end of the growing season (November/December).
The coverage of macrophytes (including filamentous macroalgae) was determined by a complete survey of the lakes: In Bleiswijkse Zoom and Zwemlust every month in summer, in Noorddiep once in summer.

Table 7.1: *Major characteristics of the three lakes studied.*

Lake	Surface area (ha)	Mean depth (m)	Total-P summer mean (mg P l^{-1})
Noorddiep			
Experimental	4.5	1.5	0.20
Reference	11.1	1.5	0.20
Bleiswijkse Zoom			
Experimental	3.1	1.1	0.25
Reference	11.4	1.4	0.25
Zwemlust	1.5	2.0	1.00

Table 7.2: *Measures taken in the experimental sites of Noorddiep and Bleiswijkse Zoom and in Zwemlust.*

lake	Fish removal (kg ha^{-1})	Fish removal (% of total)	Stocking in spring (numbers)	Species
Noorddiep				
1988	545 (Mar)	80	-	
	39 (Nov)			
Bleiswijkse Zoom				
1987	645 (Spring)	85	800	0+ pike-perch
1988	140 (Nov)		3600	0+ pike
1989	80 (Nov)		838	0+ pike
1990			300	0+ pike
1991			300	0+ pike
Zwemlust				
1987	1000	100	140	adult rudd
			1600	0+ pike
1988			1500	0+ pike
1989			169	adult roach

RESULTS

Noorddiep

Before the fish removal in March/April 1988 the fish stock amounted to approximately 700 kg ha^{-1} and was largely composed of bream and carp (> 80 %). Also roach and pike were present (Figure 7.1). After the reduction the biomass of bream and carp remained on a stable level of c. 100 kg ha^{-1}. Roach and perch increased in biomass from c. 50-75 kg ha^{-1} before the measure to 100-150 kg ha^{-1} in 1991-1992. Compared with the reference situation the total fish biomass decreased to approximately one third. The total piscivorous fish stock did not change significantly (Kruskall-Wallis), but pike-perch was replaced by pike and perch. The pike biomass increased from c. 15 to 30 kg ha^{-1} and piscivorous perch increased from 6 to 20 kg ha^{-1}.
Already in the first year after the fish removal clear water was established (Secchi depth to the bottom) and macrophyte coverage increased from 30 % to 65 % (Figure 7.2a and Figure 7.2b). The main macrophytes were floating-leafed *Nuphar lutea* and submersed *Ceratophyllum demersum*. On the bottom filamentous macro-algae developed and formed 10-15 % of the total coverage.
There was no significant difference between the total biomass of planktivorous Y-O-Y at the reference site and at the experimental site (Kruskall-Wallis), but the composition of the Y-O-Y changed significantly (Chi^2, $p < 0.05$). The contribution of perch and roach increased from 10 % (roach and perch equally present) at the reference site to 84 % at the experimental site (70 % 0+ perch, 14 % 0+ roach). The total planktivorous fish stock (including > 0+ fish) was significantly lower at the experimental site (Kruskall-Wallis, $p < 0.05$, Table 7.3). From 1988 onwards hardly any 2nd or 3rd year bream was present at the experimental site, while the survival of roach up to the 2nd and 3rd year was good.

Bleiswijkse Zoom

Before the fish removal in March/April 1987 the fish stock was approximately 700 kg ha^{-1} and was largely composed of bream and carp (> 90 %). Hardly any roach or pike were found (Figure 7.3). After the reduction to c. 100 kg ha^{-1} the biomass of bream and carp increased to c. 250 kg ha^{-1} in 1991, despite additional reductions in the following years (removal of 90 kg ha^{-1} in 1988 and 100 kg ha^{-1} in 1989). Also roach, rudd and perch increased in density and contributed c. 100 kg ha^{-1} to the fish stock. Compared to the reference situation the biomass was only little lower, but the new community consisted of more species (Figure 7.3). The total biomass of piscivorous fish did not change (Kruskall-Wallis), but as in Noorddiep pike-perch was replaced by pike and perch. The pike biomass increased from almost zero to 20 kg ha^{-1} and piscivorous perch increased from zero to 17 kg ha^{-1} (Table 7.3).
Already in the first year after the fish removal clear water was established and macrophytes increased from 2 % to 75 % coverage (Figure 7.2a and Figure 7.2b). The first year macrophytes were composed of Characeae, in later years *Potamogeton pectinatus* and *P. perfoliatus* were largely dominant. The first year the clear water and the macrophytes remained the whole summer, but in

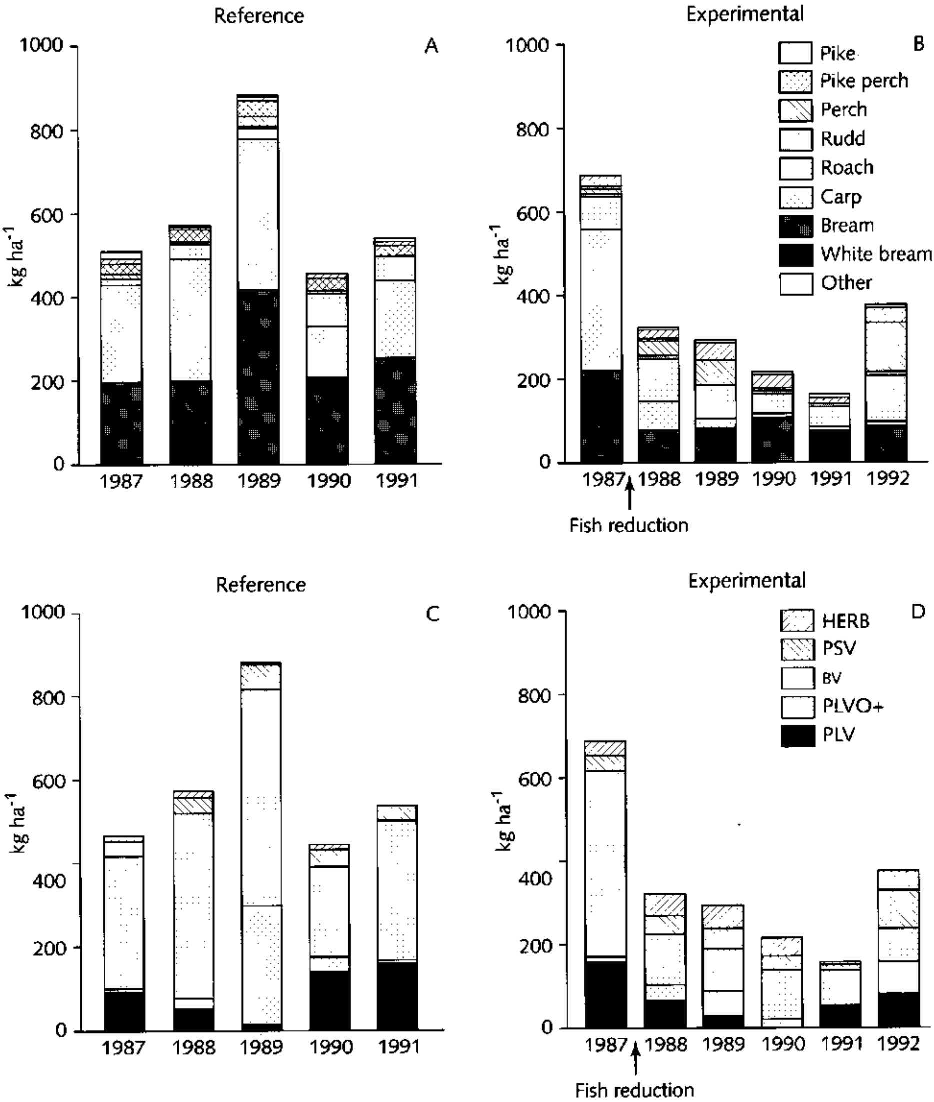

Figure 7.1: *Species composition (a & b) and feeding type composition (c & d) of the fish stock in Noorddiep in kg ha^{-1} from 1987 to 1992 in the reference site (a & c) and in the experimental site (b & d). Feeding types are: PLV 0+ = Planktivorous 0+ = 0+ bream, white bream, roach, rudd and perch < 11 cm and pike-perch < 7 cm; PLV = Planktivorous fish > 0+ = 0+ < bream < 20 cm, 0+ < rudd, roach, white bream, bream < 15 cm; BV = Benthivorous fish = bream > 20 cm, white bream > 15 cm, all carp; PSV = Piscivorous fish = all pike, pike-perch > 7 cm, perch > 11 cm; HERB = Herbivorous fish = roach, rudd > 15 cm, tench.*

later years during part of the summer the Secchi depth decreased and macrophytes disappeared. The biomass of pike increased by growth, natural reproduction and stocking, but they could not control the recruitment of Y-O-Y (Figure 7.3, Table 7.3), which reached a much higher biomass than in the reference situation (Kruskall-Wallis, $p < 0.05$). The biomass of the older year classes of planktivorous fish (bream < 20 cm, roach, rudd and white bream < 15 cm) did not significantly differ between the experimental site and the reference site (Kruskall-Wallis), but the composition had changed (Chi^2, $p < 0.05$, Table 7.3). Especially the survival of 2^nd^ and 3^rd^ year bream was low at the experimental site. Bream contributed 65 % to the biomass of 0+ fish and its share decreased to 30 % in the older year classes of the planktivorous fish stock, while the share of roach increased from 1.5 % to 52 %. The survival and growth rate of bream at the experimental site were high enough to build up a benthivorous bream population of 150 kg ha^{-1}. The biomass of carp remained between 50-100 kg ha^{-1}.

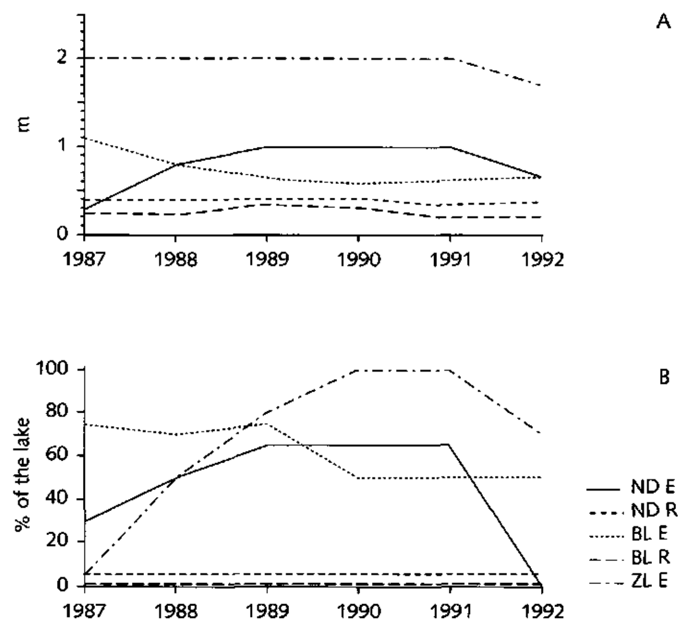

Figure 7.2: *Summer average of Secchi depth (a) and average coverage of macrophytes (b) in the experimental (E) and reference (R) part of Noorddiep (ND) and in Bleiswijkse Zoom (BL) and in Zwemlust (ZL) from 1987 to 1992. In the experimental part of Noorddiep the fish stock reduction took place in winter 1987-1988, in Bleiswijkse Zoom and Zwemlust in winter 1986-1987.*

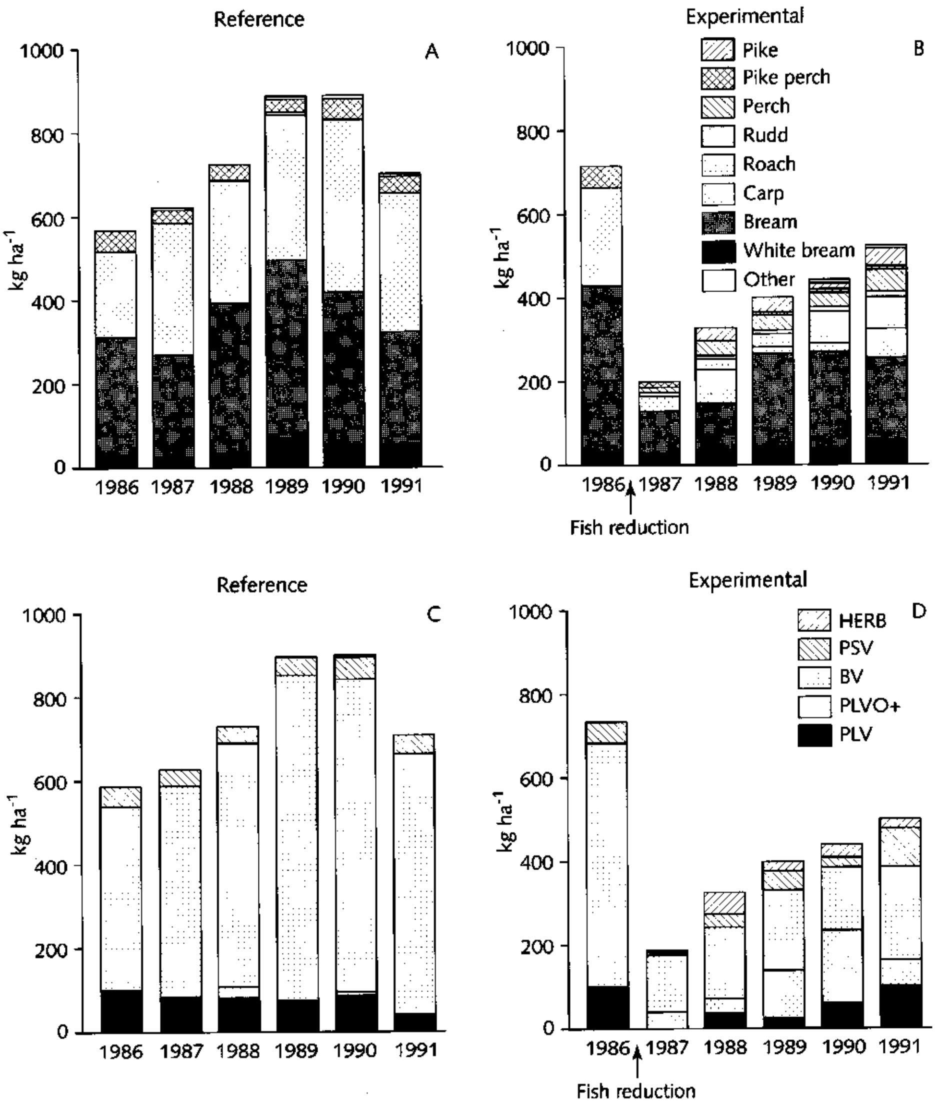

Figure 7.3: *Species composition (a & b) and feeding type composition (c & d) of the fish stock in Bleiswijkse Zoom in kg ha^{-1} from 1986 to 1991 in the reference site (a & c) and in the experimental site (b & d). For explanation of feeding types see Figure 1.*

Zwemlust

Before the fish removal in March 1987 c. 800-1000 kg ha^{-1}, largely composed of bream (> 90 %), were present. Hardly any roach or rudd were found (Figure 7.4). After the complete reduction only pike yearlings and some spawners of rudd (*Scardinius erythrophtalmus*) were introduced.
Already in the first year after the fish removal the water became clear. Macrophytes increased from 5 % lake coverage in the first year to 80 % in the years thereafter (Figures 7.2a and 7.2b). *Elodea nutallii* dominated the macrophyte population, but was replaced by *Ceratophyllum demersum* in later years (Van Donk *et al.*, 1994).
The pike biomass increased to 16 kg ha^{-1} in the first year and increased to ca. 30 kg ha^{-1} in the following years, close to the original level of 38 kg ha^{-1} prior to biomanipulation (Van Donk *et al.*, 1989). However, before the fish removal the pike population was dominated by older pike. In the first two years after the manipulation the pike population was mainly composed of small fish. Afterwards the biomass of 0+ pike decreased dramatically and the average length of the pike increased again (Table 7.4). The rudd population increased from 7 kg ha^{-1} in 1987 to 300-400 kg ha^{-1} in 1992 (Figure 7.4).

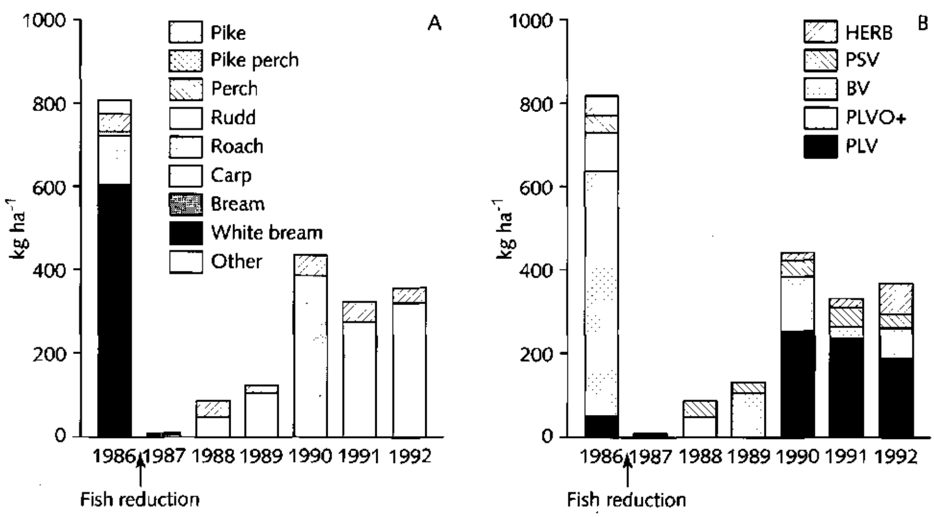

Figure 7.4: *Species composition (a) and feeding type composition (b) of the fish stock in Zwemlust in kg ha^{-1} from 1986 to 1992. For explanation of feeding types see Figure 7.1.*

Table 7.3:

Average biomass of piscivorous (A) and planktivorous (B) fish over the last three-four years in Noorddiep (ND; experimental site 1989-1992, reference site 1988-1991), Bleiswijkse Zoom (BZ; both experimental and reference site 1989-1991) and Zwemlust (ZL; 1990-1992) in kg ha^{-1}. Standard deviation of the years between brackets; exp = experimental; ref = reference.

Species	ND exp		ND ref		BZ exp		BZ ref		ZL exp	
A										
0+ pike	8.0	(5.8)	0		6.6	(0.4)	0		2.2	(1.3)
0+ pike-perch	0		1.4	(1.5)	1.5	(1.6)	0.7	(0.7)	0	
Total pike	29.8	(9.8)	16.1	(0.6)	27.0	(10.1)	3.2	(0.7)	25.6	(5.1)
Total pike-perch	0.2	(0.1)	43.5	(11.4)	6.4	(1.4)	41.6	(7.3)	0	
Perch > 11 cm	18.1	(27.1)	4.5	(5.2)	14.8	(21.7)	0		0	
Total piscivorous	48.8	(32.2)	64.4	(17.0)	53.3	(34.3)	41.7	(7.8)	25.6	(5.1)
B										
0+ fish										
Bream	5.9	(7.0)	140.3	(199.8)	76.1	(31.2)	3.8	(3.8)	0	
Roach	0.7	(1.0)	3.3	(5.7)	0.3	(0.5)	0		0	
Rudd	0.3	(0.2)	0		1.8	(1.7)	0		73.7	(50.6)
Perch	28.9	(31.5)	9.3	(14.3)	27.9	(10.3)	0		0	
Total 0+ fish	36.3	(40.0)	152.6	(219.5)	78.4	(48.5)	3.8	(3.8)	73.7	(50.6)
> 0+ fish										
Bream	1.1	(1.4)	79.0	(62.6)	14.8	(12.2)	51.4	(20.8)	0	
Roach	40.3	(21.7)	43.2	(42.0)	41.5	(17.8)	2.7	(1.3)	0	
Rudd	1.6	(1.3)	1.1	(0.3)	4.5	(0.8)	0		226.6	(36.2)
White bream	1.1	(1.9)	6.5	(1.5)	6.9	(4.4)	12.9	(7.3)	0	
Total planktivorous > 0+	43.2	(22.9)	129.9	(94.1)	67.6	(22.6)	68.7	(23.0)	226.6	(36.2)
Total planktivorous	79.5	(57.7)	282.5	(133.0)	180.4	(25.7)	72.5	(26.7)	300.4	(70.8)

DISCUSSION

Hypothesis 1: In vegetated lakes pike is able to keep the biomass of Y-O-Y low (< 20 kg ha^{-1})

The hypothesis is based on the process of predation, which usually takes place during the period May-October. The data for this study were sampled in the winter period (November-February) and, therefore, refer to the result of this process. With use of these data only statistical relationships between the pike biomass/numbers and the biomass of 0+ fish can be tested. In cases of a correlation between the data, this is indicative of effects of predation. However, causal mechanisms between the predator and its prey cannot be shown with this dataset.

Evaluating three biomanipulation cases after a period of five years it can be concluded that the survival of young-of-the-year is similar or even better in the overgrown areas than in the reference situation with turbid water. The expected large effect of pike on Y-O-Y has not been found: there is no correlation between 0+ pike and the Y-O-Y biomass. The obtained biomasses of young pike were relatively low. At all experimental sites (with or without stocking) the pike biomass remained below 45 kg ha^{-1}, while Grimm (1989) expected biomasses of 50-100 kg ha^{-1}. A biomass of 75 kg ha^{-1} was mentioned as the biomass for young pike needed to control the planktivorous cyprinid population in highly productive lakes (Grimm, 1989). The low coverage with emergent vegetation presumably formed a bottle-neck for higher pike biomasses (Grimm, 1994).

Table 7.4: *Average length of pike (cm) in experimental sites of Noorddiep, Bleiswijkse Zoom and Zwemlust at the end of the growing season (November-December).*

	Noorddiep	Bleiswijkse Zoom	Zwemlust
0+ pike			
1987	-	-	23.2
1988	22.6	17.7	21.4
1989	23.0	33.4	-
1990	23.4	25.9	27.0
1991	21.2	20.9	20.8
1992	-	-	25.1
Total pike population			
1987	-	-	23.2
1988	28.3	28.4	26.7
1989	26.0	41.2	36.9
1990	30.8	30.2	37.8
1991	29.1	28.5	34.9
1992	-	-	41.3

In this study stocking densities of pike fingerlings (4-5 cm) ranged between 300 and 900 individuals ha^{-1}. For effective predation of pike on 0+ cyprinids higher densities are suggested by several authors (Preis *et al.*, 1994; Jeppesen, unpubl. results). However, both in practice and in ponds the raising of 0+ pike is restricted by the density (see for references Raat, 1988). In ponds optimal stocking densities are not above 500 and 1000 pike fingerlings per hectare. In practice, the resident pike have a strong effect on the survival of the mixed specimens. In that situation stocking of pike larvae or fingerlings cannot enhance the resident fish stock. Therefore, we assume that the density of the 0+ pike population in the present study could not be further enhanced by stocking higher densities of pike fingerlings.

The expected large effect of pike on the Y-O-Y cyprinids was not found, partly due to the relatively low biomasses of pike, but also the clear water and macrophytes created a new situation for the cyprinids. Vegetation is not only important as refuge for young pike (Grimm, 1981b), but also creates an extra spawning area and refuge for cyprinids (Carpenter & Lodge, 1986).

Although by the end of June the density of 0+ cyprinids is even higher in Noorddiep than in Bleiswijkse Zoom (Table 7.5), the situation is reversed by the end of the growing season. Apparently the predation was higher in Noorddiep. There was no difference in the biomass of pike between the sites (Table 7.3), and apart from 1989 also the average length of pike was similar at both sites (De Jong, 1993) (Table 7.4). But the predation of pike was probably more efficient in Noorddiep than in Bleiswijkse Zoom as the vegetation was less dense in Noorddiep.

Therefore, vegetation was a better refuge for the cyprinids in Bleiswijkse Zoom than in Noorddiep (Walker, 1994).

Table 7.5: *Average number ($*10^3$ ha^{-1}) of 0+ fish by the end of June in Noorddiep (ND; 1989-1992) and Bleiswijkse Zoom (BZ; 1988-1991). Standard deviation (of 3-4 years) between brackets. exp = experimental site, c = control.*

Site	Perch		Roach		Bream		Rudd		Total	
ND exp	58.6	(44.6)	92.4	(65.5)	53.6	(45.8)	30.0	(42.0)	234.4	(172.1)
BZ exp	8.3	(9.4)	3.2	(3.4)	66.4	(50.5)	1.8	(3.1)	79.6	(41.9)
BZ c	4.6	(6.1)	1.4	(1.4)	36.8	(34.3)			42.8	(40.3)

Hypothesis 2: Species diversity of the fish stock will have increased after biomanipulation

As expected the species composition of the fish became more diverse. The share of bream and carp decreased and the abundance of perch, roach and pike increased.

The number of benthivorous fish decreased, especially in Noorddiep. The feeding conditions for benthivorous fish deteriorated as the sediment was covered with vegetation. Chironomids and oligochaetes were replaced by snails, gammarids and other insect larvae (Kornijow *et al.*, 1990; Diehl, 1993). Roach and perch are well adapted to forage in this situation (Winfield, 1986), but bream and carp prefer open water conditions (Lammens *et al.*, 1987; Lammens, 1989). The result is a different fish community mainly composed of fish adapted to living in vegetation. The shift to fish adapted to vegetation is probably caused by a combination of the effect of a change in food sources and the fact that bream is more vulnerable to predation than roach and perch, because the latter species stay in the vegetation.

After biomanipulation in Noorddiep bream was replaced by roach and perch already in the Y-O-Y population, while in Bleiswijkse Zoom a similar shift occurred in the older year classes. The spawning conditions for bream in the lakes appeared very identical, as the density of bream was high by the end of June at both experimental sites (Table 7.5), but the survival of 0+ bream in Noorddiep was much lower than in Bleiswijkse Zoom, probably due to the efficient predation of the piscivorous fish on bream in Noorddiep. In Bleiswijkse Zoom predation on 0+ bream was more difficult due to very dense vegetation in early summer and due to turbid water in late summer, which may have favoured bream.

The biomass of young bream in Noorddiep was so low, that hardly any benthivorous bream developed, while in Bleiswijkse Zoom part of the bream population escaped predation and became benthivorous. This difference in benthivorous fish is the main explanation for the difference in biomass between the experimental sites.
The newly created situation with clear water and macrophytes favoured roach. Even a very low biomass of 0+ roach (1 kg ha^{-1} in Bleiswijkse Zoom) was sufficient to build up a reasonably high population of older fish. This is surprising as many articles describe a shift from roach to perch as vegetation increases (Winfield, 1986; Persson, 1988, 1991). This shift is mainly based on the observation that perch is more adapted to foraging between the macrophytes compared to roach, which is more efficient in eating zooplankton (Persson, 1988). However, our situation differs from the lakes in that study (in Sweden). In most lakes in Sweden the main cyprinid species is roach, even in the turbid state (Persson, 1988). In the Netherlands, however, bream and carp dominate the cyprinid population in turbid waters (Lammens, 1986).
In lake Krankesjön in Sweden, where bream was abundant when the water was turbid, as in our lakes, an increase of roach as well as perch was found when the water became clear and the macrophytes developed (Blindow *et al.*, 1993). Also the abundance of rudd increased after the fish reduction.

Total piscivorous population

Our first hypothesis was mainly focused on predation of pike on cyprinids. However, also perch should be able to become predator on cyprinids when the vegetation is present (Winfield, 1986). We did find that the recruitment of perch was much higher at both experimental sites.
At all sites the share of piscivorous fish (pike and perch) increased after the fish reduction, but only in Noorddiep the share increased to more than 25 %. In Zwemlust and Bleiswijkse Zoom the piscivorous fish stock remained below 10-15 %, while in Swedish lakes with a high vegetation coverage the fish stock was for 50-80 % composed of piscivorous fish, mainly perch (Persson, 1994). In our study the biomass of piscivorous perch remains below 20 kg ha^{-1} and formed maximally 10 % of the fish stock. Some studies indicate that at higher nutrient conditions, as present in the observed cases, perch will loose from cyprinids (mainly roach), in the competition for food (Persson, 1991). Because an increase in nutrient concentrations often coincides with a decrease of vegetation, Persson suggested in 1994 that the high share of piscivorous perch may be more determined by vegetation than by nutrients. Because of that mechanism also at higher nutrient levels a stable clear water state might be possible (Persson, 1994). However, the results of this study show that macrophytes and clear water are no guarantee for high biomasses of pike or perch.

Stability of the obtained clear water state

After 5 years of biomanipulation the water in the lakes is still clear during most of the year, although the fish biomass has increased to high values (400 kg ha^{-1} in Zwemlust and Bleiswijkse Zoom). This is probably due to the macrophytes keeping the water clear (Van Donk *et al.*, 1990a, 1993).

However, in later years in both Zwemlust and Bleiswijkse Zoom the macrophytes disappeared in July-August and the water became turbid. Despite the high fish biomasses the sites could recover after periods of turbid water; each spring the water is clear. This temporary deterioration also occurred in an other biomanipulated lake, lake Væng in Denmark, but here the turbid water period lasted much shorter (Lauridsen *et al.*, 1994; Chapter 6). This might be caused by the high percentage of piscivores and the low abundance of 0+ fish in lake Væng (Chapter 6). Because of the low percentage of piscivores it is therefore questionable if an alternative stable state with clear water can be obtained in the observed eutrophic lakes.

ACKNOWLEDGEMENTS

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CHAPTER 8

EFFECTS OF BIOMANIPULATION IN THE LARGE AND SHALLOW LAKE WOLDERWIJD, THE NETHERLANDS

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EFFECTS OF BIOMANIPULATION IN THE LARGE AND SHALLOW LAKE WOLDERWIJD, THE NETHERLANDS

ABSTRACT

Since the early 1970's, Lake Wolderwijd (2650 ha, mean depth 1.5 m) suffered from cyanobacterial blooms, turbid water and a poor submerged vegetation as a result of eutrophication. From 1981 onwards the lake was flushed with water low in phosphorus and high in calcium bicarbonate. Total-P and chlorophyll-*a* in the lake more than halved, but Secchi depth in summer increased from 0.20 to 0.30 m only. In the hope of triggering a shift from the algae-dominated turbid water state to a macrophyte-dominated clear water state, the lake was biomanipulated during winter 1990/1991. The fish stock, mainly bream (*Abramis brama*) and roach (*Rutilus rutilus*), was reduced from 205 to 45 kg ha^{-1}. In May 1991, 575,000 (217 ind ha^{-1}) pike fingerlings (*Esox lucius*) were introduced. In spring 1991 the lake cleared as a result of grazing by *Daphnia galeata*. The clear water phase lasted for only six weeks. Macrophytes did not respond as expected and most of the young pike died. However, from 1991 to 1993 the submerged vegetation is gradually changing. Characeae began to spread over the lake (from 28 ha in 1991 to 438 ha in 1993). The water over the *Chara* meadows was clear, probably as a result of increased net sedimentation in these areas. It is hypothesized that expansion of the *Chara* meadows might ultimately result in a shift of the whole lake to a lasting clear water state. In order to promote the *Chara*, the fish stock reductions aimed at a spring clear water phase should be continued.

INTRODUCTION

Most shallow lakes in the Netherlands are characterised by turbid water and a lack of macrophytes, primarily as a result of eutrophication. The lake restoration strategy has been focused on the reduction of the external phosphorus loading. However, so far this strategy has not resulted in the desired clear water state (Van Liere & Gulati, 1992). Recovery is hampered by the internal phosphorus loading from the sediments (Sas, 1989; Van der Molen & Boers, 1994) and by the abundance of benthivorous and planktivorous fish (Hosper, 1989; Hosper & Jagtman, 1990). The turbid water state appears to be extremely stable and additional measures are necessary to get the recovery process started. Biomanipulation, i.e. removing or stocking of fish, has been suggested as a promising tool (Shapiro *et al.*, 1975; Benndorf *et al.*, 1984; Carpenter *et al.*, 1987; Gulati *et al.*, 1990). Biomanipulation as a tool for restoration of shallow lakes is mainly based upon the concept of 'alternative stable states'. Within certain limits of nutrient loading, there are two alternative stable states: a phytoplankton-dominated turbid water state and a macrophyte-dominated clear water state (Scheffer, 1989, 1990; Moss, 1990; Scheffer *et al.*, 1993). A drastic reduction of the planktivorous and benthivorous fish stock may induce a shift from the turbid water state to the clear water state (Hosper & Jagtman, 1990). This approach proved to be successful in the restoration of small lakes (< 50 ha) in the Netherlands (Chapter 4, 5, 6; Van Donk *et al.*, 1990a; Van Berkum *et al.*, 1995; Van Donk & Gulati, 1995), Denmark (Jeppesen *et al.*, 1990a) and the UK (Philips & Moss, 1994). Substantial fish stock reduction (> 75 %) resulted in increased zooplankton grazing, decreased sediment resuspension, clear water and as a consequence the return of submerged macrophytes. Submerged macrophytes are believed to play a key role in sustaining the clear water state by several mechanisms, such as competing with algae for nutrients, reducing the resuspension of the sediment or providing refuge for zooplankton (Moss, 1990; Jeppesen *et al.*, 1990b; Scheffer *et al.*, 1993; Chapter 6).

Stimulated by the successful case studies in small lakes, biomanipulation was suggested to restore the large Lake Wolderwijd (2650 ha, $z = 1.5$ m). It is clear that the results from small lakes cannot be applied to large lakes, without due consideration. In Lake Breukeleveen (180 ha) fish reduction failed to result in clear water, possibly due to the insufficient removal of fish, the abundance of filamentous cyanobacteria and the strong impact of wind-induced resuspension of the peaty lake sediments (Van Donk *et al.*, 1990b, 1994). Filamentous cyanobacteria, such as *Oscillatoria agardhii* Gomont, are a less favourable food source for zooplankton (Gliwicz, 1990). In comparison to Lake Breukeleveen, Wolderwijd offers better chances for biomanipulation, due to the lower abundance of filamentous cyanobacteria and the predominantly sandy lake sediments. Furthermore, enclosure experiments (2 x 1 ha) in Wolderwijd, showed a rapid colonization by *Chara* spp. after removal of the fish stock (unpubl. results).

Our objective was to test biomanipulation as a tool for restoring a large and shallow lake. In early 1991, the fish stock was substantially reduced and pike (*Esox lucius* L.) fingerlings were stocked to support the control of young-of-the-year (YOY) cyprinids. We expected an increase in transparency, due to high zooplankton grazing and reduced sediment resuspension by fish, and consequently an increase in the abundance of submerged macrophytes. The new clear water state would be sustained by a developing pike stock and an extensive submerged vegetation. Responses of transparency, nutrients and the biotic components of the lake ecosystem were studied. Three years after the main intervention (1991-1993) were compared to two preceding years (1989-1990).

STUDY SITE

Wolderwijd is a large and shallow lake in the central part of the Netherlands with an area of 2650 ha (Figure 8.1). Water depth varies from 0.5 m to 2.5 m, mean depth is 1.5 m and maximum depth is 5.0 m. The lake was created in 1968 along with the construction of the polder of Flevoland in IJsselmeer

(Meijer *et al.*, 1994b). Several small streams from a predominantly agricultural area flow into the lake. Sluices in the south of the lake provide the outflow into Nijkerkernauw. A sluice in the north connects Wolderwijd with Veluwemeer. The first year of its existence the water of the lake was clear. Since 1970 the lake is characterized by blooms of *Oscillatoria agardhii* (Berger & Bij de Vaate, 1983) and a poorly developed submerged vegetation of *Potamogeton pectinatus* L. and *Pot. perfoliatus* L. The external P-loading is 0.5-1.0 g $Pm^{-2}y^{-1}$ and varies with the inflow from streams. From 1981 onwards the lake has been periodically flushed with excess polder water, that is low in phosphorus (< 100 $\mu g\ l^{-1}$) and high in calcium bicarbonate (Figure 8.2). In the adjacent Veluwemeer the flushing with polder water started already in 1979 and was very successful (Hosper, 1984; Hosper & Meijer, 1986; Jagtman *et al.*, 1992). Internal P-loading strongly decreased due to the pH buffering effect of the calcium bicarbonate. Particularly during cold winters with long periods of ice-cover, the number of cyanobacteria in Veluwemeer significantly reduced by the flushing (Jagtman *et al.*, 1992). Although the flushing of Wolderwijd was less intense, total-P and chlorophyll-*a* more than halved (Figure 8.4) and the phyto-plankton became more diverse. Summer Secchi depth increased from 0.20 to 0.30 m only (Figs. 8.3 and 8.4).

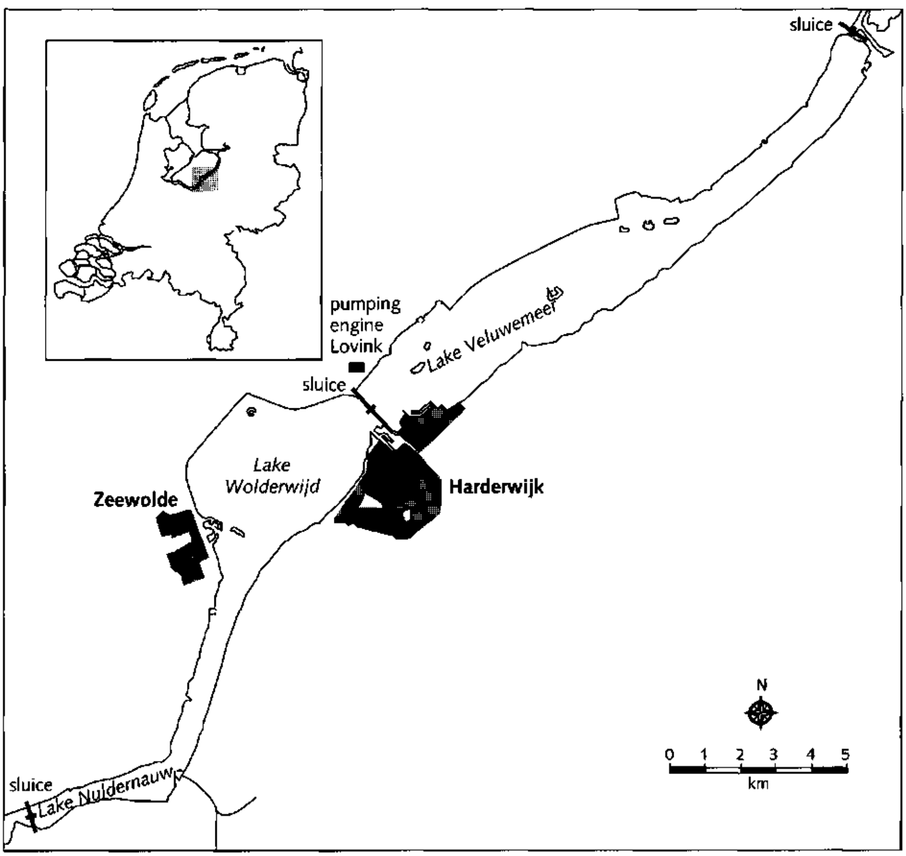

Figure 8.1: *Lake Wolderwijd in the Netherlands.*

MATERIALS AND METHODS

Biomanipulation

The objective of the fish stock removal was to reduce the planktivorous fish stock to < 20 kg ha^{-1} and the benthivorous fish stock to < 25 kg ha^{-1}. These objectives were based upon the following empirical data: (1) results from enclosure experiments (McQueen & Post, 1988) indicate that above 20 kg ha^{-1} of planktivorous fish, the abundance of zooplankton is strongly depressed and (2) results from pond experiments (Chapter 3) showed that significant effects on turbidity can be expected above 50 kg ha^{-1} of benthivorous fish. This level was reduced to 25 kg ha^{-1} to account for the reinforcing effect of wind-induced waves on turbidity in large lakes. The fishery was carried out between November 1990 and July 1991, using large seine nets (180 m, 770 m and 1200 m in length), trawls and fykes. The initial fish stock of about 205 kg ha^{-1} (190-220 kg ha^{-1}) was reduced to about 45 kg ha^{-1}(33-63 kg ha^{-1}). Approx. 425,000 kg of fish were removed, of which about 95,000 kg of bream (*Abramis brama* L.) and roach (*Rutilus rutilus* L.) were restocked elsewhere. The rest was transported to a fish processing plant. The original objectives were accomplished. For detailed information on the planning and implementation of the fish removal, see Grimm & Backx (1994) and Backx & Grimm (1994). On 8 May and 28 May 1991 in total about 575,000 pike fingerlings (3-4 cm) were introduced. The next year, from January to May 1992, additional removal of small fish (< 15 cm) from the harbours and the deeper parts of the lake was undertaken. In May 1992, 42 kg ha^{-1} of large bream (> 25 cm) were removed from the spawning areas by fyke nets. From February to August 1993, small fish (< 15 cm) and larger bream were again targeted and about 73 kg ha^{-1} was removed.

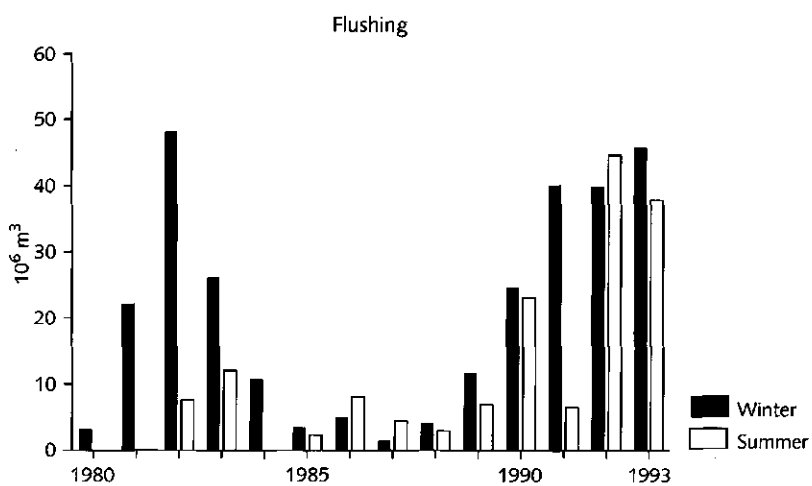

Figure 8.2: *Flushing of Wolderwijd. Total flushing in winter (October-March) and summer (April-September) from 1975 to 1993.*

Lake flushing

To reduce the number of filamentous cyanobacteria and thus enhancing the chances for biomanipulation, flushing of the lake with polder water was intensified from April 1990 onwards. Flushing increased from monthly 1-2.10^6 m^3 in 1988-1989, to 4-7.10^6 m^3 in 1991-1992 (Figure 8.2). As a result of the flushing, the hydraulic residence time of Wolderwijd, on the basis of inflow, reduced from about 1 year to 0.5 year. To prevent fish from entering the lake, the water was flushed through an iron grid (mesh size 3 x 0.5 cm) in the sluice. During summer the water was pumped into the lake after sieving through stones and a Nicolon net (mesh size < 1 mm).

Table 8.1: *Water quality inside and outside the Chara vegetation in June-July 1993. Standard deviation within brackets (n = 4 or n = 5).*

	Inside vegetation		Outside vegetation	
Secchi depth (m)*	0.60***	(0.13)	0.30	(0.00)
Chlorophyll-*a* ($\mu g\ l^{-1}$)*	12.00	(5.00)	38.00	(5.00)
Total-P ($mg\ l^{-1}$)	0.06	(0.02)	0.10	(0.03)
Total N ($mg\ l^{-1}$)	1.37	(0.25)	1.80	(0.05)
SRP ($mg\ l^{-1}$)*	0.003	(0.00)	< 0.001	(0.00)
Dissolved-N ($mg\ N\ l^{-1}$)**	0.0045	(0.015)	0.06	(0.013)
Inorganic suspended solids ($mg\ l^{-1}$)	2.75	(1.30)	7.00	(1.20)

* significant difference between inside and outside the vegetation ($p < 0.05$)
** dissolved N= $NO_3 + NO_2 + NH_4$
*** Secchi depth to the lake bottom

Sampling and analysis

Every fortnight, three parts of the lake were sampled (deep, shallow and centre of the lake). In each part 10-15 samples were taken over a length of 500 m with a transparent 1.5 m perspex tube (Ø 5 cm). Analysis showed no significant difference between the parts (Van Nes *et al.*, 1992). Only above the Characeae vegetation (after 1991) differences were found, which are separately presented in Table 8.1. In the rest of this paper data are presented from the centre of the lake. The 10-15 samples were mixed to a composite sample of 25-30 l for analysis of nutrients, chlorophyll-*a* and phytoplankton. Nitrogen, phosphorus, suspended solids and chlorophyll-*a* were measured according to the Netherlands standard methods (NEN), which comply with International Standards (ISO). For analysis of zooplankton a composite sample of 25 l was filtered over a net with mesh size 55 µm and fixed with 96 % ethanol. Density, length and fecundity (number of eggs adult ind^{-1}) of *Daphnia* sp. were determined. The composition of phytoplankton was determined by taking a 1 l sample that was then fixed with lugol solution. At least 200 individuals were determined. The vegetation was estimated in three density classes (0-15 %, 16-50 % and 51-100 % coverage of the lake bottom) by extrapolating from gridpoints in the lake (grid 50 x 100 m). The density of the mysid shrimp, *Neomysis integer* Leach, was monitored monthly by sampling 10 parts of the lake (different sediment type and depth) with five replicates each. The samples were taken by pulling a net with an opening of 0.50 x 0.25 m and a mesh size of 0.5-2.0 mm over 40 m^2. The fish stock was estimated by trawling (35-70 trawls covering 45-70 ha), using the catch per surface area and estimates for the efficiency of the nets (Grimm & Backx, 1994). The fish biomass has an estimated inaccuracy of 10-25 % (Backx & Grimm, 1994; Backx, unpubl. data).

RESULTS

Transparency, nutrients and phytoplankton

In 1989 and 1990, before the fish removal, the summer Secchi depth was about 0.30 m. After the fish removal in May 1991, an extraordinary high Secchi depth of 1.7 m was observed throughout the lake (Figure 8.3). This clear water phase lasted for six weeks.

The high transparency coincided with extremely low concentrations of chlorophyll-*a* (3 $\mu g\ l^{-1}$, Figure 8.3) and inorganic suspended solids (4 $mg\ l^{-1}$, not in figure). The next year, in May 1992, the transparency reached a peak value of 0.9 m, but this clear water phase lasted for two weeks only. However, in the part of the lake covered with Characeae (see below), the water remained clear until August. In 1993 only during one week a Secchi depth of 0.9 m was observed in the open water, but again above the Characeae, the water remained clear for about six weeks. A sharp distinction was observed between the turbid water and the clear water and aerial photographs showed that the transition zone may be less than 10 m (Scheffer *et al.*, 1993). In summer 1991 the mean Secchi depth in the open water was significantly higher ($p < 0.05$) than in all other years (Figure 8.4). In May-June, at the start of the growing season for vegetation, Secchi depth was about twice as high as in all other years (Figure 8.5). In 1991 the concentration of total phosphorus and total nitrogen was relatively low (resp. 0.07 $mg\ P\ l^{-1}$ and 1.4 $mg\ N\ l^{-1}$, Figure 8.4).

In 1989 and 1990 the phytoplankton was dominated by cyanobacteria, predominantly *Planktothrix agardhii*, with densities of 10,000-70,000 ind ml^{-1}. The dominance of cyanobacteria was broken after the fisheries in 1991, but returned in the summer of 1993 (Figure 8.6).

Daphnia and Neomysis

Each year, *Daphnia* developed a high density in spring (Figure 8.3). Before and after the fish reduction the *Daphnia* population was mainly composed of *Daphnia galeata* (Sars). In 1991 and 1992 the highest density coincided with the clear water phase. Only in 1992 *Daphnia* slightly recovered in summer, while in all the other years *Daphnia* was almost absent from July onwards. Each summer the average length of *Daphnia* decreased (Figure 8.7), probably as a result of selective fish predation by Y-O-Y fish (Lammens *et al.*, 1985).

During the clear water phase in 1991, the density nor the length of *Daphnia* was higher than in the years before the fish reduction. In July 1991, however, the average length was relatively high. The

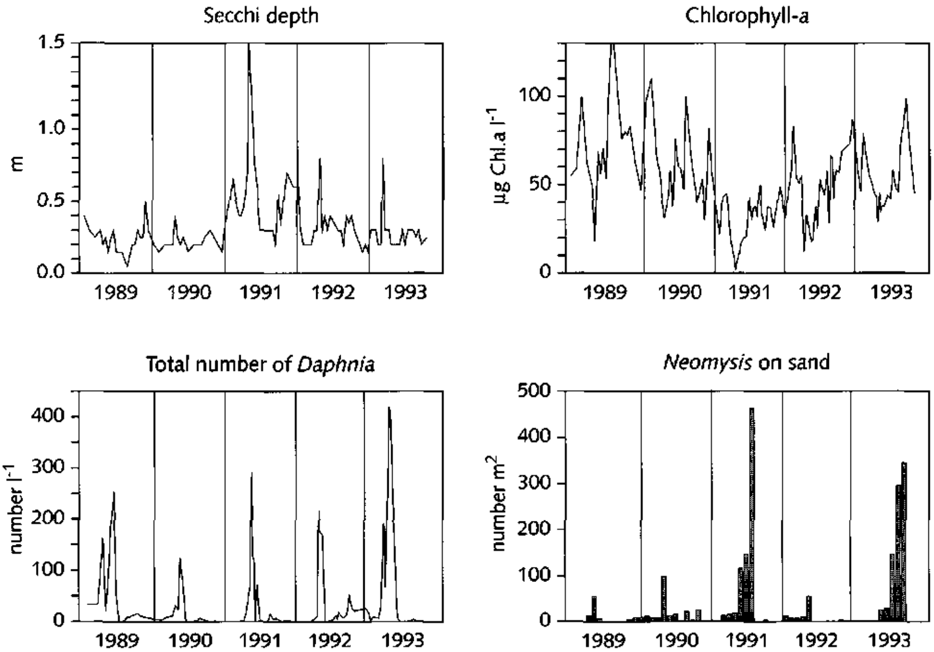

Figure 8.3: *Secchi depth, chlorophyll-*a, Daphnia *and* Neomysis *in 1989-1993, before and after the drastic fish stock reduction (November 1990-June 1991).*

mysid shrimp *Neomysis integer* reached high densities in July 1991 and 1993 (over 400 ind m^{-2} on sand) (Figure 8.3). In other years *Neomysis* was present, but the densities were low (< 100 ind m^{-2}).

Macrophytes

Over the years 1989-1993, the total vegetated area of the lake remained the same, about 1000 ha (Figure 8.8), but a shift in species and density was observed. Before the fish removal (1989-1990) the main species were *Potamogeton pectinatus* and *P. perfoliatus*. In 1992-1993 the dense parts of the *Potamogeton* vegetation almost disappeared and became replaced by Characeae (Figures 8.8 and 8.9). The *Chara* vegetation consisted mainly of *Chara contraria* A. Braun ex Kütz and *C. vulgaris* L.. In 1991 *Chara* occupied 28 ha, in 1992 141 ha and in 1993 the area had expanded to 438 ha of the lake. In 1993, the water remained clear in an area of 200-300 ha above the Characeae (see above). The concentration of chlorophyll-*a* and inorganic suspended solids was lower within the *Chara* meadows than outside the vegetation (Table 8.1). No significant difference was found in total-N and total-P, but the concentration of SRP was higher inside the vegetation area ($p < 0.05$, Wilcoxon signed rank test).

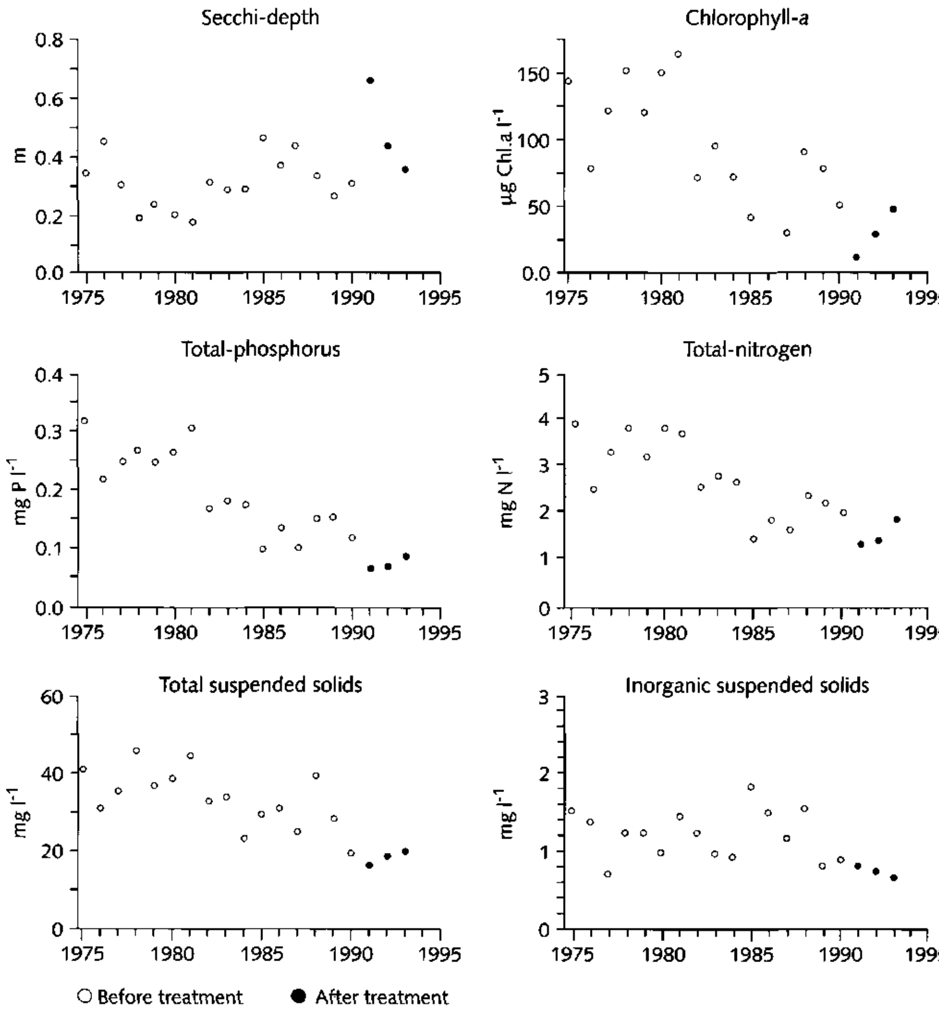

Figure 8.4: *Secchi depth, chlorophyll-a, total-P, total-N, total suspended solids and inorganic suspended solids in the open water. Mean values (April-September) for 1975-1993, before and after the drastic fish stock reduction (November 1990-June 1991).*

Fish

The initial fish stock of 205 kg ha^{-1} was reduced to 45 kg ha^{-1} (Figure 8.10). During the summer of 1991, the fish stock increased again to 100 kg ha^{-1} by September, mainly as a result of the production of 0+ fish (Y-O-Y), of which 30 kg ha^{-1} consisted of ruffe (*Gymnocephalus cernua* L.). The dominant

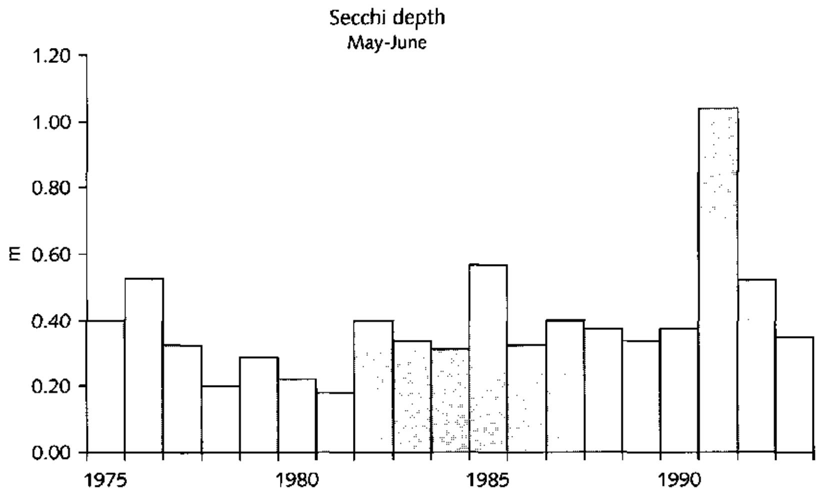

Figure 8.5: *Secchi depth in May-June from 1975 to 1993, before and after the drastic fish stock reduction (November 1990-June 1991).*

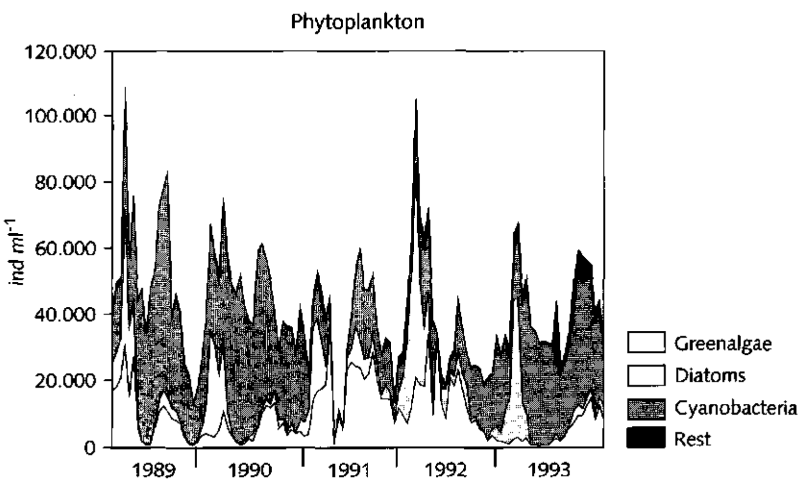

Figure 8.6: *Phytoplankton in 1989-1993, before and after the drastic fish stock reduction (November 1990-June 1991).*

species of the fish stock in September were ruffe (30 %) and bream > 25 cm (23 %). In June 1992, after the additional fish removal, the remaining population was estimated at 70 kg ha^{-1}, which at the end of the growing season, in September 1992, had increased to 105 kg ha^{-1}. During the summer 45 kg ha^{-1} of Y-O-Y recruited, dominated by perch (*Perca fluviatilis* L.) (58 %).

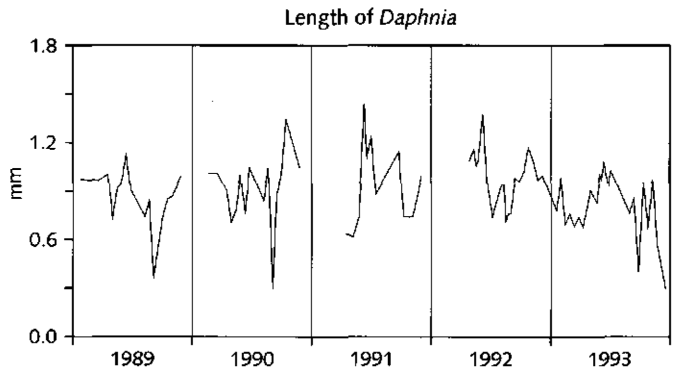

Figure 8.7: *Length of* Daphnia *in 1989-1993, before and after the drastic fish stock reduction (November 1990-June 1991).*

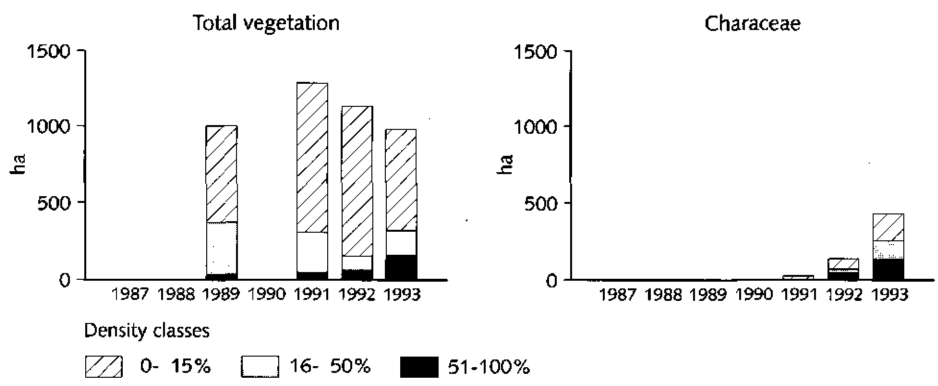

Figure 8.8: *Submerged macrophytes in 1989-1993, before and after the drastic fish stock reduction (November 1990-June 1991). Indicated are vegetated area (ha) and density classes (% of bottom covered by vegetation).*

In January 1993 the total fish stock had increased to 165 kg ha^{-1}, partly due to immigration of bream > 25 cm. In winter 1993 mainly large bream was removed. The remaining population in June 1993 was about 85 kg ha^{-1}, while at the end of the growing season the total biomass had hardly changed. In September 1991, electro-fishing indicated a pike biomass of less than 3 kg ha^{-1}.

DISCUSSION

The objective of this study was to test the concept of biomanipulation in a large and shallow lake. Biomanipulation has been successfully applied in small lakes (< 50 ha) (Van Donk *et al.*, 1990a;

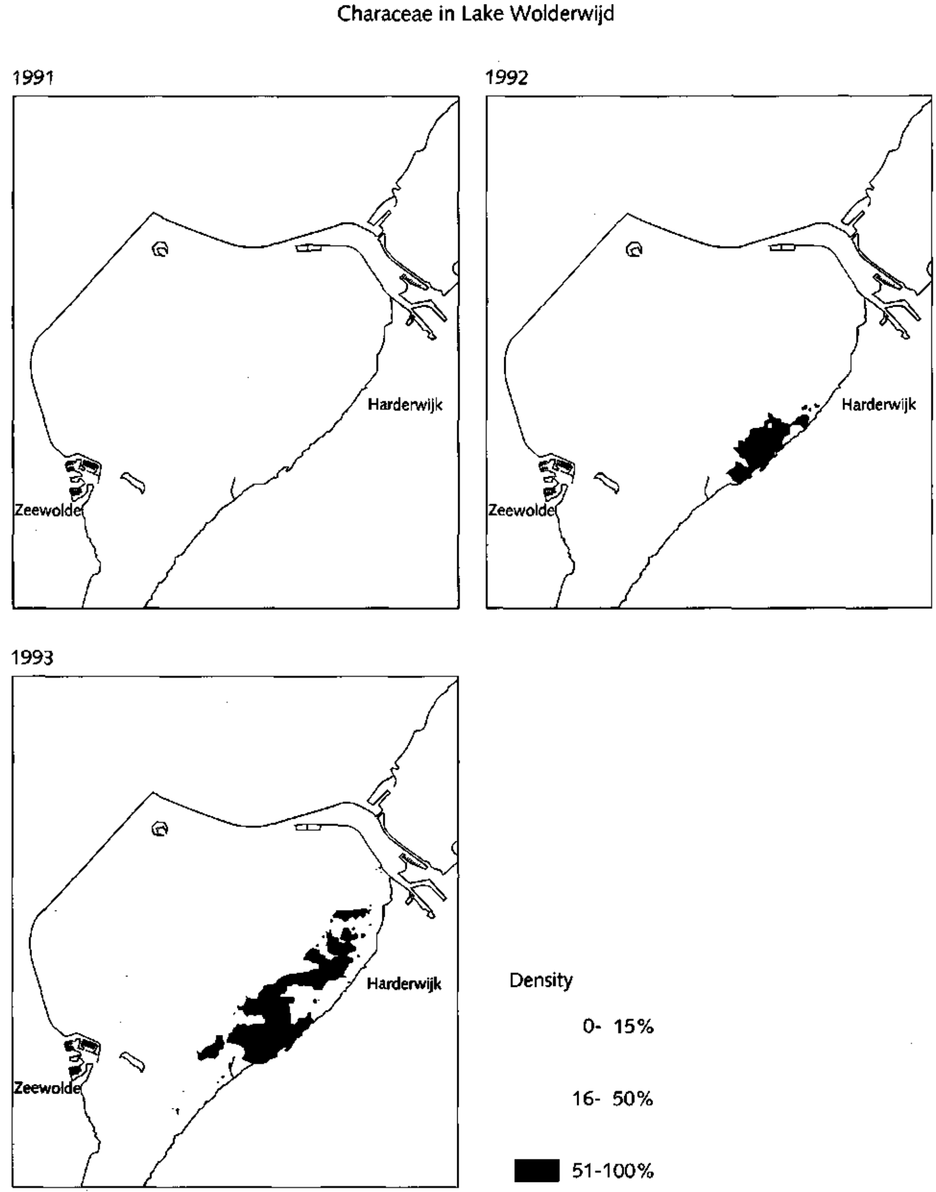

Figure 8.9: *Characeae in 1990-1993. In 1989: no Characeae were present. In 1990: 1 ha.*

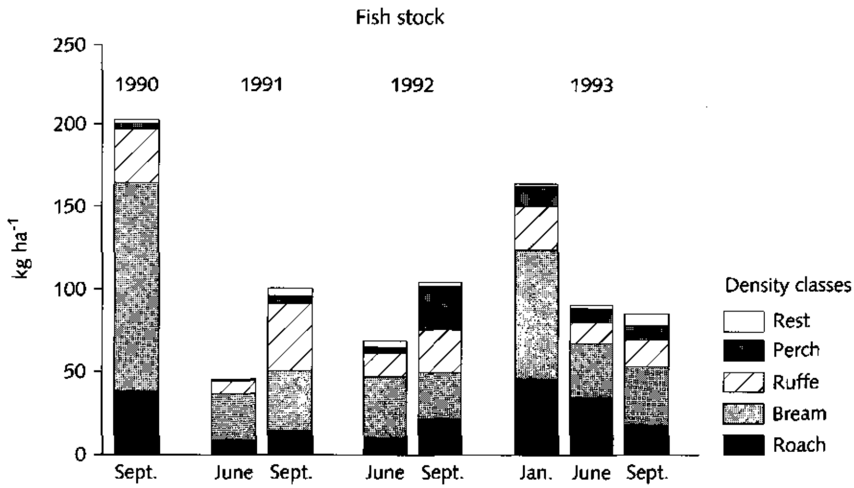

Figure 8.10: *Fish stock in 1990-1993. Drastic fishery was carried out from November 1990-June 1991. Additional fisheries took place from January-May 1992 and February-August 1993.*

Jeppesen *et al.*, 1990a, Chapter 6; Van Berkum *et al.*, 1995, Philips & Moss, 1994). Apart from the technical feasibility of the fish removal, in larger lakes factors such as wind-induced resuspension of sediments and the more difficult recolonisation by macrophytes, may reduce the chances for successful biomanipulation (Hosper & Meijer, 1993; Reynolds, 1994).

The results of 1991 showed that it was technically feasible to remove the bulk of the fish stock and to realise the objectives for planktivorous and benthivorous fish. In 1992 and 1993 the objective of the fish reduction was not achieved because the fish reduction started too late in the season. For optimal fish reduction the fishery should start in November at the latest (Perrow *et al.*, 1997) in order to spread the fishery over a longer period with more intervals without fisheries.

Wolderwijd cleared in spring 1991, demonstrating that attainment of clear water is possible in a large and shallow lake. This was also shown in the large Lake Christina (1650 ha; Hanson & Butler, 1994), Finjasjön (950 ha; Annadotter, 1993) and Sätofta Bay of Ringsjön (400 ha; Hamrin, 1993). Apparently, in Wolderwijd the impact of wind-induced resuspension on turbidity is not as dominant as in other large lakes in the Netherlands, such as Lake Breukeleveen, where biomanipulation was not successful (Van Donk *et al.*, 1990b, 1994). Based on results of biomanipulation in smaller lakes, it was expected that the reduction of benthivorous fish would lead to a reduction of the resuspension of sediment (Chapter 5; Breukelaar *et al.*, 1994; Van Berkum *et al.*, 1995). However, the original biomass of benthivorous fish in Wolderwijd (90 kg ha^{-1}) was low as compared to the biomass in the small lakes (300-450 kg ha^{-1}) (Chapter 5). This explains why no significant decrease in inorganic suspended solids was found after the fish reduction in Wolderwijd.

In this discussion attention will be focused at the dynamics of *Daphnia*, the role of predation by piscivorous fish, the development of Characeae and the high transparency of the water above the Characeae.

Daphnia grazing

In most biomanipulation case studies the reduction of the fish stock led to an increase in large-bodied *Daphnia* in spring (Van Donk *et al.*, 1990a; Faafeng & Braband, 1990; Hanson & Butler, 1994; Chapter 6). However, in Wolderwijd no change in *Daphnia* species, nor a significant difference in length or density was found in the *Daphnia* population in that important period. Nevertheless, the obtained clear water period, coincided with high *Daphnia* densities. Possible explanations for the minor difference in *Daphnia* length and density between 1989 and 1991 are food limitation of *Daphnia* in 1991 and a non-representative sampling of *Daphnia*. Food limitation is indicated by the extremely low chlorophyll-*a* levels and the low fecundity of the *Daphnia* (< 2 eggs ind^{-1} adult *Daphnia*) (Taylor, 1985), during the clear water phase. In that period also the grazing exceeded two to eight times the primary production (Meijer *et al.*, 1994b). Another option is that large *Daphnia* were underestimated during sampling, because they might have been concentrated near the bottom during the clear water period, as was shown in enclosure experiments in Denmark (Schriver *et al.*, 1995).

Apart from the high *Daphnia* peak during the clear water phase, also other factors contributed to the low algal biomass and high transparency in May-June 1991, such as the long period with ice-cover in February 1991 (28 days), the intensified flushing and the low phosphorus concentration. However, in earlier years with a long ice-cover (1979, 1982, 1985 and 1987) or flushing (1981-1983), but without fish reduction, no large increase of transparency was observed in May-June (Figure 8.5). Each year *Daphnia* was absent from July onwards and the algal biomass increased. Considering the summer chlorophyll-*a* levels, food limitation is out of the question and therefore predation by Y-O-Y fish (perch and bream) and invertebrates, such as *Neomysis*, is the most likely explanation for the absence of *Daphnia* during the summer. Unfortunately, due to the minor differences in zooplankton biomass between the years and the few fish data (only 4 years), we are not able to demonstrate a correlation between the density of planktivorous fish and *Daphnia*.

In summer 1991 and 1993 high densities of *Neomysis* were found. An earlier paper stressed the importance of *Neomysis* for predation on *Daphnia* in 1991 (Meijer *et al.*, 1994b). Recent results, however, indicate that in periods with very high densities the biomass of *Neomysis* was formed for 60 % by juveniles, which do not consume *Daphnia* (Siegfried & Kopache, 1980). Therefore, in that period *Neomysis* probably consumed 8 % of the biomass of *Daphnia* per day, compared to 20 % mentioned earlier (Meijer *et al.*, 1994b). Consequently the total predation pressure decreases from 26 % to 14 % of the *Daphnia* biomass per day, which is still in the range of the daily production of *Daphnia*.

Role of piscivorous fish

The increase of the fish biomass in summer was mainly caused by the production of Y-O-Y of perch and ruffe. The biomass of Y-O-Y of bream and roach was relatively low. Also the share of piscivorous fish was very low. A survey of 300 Danish lakes indicated that at total-P levels of 0.07-0.10 mg l^{-1}, a stable situation with a high percentage of piscivorous fish (30 %) is possible (Jeppesen *et al.*, 1990b). However, in Wolderwijd with total-P of 0.07-0.09 mg l^{-1}, the proportion of piscivorous fish only increased from 2.5 % in 1990 to 5-8 % in 1991-1993. The biomass of pike was low, probably because of the lack of suitable habitat, such as emergent and submerged vegetation (Grimm & Backx, 1990). In the Danish lakes the piscivorous fish population is mainly composed of perch. In Wolderwijd the biomass of piscivorous perch has slightly increased, but is still quite low (6 kg ha^{-1}). According to Persson (1994), perch can only become important if the phosphorus load is low and macrophytes are abundant. In most of the Danish lakes with a high percentage of piscivorous fish also the coverage of macrophytes was high. Possibly, in Wolderwijd not the nutrient levels, but the limited abundance of submerged and emergent vegetation restrict the development of pike and perch. Therefore, on the short term we do not expect these predators to be able to control the planktivorous fish. Besides, there is hardly any evidence from the field, that demonstrates the role of pike as a regulator of the food web in lakes. In Finjasjön the pike biomass is also quite low (about 3 kg ha^{-1}) and as in Wolderwijd the perch was mainly small and planktivorous (Annadotter, 1993). Even in biomanipulation experiments in small lakes with higher biomasses of pike, the pike was not able to control the production of planktivorous fish after the fish reduction (Chapter 6 and 7). This is partly caused by the lack of emergent vegetation but also by the higher nutrient levels and thus a higher production of planktivorous fish in those small lakes (Klinge *et al.*, 1995). Only in Lake Noorddiep with a more varied vegetation and a pike stock which was already present before the measures, some control of planktivores by piscivores occurred (Chapter 7). Apart from fish removal also measures should be taken to reduce the spawning success of the cyprinids by removal of eggs after spawning on artificial spawning substrate or the removal of fish from the spawning grounds (Perrow *et al.*, 1997; Grimm & Backx, 1994).

Despite the high biomasses of planktivores in Lake Zwemlust en Bleiswijkse Zoom, the water in these small lakes remained clear during summer, due to the abundant macrophyte growth (Van Donk *et al.*, 1990a, Chapter 6).

Development of Characeae

In Wolderwijd no increase in the total area covered by macrophytes was found, but a shift from *Potamogeton* species to Characeae occurred. *Chara* is known to react to increased water transparency and these species are particularly able to persist in large, shallow wind-exposed lakes (Blindow, 1992; Blindow *et al.*, 1993). In Wolderwijd the area covered by Characeae increased from 28 ha in 1991 to 438 ha in 1993. Probably, the availability of oospores limited the colonisation by *Chara* in 1991. Experiments in 1993 showed a marked response after the introduction of oospores or plants (Stam, unpubl. data). The density of the oospores appears to be high inside the vegetated areas, but drops sharply with increasing distance from the *Chara* meadows: at a distance of > 100 m the density if 10-100 fold lower than inside the meadows (Stam, unpubl. data). It is likely that the probability of a dense canopy of *Chara* is highest on sites with a high spore density (Van den Berg, 1999). Given the limited temporal window for establishment (the clear water phase in spring), expansion of the meadows can therefore only occur along the borders of the existing area. The expansion rate will probably increase with a higher availability of light. As soon as a reasonable area of *Chara* is present, *Chara* itself creates a high transparency of the water column (Van den Berg, 1999; Blindow, 1991; Blindow *et al.*, 1993).

Macrophytes and high transparency

In Wolderwijd, high transparency is restricted to the water column above the *Chara* vegetation. In smaller lakes the presence of macrophytes over at least 50 % of the surface area was sufficient to keep the water clear, also in areas without macrophytes (Chapter 6). Obviously, in Wolderwijd the mechanisms causing clear water are limited to the vegetated locations. It is quite difficult to identify the key mechanisms that cause the differences in transparency observed. Many mechanisms may interact and this multiple causality prevents a simple sorting out of hypotheses (Scheffer & Beets, 1994). Possible mechanisms include: macrophytes reduce resuspension of bottom material and increase sedimentation of suspended matter (James & Barko, 1990; Petticrew & Kalff, 1992); macrophytes can act as refuge for zooplankton (Timms & Moss, 1984); macrophytes can reduce algal growth by nutrient competition (Ozimek *et al.*, 1990) or by allelopathy in particular by Characeae (Hootsmans & Blindow, 1993) and macrophytes may stimulate the development of small herbivorous organisms living among plants such as bryozoans and protozoans. In smaller lakes (with less wind resuspension) the water stayed clear in the presence of macrophytes like *Potamogeton pectinatus* (Bleiswijkse Zoom), *Elodea nutalli* or *Ceratophyllum demersum* (Zwemlust), Characeae (Duinigermeer), *Ceratophyllum demersum* and *Nuphar lutea* (Noorddiep). For Lake Zwemlust competition for nitrogen between macrophytes and algae, seems the most likely explanation for the low algal biomass in the presence of macrophytes (Van Donk *et al.*, 1993). Also in the Bleiswijkse Zoom and Noorddiep a decrease in nitrogen is found at the moment that the macrophytes become abundant (Chapter 6). However in those small lakes, the processes which keep the water clear are not necessarily the same as in the large and wind-exposed Wolderwijd. In the large Lake Krankesjön (Sweden, 3200 ha) a decrease of the water level resulted in an abundance of Characeae followed by an increase in transparency (Blindow *et al.*, 1993). Here increased sedimentation and reduced availability of phosphorus may have contributed to the high transparency (Blindow *et al.*, 1993). In Wolderwijd there is no evidence for a lower availability of phosphorus within the vegetation. In Lake Christina (USA, 1600 ha), the fish stock reduction also led to an increase in macrophytes. In the first two years only a spring clear water phase was obtained, but in the third year macrophytes kept the water clear. An increased net sedimentation was suggested as one of the reasons for the clear water above the macrophytes (Hanson & Butler, 1990; 1994). As in Wolderwijd the vegetated areas in this Minnesota lake show a higher transparency than the areas without vegetation.

The clear water in Wolderwijd occurred especially in the areas covered by Characeae, while in the parts with *Potamogeton pectinatus* or *P. perfoliatus* the water was turbid. The reason for this difference may stem from the canopy structure of the plants. The canopy of Characeae covers the lake bottom completely, whereas the *Potamogeton* species leave a lot of open spaces. Monitoring in 1994 showed that during high wind speeds the water above the Characeae became turbid. After a storm the water cleared within one day, indicating that increased net sedimentation within the *Chara* meadows may explain the difference in transparency.

CONCLUSIONS

This case study showed that in large and shallow lakes drastic fish stock reduction may lead to clear water. However, in Wolderwijd this was limited in time and space. The open water area was clear only during the *Daphnia* spring peak. The limited period of clear water stimulated the expansion of Characeae. In the area with Characeae the water stayed clear as long as plants were present. In the current situation, with the lack of spawning and hiding places the abundance of piscivores will probably remain too low to control the production of planktivores. Therefore, a prolonging of the presence of *Daphnia* throughout the summer cannot be expected. The most promising way to achieve a shift from the turbid water state into the clear water state will be the expansion of the area with a dense *Chara* vegetation. Above the *Chara* plants the water remains clear, probably due to increased net sedimentation. To stimulate *Chara*, spring clear water periods are necessary. For that reason, the lake manager is recommended to continue the fish stock reductions. The fish removal should be substantial in order to get a spring clear water phase. Additionally, removal of eggs of cyprinids after the spawning, may lower the production of planktivores. Moreover, the nutrient load should be reduced further in order to get a lower production of planktivorous fish and less problems with cyanobacteria. On the short term the best obtainable situation is a period with clear water in spring and locally large areas with clear water above the Characeae.

ACKNOWLEDGEMENTS

We thank the commercial fishermen, the angling clubs and Map Grimm and Joost Backx of Witteveen+Bos Consulting Engineers for the fruitful co-operation. Without them this project would have been impossible. Rijkswaterstaat-Directorate IJsselmeergebied, the lake manager, did the time-consuming organisation of the fisheries and a great deal of the sampling and analysis. Valuable contributions to the project came from Kees Bruning of AquaSense, Ramesh Gulati of the NIE-Centre for Limnology and our colleagues from the RIZA Lake Restoration Research Programme. Thanks are due to Eddy Lammens, Carolien Breukers, Thea Helmerhorst and Hugo Coops for comments on and contributions to the manuscript. Wim Stam is thanked for the data on the oospores and Marcel van de Berg and Roel Doef for the data on Characeae.

BOX 2. A LAKE WOLDERWIJD FROM 1993 ONWARDS IN COMPARISON WITH THE ADJACENT LAKE VELUWE

From 1993 onwards the *Chara* expansion continued in the lake. Until 1995 the Secchi depth remained relatively low, but in accordance with the conclusions of this chapter (which were drawn in 1995) further expansion of the *Chara* did lead to an increase of the water clarity also outside the *Chara* meadows. *Chara* expanded from 470 ha (17% of the lake area) in 1993 to 1300 ha (43 % of the lake area) in 1998 and from 1995 onwards the Secchi depth outside the *Chara* meadows increased (Figure 8.11, Meijer *et al.*, 1999).

This increase of the Secchi depth in relation to the expansion of *Chara* appeared even stronger in the adjacent Lake Veluwe (Figure 8.11). In both lakes the higher transparency from 1995 onwards is caused by a reduction in resuspended sediment and algal biomass. The chlorophyll-*a* concentration decreased from 40 μg l in 1993 to 6-10 μg l in 1996-1998. In Lake Wolderwijd the Secchi depth decreased again in 1998.This was not caused by a higher algal biomass, but presumably by disturbance of the bottom sediment by dredging of the shipping canal near the sampling point.

In Lake Veluwe *Chara* covers a larger part of the lake and the higher transparency seems more stable than in Lake Wolderwijd. A regression model suggested that the whole lake is likely to have a Secchi depth of more than 1 m (the goal of lake restoration in Dutch shallow lakes), if more than 70% of the lake is covered with *Chara* (Meijer *et al.*, 1999).

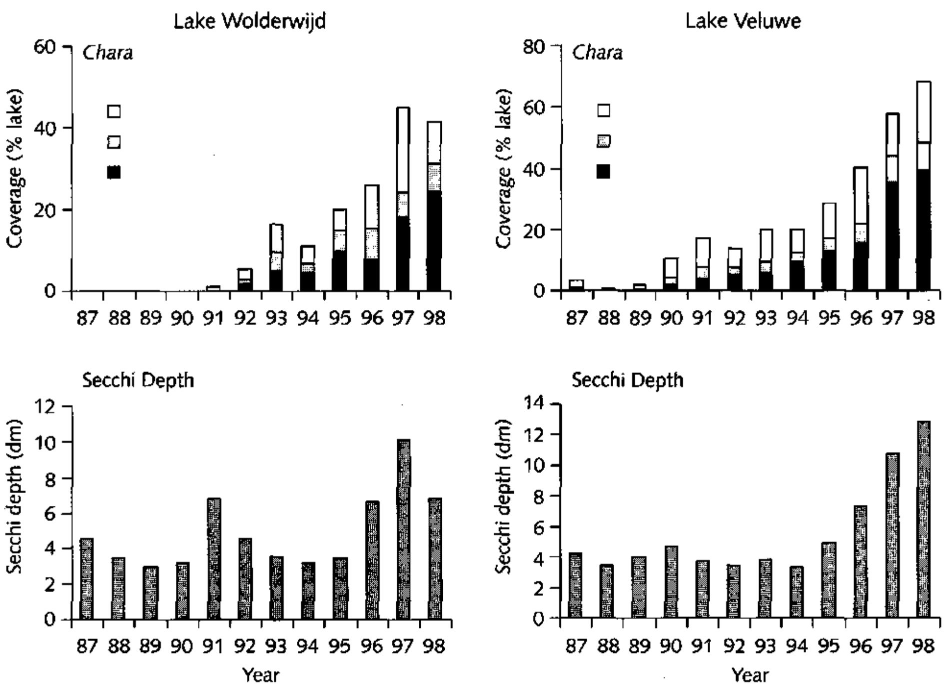

Figure 8.11: *Summer average Secchi depth and areal coverage of the lake with different densities of Chara vegetation for Lake Wolderwijd and the adjacent Lake Veluwe (adapted from Van den Berg, 1999).*

With the expansion of Charophytes the system changed. In addition to the changes in transparency, the P-concentration decreased, the cyanobacteria *Planktothrix agardhii* disappeared, zebramussels returned to the lake, and bream became less abundant (Meijer *et al.*, 1999). All of these changes in the ecosystem may be expected to have contributed to the increase in transparency. The lower biomass of large bream reduced the resuspension of the sediment. The decrease of the P-concentration has reduced algal production. The disappearance of *Planktothrix* caused the chlorophyll-a- concentrations to decrease, as other algae are less efficient in taken up the phosphorus and the mussels help filtering algae from the water. The combination of these mechanisms is thought to have moved the system towards a stable clear water state.

In this chapter (written in 1995) it was concluded that in Lake Wolderwijd additional fishery might be required to get a further expansion of the *Chara*. However, there has been no drastic fish removal from 1993 onwards. Nonetheless, (the fish biomass decreased from 85 kg ha^{-1} in 1993 to 50 kg ha^{-1} in 1998 (Figure 8.12) and the biomass of bream became less than 20 kg ha^{-1}. In Lake Veluwe from 1975 onwards professional fisherman removed about 15 kg ha^{-1} of large bream and roach each year However, from 1993 onwards this fish removal was extended to a removal of 40 kg ha^{-1} each year. The fish biomass decreased from 150 kg/ha in 1992 to 40 kg ha^{-1} in 1998. This may well have accelerated the expansion of *Chara*. Importantly, the *Chara*

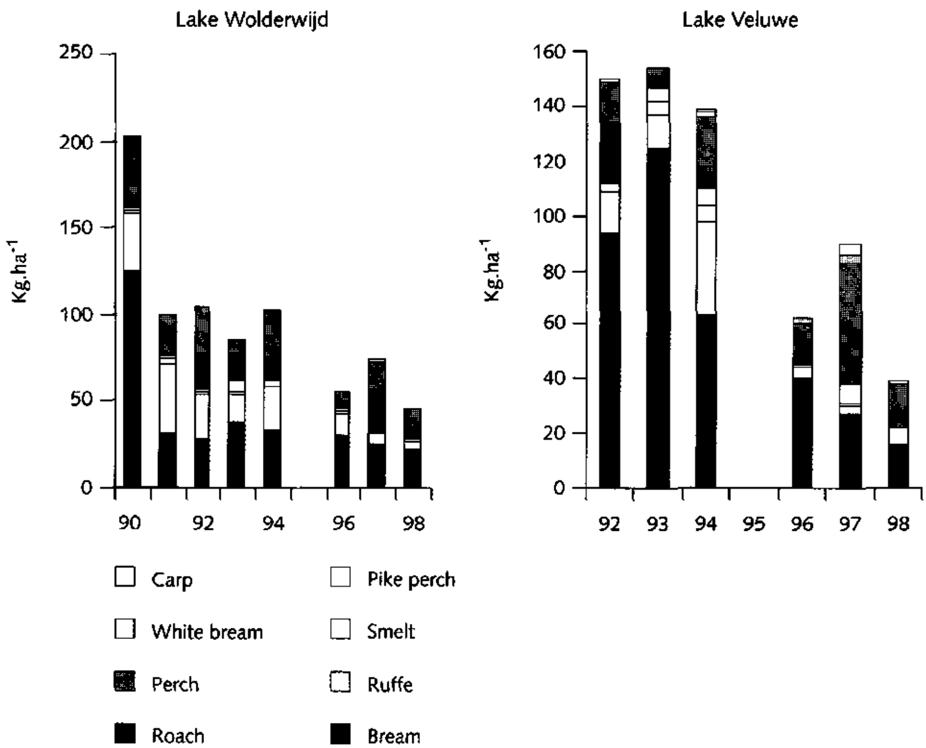

Figure 8.12: *Development of the fish stock in Lake Wolderwijd and Lake Veluwe from 1990-1998.*

expansion in both lakes is likely to have reduced the regrowth of bream as these fish can not forage in the densly vegetated areas.

Historic data showed that the shift from the clear water state to the turbid water state in the 1960's and the recent shift back towards the clear water state showed a hysteresis pattern (Figure 8.13). In Lake Veluwe the clear water state ended when the *Chara* population collapsed at a total phosphorus concentration of about 0.15 mg P l^{-1}. The turbid state lasted for about 20 years and the recovery of the clear water state (first only locally, later in the whole lake) did not start until the total P-concentration dropped below 0.10 mg P l^{-1}. At this level the algal biomass was low enough to create a light climate sufficient for the re-colonisation of *Chara* in the shallow areas of the lakes. The *Chara* expansion initiated a further reduction of the total phosphorus concentration. Because Lake Veluwemeer and Lake Wolderwijd have shallow areas the colonisation could start at relatively low Secchi depth. Due to the large scale of the lakes and the lack of propagules the expansion of *Chara* went gradually.

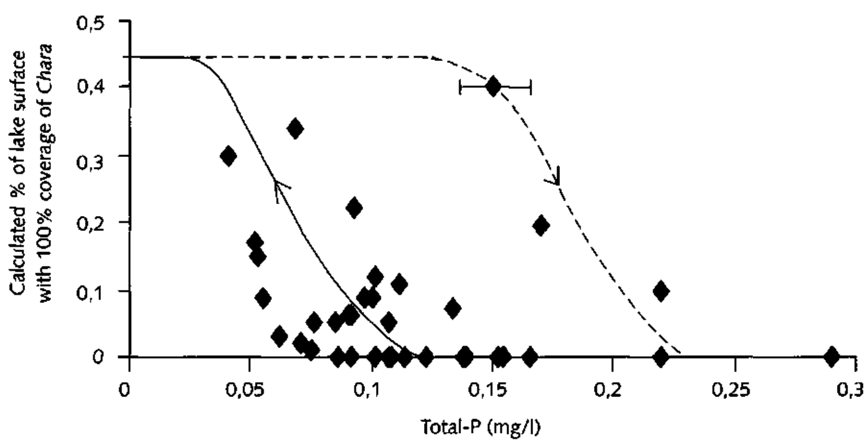

Figure 8.13: *Fall and rise of Charophytes in relation to the summer average total P-concentration. In Lake Veluwe and Lake Wolderwijd. The figure shows a typical hysteresis pattern. A calculated coverage of Chara is used. An areal coverage of 70 % of the lake with an average plant-density of 50 % gives a calculated full coverage of 35 %.*

In both lakes the reduction of the P-loading formed the basis of the recovery processes, which has taken over 20 years. In Lake Wolderwijd biomanipulation did probably speed up the restoration process by reducing the P-concentration and by initiating the development of *Chara*. In Lake Veluwe the extra fish removal by the professional fisherman since 1993 may have helped the restoration process.

Obviously, although it is likely that in both lakes the reduction of the fish stock have accelerated the restoration process, it is not clear what would have happened without the fish reductions.

CHAPTER 9

BIOMANIPULATION IN SHALLOW LAKES IN THE NETHERLANDS:

AN EVALUATION OF 18 CASE STUDIES

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BIOMANIPULATION IN SHALLOW LAKES IN THE NETHERLANDS:

AN EVALUATION OF 18 CASE STUDIES

SUMMARY

Eighteen shallow lakes in the Netherlands were subjected to biomanipulation, *i.e.* drastic reduction of the fish stock, for the purpose of lake restoration. The morphology and the nutrient level of the lakes differed, as did the measures applied. In some lakes biomanipulation was accompanied by reduction of the phosphorus loading. In all but two lakes, the Secchi disk transparency increased after the fish removal. Eight lakes (no phosphorus loading reduction, except for one lake) showed a strong and quick response to the measures: the bottom of the lake became visible ("lake-bottom view") and there was a massive development of submerged macrophytes. In eight other lakes the water transparency increased, but lake-bottom view was not obtained. In the biomanipulated lakes the decrease in total phosphorus and chlorophyll-*a* and the increase in Secchi disk transparency were significantly stronger than the general trend occurring in Dutch lakes where no measures had been taken. The improvement in the Secchi depth and chlorophyll-*a* was also stronger than in lakes where only the phosphorus loading was reduced.

The critical factor for obtaining clear water was the extent of the fish reduction in winter. Significant effects were observed only after > 75 % fish reduction. Success seems to require substantial fish manipulation. In such strongly biomanipulated lakes, wind resuspension of the sediment never prevented the water from becoming clear. No conclusion can be drawn with respect to the possible negative impact of cyanobacteria or *Neomysis* on grazing by *Daphnia* and consequently on water clarity. In all lakes where there had been a high density of cyanobacteria or years with a high density of *Neomysis* other factors such as insufficient fishery may explain why lake bottom view was not obtained. In all lakes with additional phosphorus loading reduction the fish stock has been reduced less drastically (15-60 %). In these lakes the effects on transparency were less pronounced than in the lakes with > 75 % fish removal.

Daphnia grazing seems responsible for spring clearing in all clear lakes but one. In three lakes the reduction of benthivorous fish also increased the transparency. The factors that determine water clarity in summer are less obvious. In most clear lakes a low algal biomass coincided with a macrophyte coverage of more than 25 % of the lake surface area. However, it was not clear what mechanism caused the low algal biomass in summer, although inorganic nitrogen concentrations were regularly found to be very low. *Daphnia* grazing in open water seemed to be of little

importance for suppressing the algal biomass in summer. Although in most lakes the total phosphorus concentration decreased after the biomanipulation, the dissolved phosphorus concentration remained too high to cause phosphorus limitation of the algal growth. In four out of six clear lakes for which there are long-term data the transparency decreased again after 4 years. In one lake with lower nutrient levels the Secchi disk transparency increased over the years. However, the number of lakes with low nutrient levels is too small for conclusions to be drawn regarding the impact of nutrient levels on the stability of the clear water state.

INTRODUCTION

Biomanipulation as a possible method of lake restoration was introduced by Shapiro in 1975 (Shapiro *et al.*, 1975). It is only in the past ten years that the technique of biomanipulation has become more generally applied in water quality management (Chapter 6; Carpenter & Kitchell, 1993; Philips & Moss, 1994; Van Berkum *et al.*, 1995; Hosper, 1997; Perrow *et al.*, 1997; Jeppesen, 1998; Hansson *et al.*, 1998). The first experiments with biomanipulation were performed in relatively deep lakes (Benndorf *et al*, 1984; Carpenter & Kitchell, 1993) and were concerned with the removal of all fish with rotenon or with stocking of predatory fish (Henrickson *et al*, 1980; Shapiro & Wright, 1984; Benndorf *et al.*, 1988). In the Netherlands, biomanipulation measures usually involve the substantial reduction of planktivorous and benthivorous fish in shallow lakes. A reduction of the overwintering planktivorous fish stock cause large filter-feeding zooplankton to exert a higher grazing pressure on phytoplankton, thus forcing a spring clear-water phase. Reduction of benthivorous fish further supports the clearing of the lake, as the resuspending of the sediment and the release of nutrients in the water due to these bottom-feeders will be reduced (Breukelaar *et al.*, 1994; Havens, 1993). Clear water during spring allows the submerged vegetation to grow and creates a sustainable clear water state. Stocking of lakes with pike fingerlings (*Esox lucius L.*) may help to reduce the young-of-the-year fish during summer. In the Netherlands, the first biomanipulation experiments were conducted in 1986 in small drainable ponds of 0.1 ha, where the impact of 0+ fish on zooplankton was investigated (Chapter 3). Since 1987 experiments have also been carried out in natural lakes and ponds (Chapter 4; Van Donk *et al.*, 1990; Driessen *et al.*, 1993; Van der Vlugt *et al.*, 1992). Later, guidelines were formulated for the assessment of chances for clear water and macrophytes, based on the results of nine biomanipulation cases (Hosper & Meijer, 1993). Five out of these nine cases were successful: in those five lakes biomanipulation led to clear water and a rich submerged vegetation (Hosper, 1997). Several factors may prejudice successful biomanipulation in the other cases: insufficient fish reduction, wind-induced resuspension, inedible cyanobacteria and predation of *Daphnia* by invertebrates (Hosper & Meijer, 1993; Hosper, 1997).

The number of projects involving biomanipulation, whether or not accompanied by P load reduction, has increased considerably during the past ten years. In this paper we evaluate the results of 18 cases, which differ in morphology, nutrient level and the measures applied. We compare the effect of biomanipulation with the effects of phosphorus loading reduction in Dutch lakes.

Furthermore the following questions will be discussed: (i) How does successful biomanipulation work? (ii) Can we explain the lack of success in other lakes? and (iii) What factors determine the long-term stability of clear water?

SITES STUDIED

The 18 lakes subjected to biomanipulation differ in morphology (surface area, sediment type, shape, degree of isolation), nutrient level and in the measures applied (extent of fish reduction, number of times fish reduction was applied and possible extra phosphorus reduction measures) (Table 9.1). The surface area ranges from 1.5 to > 2000 ha. All lakes have an average depth of < 2.5 m and the lakes range from eutrophic to hypertrophic. Before the measures the summer average total-P concentration in all lakes was higher than 0.1 mg P l^{-1}. Besides fish reduction, phosphorus load reduction in the form of dredging or the addition of $FeCl_3$ to the water inlet was applied to 6 of the 18 lakes. In four lakes at least three different measures were taken (Table 9.1). More details on measures and lake characteristics can be found in the papers on each of the projects (references are given in Table 9.1). In only nine lakes was the aim of a 75 % reduction in the original fish stock and no fish immigration achieved. In all other lakes the fish reduction was less drastic, due to insufficient time or money, immigration of fish through malfunctioning fish barriers, fish nets with too large mesh size, or high stock of small fish in adjoining small waters that re-entered the lake after the fish reduction. In eight lakes one single fish reduction procedure was carried out; in the other lakes additional fish reductions were applied in the following years (Table 9.1).

METHODS

Zooplankton

The potential impact of zooplankton grazing on algae is determined by the potential grazing pressure (PGP), calculated as the ratio of *Daphnia* biomass to algal biomass, on the assumption that *Daphnia* can consume its own biomass per day (Schriver *et al.*, 1995). The algal biomass was calculated from a carbon/chlorophyll-*a* ratio of 0.07 mg C μg^{-1} chlorophyll-*a*. The *Daphnia* biomass W (mg C) was calculated as $\ln(W) = 2.46 + 2.52 \ln(L)$ (Bottrell *et al.*, 1976), L being the length in mm.

In six lakes the length of *Daphnia* was measured, in other lakes only data on the species composition of *Daphnia* were available. Here, the following average lengths per species were assumed: *Daphnia* magna (2.75 mm), *Daphnia cucculata* (0.8 mm), *Daphnia longispina/pulex* (1.5 mm), *Daphnia hyalina/galeata* (1.0 mm). Although Schriver *et al.* (1995) used the total biomass of *Daphnia* and *Bosmina*, we used only the biomass of *Daphnia*, because in the observed lakes the potential grazing pressure of *Bosmina* and copepods was negligible compared to that of *Daphnia* (Meijer & de Boois,

Table 9.1: *Lake characteristics.*

Lake	Surface area (ha)	Depth (m)	Soil type	Year of bioman	Total P before (mgl^{-1})	% fish reduction first year	Other measures	Bottom view	References
Bleiswijkse Zoom; Galgje	3	1.1	clay	1987	0.25	84[1]		+	chapter 4, 5, 6, 7
Boschkreek	3	2.0	sand	1993	0.7	52[1]	d, p		Van Scheppingen (1997; 1998)
Breukeleveense Plas	180	1.5	peat	1989	0.1	62*			Van Donk *et al.* (1990b)
Deelen	45-65	1.0	peat	1994	0.25	15-28	p		Claassen (1994)
Duinigermeer	30	1.0	peat	1994	0.11	77[1]		+	Van Berkum *et al.* (1995)
Hollands Ankeveense Plas	92	1.3	peat	1989	0.13	60[1]	d, p		Scheffer-Ligtermoet (1997)
Klein Vogelenzang	11	1.5	peat	1989	0.35	26[1]			Van der Vlugt *et al.* (1992)
Nannewijd	100	1.0	peat	1995	0.39	82 **	d, p	+/-	Veeningen (1997); Claassen (1997)
Noorddiep 3	4.5	1.5	clay	1988	0.22	79		+	Van Berkum *et al.* (1996); chapter 5, 6, 7;
Oude Venen; 40-Med	10	1.4	peat	1991	0.44	45[1]	d, i		Claassen & Maasdam (1995)
Oude Venen; Izakswijd	26	1.5	peat	1991	0.23	76	i		Claassen & Maasdam (1995)
Oude Venen; Tusken Sleatten	11	0.8	peat	1991	0.23	451	i		Claassen & Maasdam (1995)
Sondelerleien	27	1.0	clay	1991	0.29	93*[1]			Claassen & Clewits (1995)
Waay	4	2.5	clay	1994	0.11	79[1]		+	Barten (unpubl.)
Wolderwijd	2650	1.5	sand	1991	0.13	77[1]	f	+	Meijer *et al.* (1994b); chapter 8
IJzeren Man	11	2.2	sand	1991	0.27	100		+	Driessen *et al.* (1993)
Zuidlaardermeer	75	1.0	sand	1996	0.29	80	p	+	Torenbeek & De Vries (1997)
Zwemlust	1.5	1.5	clay	1987	1.2	100	p	+	Van Donk *et al.* (1989, 1990a, 1993); Van Donk & Gulati (1995), Van Donk & Otten, (1996); Van Donk, (1997)

Legend

*	fish migrated into the lake directly after biomanipulation		
**	only large fish, percentage removal of small fish is unknown, total fish removal < 75 %		
1	additional fish removal in later years		
d	dredging	f	flushing
i	isolation	p	reduction external phosphorus load.

Because of expected differences between spring and summer, we considered the periods May-June and July-September separately. In the Netherlands the highest *Daphnia* density and the highest transparency are generally found in May-June.

Macrophytes

The abundance of macrophytes was calculated as the percentage of the surface area of the lake covered with macrophytes. Very sparse vegetation with a density of < 15 % as not been taken into account. No data were available on the biomass of the macrophytes nor on the volume of the water column infested with macrophytes. A survey of macrophytes is generally carried out once a year in July-August, and therefore no distinction can be made between spring and summer.

Fish

Long-term quantitative data on fish biomass and species composition were available for only six lakes. In this paper the data on total fish biomass, percentage of piscivorous fish and biomass of 0+ fish are presented. In Noorddiep, Galgje and Zwemlust the fish biomass was estimated in December/January with a mark-recapture method (Chapter 7). In Lake Waay, Wolderwijd and Duinigermeer the biomass was estimated with a catch per unit effort method in September/October (Grimm & Backx, 1994).
Perch > 0+ and all pike and pike-perch were assumed to be predatory fish. The biomass of 0+ fish is based on the estimation of the young-of-the-year (YOY) fish at the end of the growing season (in September or December).

Trend analysis

Trends for biomanipulation cases were compared with the general development in the water quality in 160 lakes where no measures were taken. Also trends in lakes in which specific phosphorus reduction measures had been taken but no biomanipulation had been applied, were compared with the general trend (Portielje & van der Molen, 1999).
Trend analysis was performed for lakes for which there were at least 8 years of data. The Mann-Kendall test was used for the trend analysis. In this non-parametric test the trend is estimated by the median of the set of the slopes (Theil slope estimator, Theil, 1950; KIWA, 1994) that are calculated from all possible pair-wise combinations of the summer mean concentrations. An effect of measures can be calculated if data are available for at least two years before and two years after the measures. The instantaneous effect of a measure is thus incorporated in the calculated trend. Sufficient data were available from eight biomanipulation cases (Figure 9.1). In Hollands Ankeveense Plas extra phosphorus reduction measures were taken, but they did not lead to a decrease in the phosphorus concentration in the lake in the observed period of biomanipulation.

The analysis was based on relative trends, where a relative trend was defined as the absolute trend divided by the historical means.

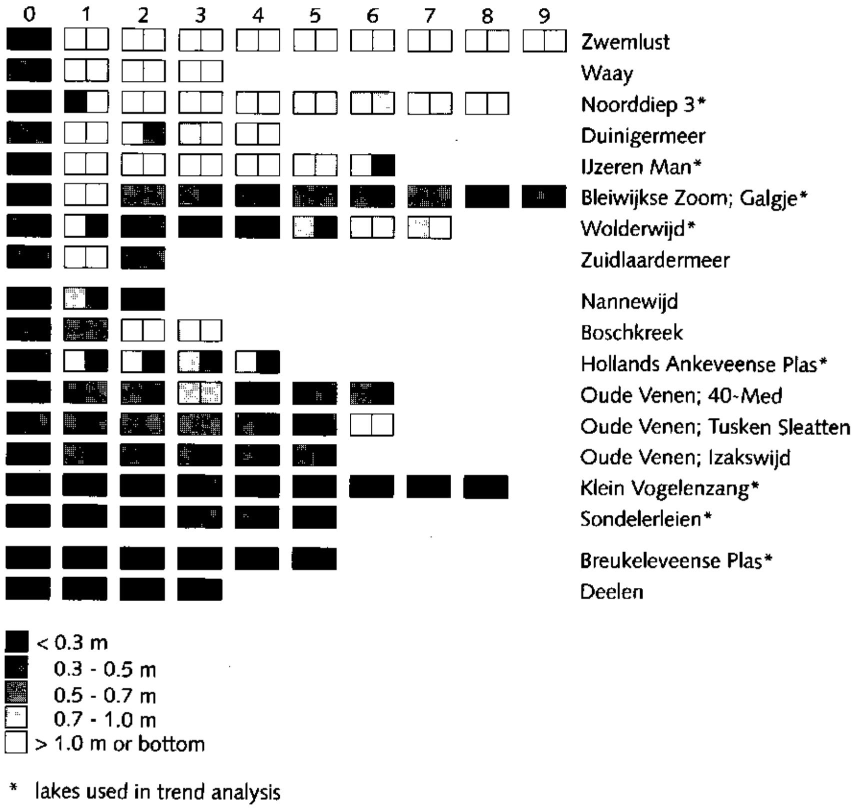

Figure 9.1: *Secchi depth in all lakes in years after biomanipulation (first square is average of May-June, second square is average of July-September).*

Table 9.2: *Average of Secchi-depth (summer mean) after the measures divided by the average Secchi-depth before the measures.*
Successful: > 1.3 & bottomview; Partially successful: > 1.3, no bottom view; Failures: < 1.3.

Lake	Improvement of Secchi-depth
Successful	
Zwemlust	9.4
Waay	2.6
Noorddiep 3	2.6
Duinigermeer	2.2
IJzeren Man	8.4
Bleiswijkse Zoom; Galgje	3.3
Wolderwijd	2.1
Zuidlaardermeer	1.6
Partially successful	
Nannewijd	1.6
Boschkreek	1.7
Hollands Ankeveense Plas	1.5
Oude Venen; 40-Med	2.5
Oude Venen; Tusken Sleatten	1.5
Oude Venen; Izakswijd	1.6
Klein Vogelenzang	1.4
Sondelerleien	1.4
Failures	
Breukeleveense Plas	1.1
Deelen	1.2

RESULTS

Transparency

In all but two lakes the Secchi depth improved after the measures. The extent of the improvement differed from lake to lake (Figure 9.1, Table 9.2). Before the measures the average Secchi depth was ca. 0.2-0.4 m. After the measures lake bottom view was achieved in eight lakes. In those lakes the biomanipulation was called successful. In five of these eight lakes, the bottom view was achieved in the spring directly after the fish removal. In the other lakes the process took several months to one year (Platform Ecologisch Herstel Meren, 1997). In Lake Wolderwijd in the first year the water remained clear only for about six weeks in May-June (Chapter 8), but six years later the Secchi depth remained high (> 1 m) during the summer. In most lakes with long-term data the average

Secchi depth starts to decrease after 3-4 years, with the exception of Lake Wolderwijd where the Secchi depth starts to increase after five years (Figure 9.2). In the lakes with lake bottom view the Secchi depth improved considerably (60-800 %). In eight other lakes the transparency improved also (40-150 %), but the lake bottom did not become visible. In those lakes the biomanipulation is called partially successful. The Secchi depth often reached 0.5-0.9 m in spring, but decreased in summer. In two lakes (Deelen and Breukeleveense Plas) there was no significant improvement in water transparency (improvement < 25 %) (Figure 9.1, Table 9.2).

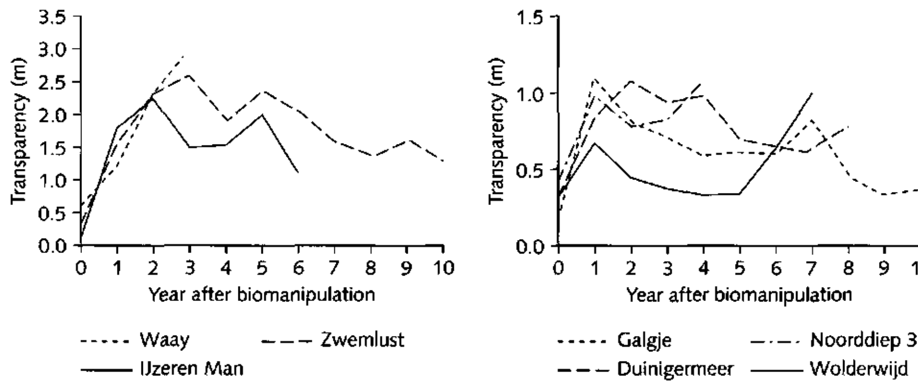

Figure 9.2: *Summer mean Secchi depth in seven successfully biomanipulated lakes.*

Chlorophyll-*a*

In 13 out of 18 lakes the chlorophyll-*a* concentration decreased (Figure 9.3). In lakes with bottom-view the summer average chlorophyll-*a* concentration generally became lower than 30 $\mu g\ l^{-1}$. In the lakes where the Secchi depth improved without lake bottom view the chlorophyll-*a* concentration was often low in spring (May-June) but increased from July onwards. In Klein Vogelenzang and Sondelerleijen the chlorophyll-*a* concentration remained quite high, despite improvement of the Secchi depth.

Daphnia

In general the *Daphnia* biomass increased slightly after the measures (Figure 9.3). In one lake (Noorddiep) there was a decrease of the *Daphnia* biomass (Chapter 6). However, the potential grazing pressure (PGP) became larger after the measures due to a simultaneous reduction in algal biomass in most lakes. The highest PGP was found in lakes with the highest Secchi depth (Figure 9.4). In all lakes with bottom view the PGP is high in May-June and decreases in July-September. Only in 3 out of 16 lakes with zooplankton data could a high PGP of *Daphnia* also be found in summer.

Both the chlorophyll-a: total-P ratio ($p < 0.01$) and the chlorophyll-a : total-N ratio ($p < 0.001$) were significantly lower at a PGP of *Daphnia* of > $1.0.d^{-1}$ compared to lower potential grazing pressures (Figure 9.5).

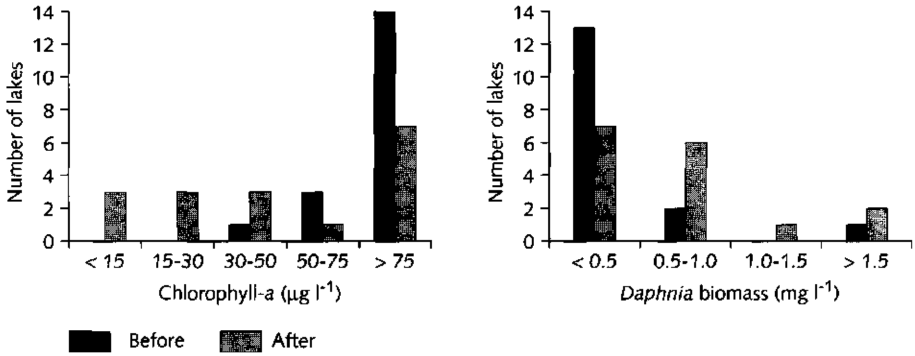

Figure 9.3: *Distribution of summer average chlorophyll-a concentration and summer average* Daphnia *biomass before and after the measures.*

Macrophytes

In all eight lakes with bottom view macrophytes developed. The colonisation by Characeae was very rapid. In three small lakes (Galgje, IJzeren Man, Duinigermeer) more than 70 % of each lake was colonised within two months. In the large Lake Wolderwijd it took 3 years for 40 % of the lake to become covered with dense vegetation. The species composition of the macrophytes changed from a dominance of *Potamogeton* sp. to a dominance of *Chara* sp. In Zwemlust and Noorddiep *Chara* hardly developed at all, but species like *Elodea* sp. and *Ceratophyllum* sp. colonized the lake more gradually (Figure 9.6). In Zuidlaardermeer the macrophytes developed during the first two years in very low densities (< 15 %). In the third year densities of more than 20 % were found at 80 % of the surface area. In Noorddiep submerged macrophytes developed only in the shallow part of the lake (ca. 45 % of the lake surface).

In the lakes without bottom view macrophytes occurred after the biomanipulation only in Hollands Ankeveense Plas (25 % of the lake surface area); in all other lakes macrophytes remained absent.

The chlorophyll-a : total-P ratio seems to be lower when > 25 % of the surface area of the lake is covered with macrophytes ($p < 0.001$). The chlorophyll-*a* : total-N ratio seems to become lower with decreasing abundance of macrophytes (Figure 9.7), as is found in a comparable analysis of a larger data set (Portielje & van der Molen, 1999). A strong decrease is found at a coverage of > 25 % (Figure 9.7) ($p < 0.001$).

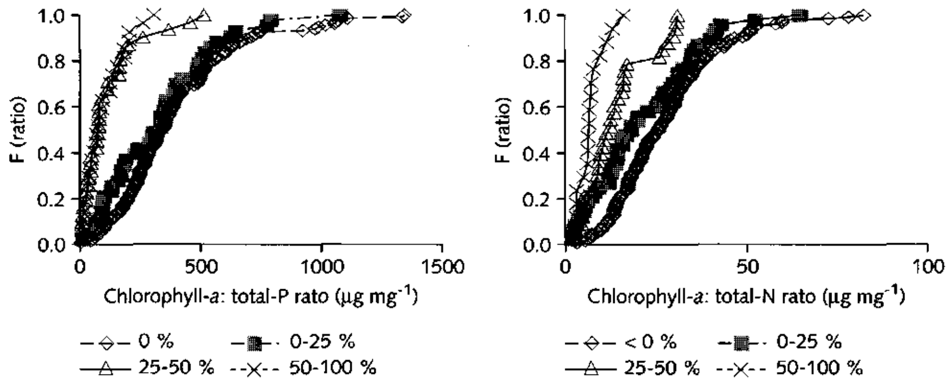

Figure 9.7: *Impact of a high coverage of macrophytes on the chlorophyll-*a *nutrients ratio. F(ratio) is the distribution function of the chlorophyll-*a*-nutrients ratio.*

Fish

In two out of six lakes with long-term fish data the fish biomass gradually decreased after the fish reduction (Waay, Wolderwijd), whereas in all other lakes the fish stock increased (Figure 9.8). In Zwemlust and Noorddiep the increase seemed to stabilise at a level of about half the original biomass.

The biomass of 0+ fish is high (> 100 kg ha^{-1}) in Zwemlust and Bleiswijkse Zoom/Galgje, and in the first year in the Waay. In the other lakes the biomass of Y-O-Y fish remains below 40 kg ha^{-1}. The biomass of 0+ fish seems to increase after the measures, whereas the benthivorous fish stock is reduced. The percentage of predatory fish is low in all lakes except in the first years in lake Zwemlust from which all fish had been removed and only pike and rudd had been stocked.

Trend analysis

In the biomanipulation cases a significantly stronger decrease in concentrations of phosphorus ($p < 0.05$) and chlorophyll-*a* ($p < 0.05$) and increase in Secchi depth ($p < 0.01$) was found compared to the general trend occurring in lakes where no specific measures had been taken (Figure 9.9). Although the total-N concentration decreased in most biomanipulation cases, the decrease was not significantly stronger (at $p < 0.1$) than the general trend. Lake-specific measures that reduced the phosphorus load led only to a significantly stronger decrease in the total-P concentration ($p < 0.01$) compared to the general trend, but not with respect to transparency, chlorophyll-*a* and total-N (Van der Molen & Portielje, 1999). Strong decreases in total-P were found in lakes with biomanipulation, whereas an additional P-reducing measure (dredging) was applied only in one biomanipulated lake.

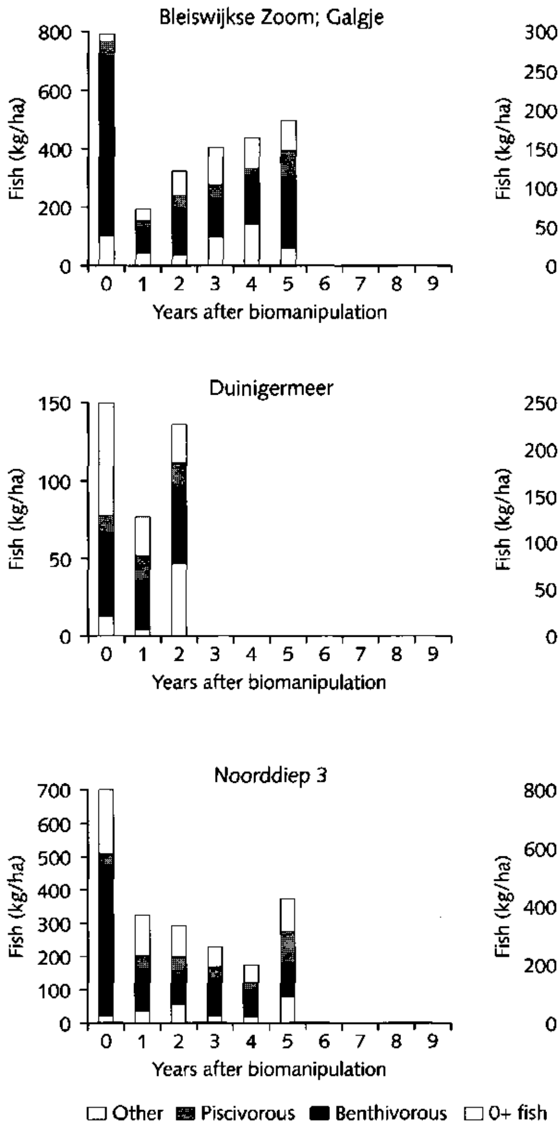

Figure 9.8: *Development of the fish community in six lakes.*

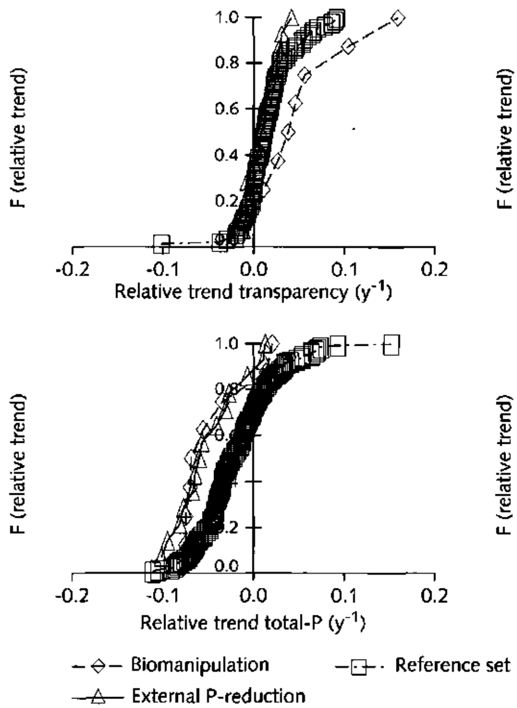

Figure 9.9: *Comparison of trends in Secchi depth, nutrients and chlorophyll-*a *between manipulated lakes (biomanipulation or reduction of the phosphorus load) and lakes without measures.*

DISCUSSION

How does successful biomanipulation work?

In all lakes with successful biomanipulation the algal biomass dropped to very low levels, leading to a strong increase in transparency. In only three lakes had benthivorous fish been a major cause of turbidity (Table 9.3). In those lakes more than 150 kg/ha of benthivorous fish had been removed, which led to a reduction in the resuspended sediment (Chapter 5; Havens, 1993). In the other lakes the benthivorous fish stock was relatively low before the measures.

In all successful cases the clear water in spring caused a drastic increase in macrophytes, which contributed to the persistence of high transparency.

In practice it is difficult to unravel the specific mechanisms involved in clearing the water, since several processes occur simultaneously, and data-sets are frequently not detailed enough to sort between the alternative hypotheses.

In spring the potential grazing pressure (PGP) of *Daphnia* was high in almost all clear lakes, indicating that *Daphnia* is an important initiator of the spring clearing of the water (Table 9.3). The biomass of *Daphnia* did not always increase after the measures, possibly because the food for *Daphnia* became limited when the algal biomass dropped to low levels. The PGP, however, is a better criterion than *Daphnia* biomass for determining the possible impact of *Daphnia* on algae. Also low dissolved nitrogen concentrations were found regularly in spring (Table 9.2). This suggests nitrogen limitation of the algal growth, but it is not conclusive because part of the nitrogen may have been recycled.

Table 8.3: *Mechanisms that keep the water clear.*

	May-June				July-September			
	benth. fish reduction > 150 kg ha^{-1}	**grazing press. > 1.0**	**diss. N < 0.1 mg l^{-1}**	**ortho P < 0.01 mg l^{-1}**	**grazing press. > 1.0**	**diss. N < 0.1 mg l^{-1}**	**ortho P < 0.01 mg l^{-1}**	**macrophytes > 25 %**
Zwemlust	●	○	○	●	●	◍	●	○
Waay		○	○	●	●	○	●	○
Noorddiep 3	○	◍	○	●	●	○	●	○
Duinigermeer	●	●	●	●	●	●	◍	○
IJzeren Man	○		○	●	●	◍	●	○
Bleisw. Z.; Galgje	○	○	○	●	●	◍	●	○
Zuidlaardermeer	●	◍	●	●	●	●	●	●
Wolderwijd	○	○	◍	●	●	○	●	◍

Legend:	○	◍	●	
benthivorous fish reduction > 150 kg ha^{-1}	yes		no	
for the other criteria	> 60	30-60	0-30	% of clear periods that the criterion is valid

Whereas *Daphnia* grazing is probably the most important mechanism causing clear water in spring, it is more difficult to determine the factors responsible for clear water in summer.

Macrophytes are considered to be important for keeping the water clear in summer. Macrophytes generally appeared quite rapidly after the clearing of the lake. Only in lake Zuidlaardermeer, the Waay and Lake Wolderwijd did it take three years to get a substantial macrophyte growth. Our results show a strong reduction in the chlorophyll-a : nutrients ratio at a coverage of > 25 % of the lake surface area. This corresponds to the reduction in algal biomass found in Denmark at a PVI (plant volume infested) of 20 % (Schriver *et al.*, 1995; Sondergaard & Moss, 1997). In the Danish experiments zooplankton grazing seems to be the major mechanism involved. However, it is not clear which mechanisms cause the increase in transparency or the reduction in the algal biomass in the presence of macrophytes in the Dutch lakes. Several mechanisms are possibly involved, e.g. increased sedimentation and reduced resuspension of the sediment (Van den Berg e*t al.*, 1997; Scheffer, 1998), which provide refuge for zooplankton (Moss, 1990), competition with algae for nutrients, especially nitrogen (Ozimek *et al.*, 1990; Van Donk *et al.*, 1993) and allelopathy (Wium-Anderson *et al.*, 1982).

We have no data on increased sedimentation or reduced resuspension in the lakes studied , but these aspects were shown to be important in *Chara* meadows in Lake Veluwe, which is comparable to Lake Wolderwijd in many respects (Van den Berg, *et al.*, 1997). In the early biomanipulation cases an increase in macrophytes coincided with a decrease in total nitrogen (Zwemlust, Galgje, Noorddiep) (Chapter 6; Scheffer, 1998). In those lakes N-limitation could be confirmed with bioassays (Chapter 5; Van Donk *et al.*, 1993). In the other successful biomanipulation cases low dissolved nitrogen concentrations occurred regularly too, but this does not necessarily imply nitrogen limitation of the algal growth.
Although in most lakes the total-P concentration decreased, the dissolved-P concentration never reached very low values, except in lake Wolderwijd. Thus phosphorus limitation of the algal growth is unlikely to have played a role in the cases studied.

Our results suggest that in summer *Daphnia* grazing is not really important (Table 9.3). This is not in line with the dominant role of zooplankton in Danish lakes (Schriver *et al.*, 1995; Jeppesen *et al.*, 1997). This discrepancy may be due to a better sampling method for zooplankton in Denmark, where the sampling is often done during the night. In the Netherlands, sampling of zooplankton is carried out during the day. *Daphnia* is difficult to sample in daytime particularly in clear water, since the species tend to hide against predation of fish near the bottom and between the macrophytes (Schriver *et al.*, 1995; Lauridsen & Beunk, 1996;). Often the sampling for zooplankton in Dutch lakes is carried out in the open water only, and consequently zooplankton densities may have been underestimated. Also macrophytes associated zooplankton (e.g. *Simocephalus, Sida, Eurycercus*) are not sampled, so the impact of these zooplankton species among the macrophytes is not known. No data were available on allelopathic effects.
An evaluation of 20 biomanipulation cases in the USA and Europe had led to the conclusion that in many cases the increased water clarity could not be related to increased zooplankton grazing (De Melo *et al.*, 1992). They suggested that the results are often a consequence of changes in the nutrient levels due to the fish removal. Also for lake Pohjalampi it was suggested that the high transparency in the lake after fish reduction was caused not by increased *Daphnia* grazing, but by a reduction in nutrient due to the removal of benthivorous fish (Karjalainen *et al.*, 1999). However most observations on the impact of *Daphnia* were based on *Daphnia* biomass, whereas the potential grazing pressure is a better instrument for determining the impact of *Daphnia* on algae.
Our results show that in spring *Daphnia* grazing is important. No conclusions can be drawn from our results with regard to nitrogen limitation, but phosphorus limitation of the algal growth does not seem to be important. However, the decrease in total nutrient concentrations confirms the idea that the change in nutrient fluxes due to the manipulation of the food chain may play a role in the success of the biomanipulation (Carpenter *et al.*, 1992; Jeppesen, 1998).

Can we explain the lack of success in the other lakes?

In the ten lakes without lake bottom view, the goal of high transparency and macrophytes was not achieved, but only the two lakes where no improvement of the transparency was found at all can be called real failures. The eight lakes where an improvement of the transparency was found, but no bottom view and no macrophytes occurred, are not fully successful, but cannot be regarded as complete "failures". As we have seen in Lake Wolderwijd a relatively small increase in transparency may lead in the shallow parts of the lake to a development of macrophytes and clear water (Chapter 8). The part with macrophytes and clear water may gradually expand and after a number of years the whole system may change to a clear water system (Figure 9.2).

The lack of bottom view in the ten lakes, may have been caused by several factors:

i. insufficient fish removal (Carpenter & Kitchell, 1992; Hosper & Meijer, 1993)
   Substantial (more than 75 %) reduction of the fish stock is thought to be important for getting clear water in spring. This drastic reduction should take place in one winter and no fish must be able to migrate into the lake afterwards.

ii. presence of peat (Portielje & van der Molen, 1999)
   In lakes with peaty sediment a high transparency may be hard to achieve, because of the presence of a higher back-ground (non-algal, humic) turbidity.

iii. high wind resuspension (Hosper & Meijer, 1993)
   When a lake is turbid because of resuspension of the sediment by wind, it may be difficult to get clear water by biomanipulation. The criteria for high wind resuspension are based on fetch in prevailing wind direction (WSW-ENE in the Netherlands), water depth and absence/presence of sandy bottom.

iv. high surface area (Reynolds, 1994; Benndorf, 1995)
   A lower chance of high transparency in large lakes may occur because of higher susceptibility to wind resuspension and because drastic fishery may be more difficult to achieve in larger lakes.

v. high nutrient concentration (Jeppesen *et al.*, 1990; Reynolds, 1994; Benndorf, 1995)
   At high nutrient concentrations the chances on success are thought to be lower , because of higher chances on inedible cyanobacteria (Reynolds, 1994; Benndorf, 1995) or because of lower chances on a good piscivorous fish population (Jeppesen *et al.*,1990)

vi. high density of cyanobacteria (Hosper & Meijer, 1993; Gliwicz, 1990)
   At densities of cyanobacteria of > 80,000 ind/ml *Daphnia* may not be able to consume the algae and reproduction of *Daphnia* may be reduced.

vii. presence of invertebrate predators, such as *Neomysis* or *Leptodora* (Hosper & Meijer, 1993)
   Neomysis and *Leptodora* can consume *Daphnia* and may therefore limit the *Daphnia* grazing.

A **75 % reduction in the fish stock** seems critical for achieving lake bottom view. In fact, in all but two instances the percentage of fish removal may explain which cases are successful and which are not (Figures 9.10 and 9.11). Other evaluations have also shown that substantial (more than a 75 %) fish reduction is required for success (Hansson *et al.*, 1998). Nonetheless, some comments can be made concerning the other "risk factors" too:

A high Secchi depth is rarely achieved in lakes with **peaty sediment** (Figure 9.10), but we cannot conclude that this has hampered recovery, since these lakes also appear to have been subjected to a relatively low fish reduction (Table 9.1). In the Netherlands a drastic fish stock reduction is generally more difficult to achieve in peaty sediment than in other lakes, as peat digging created many small canals and ditches where small fish can concentrate during winter and escape the fish nets.

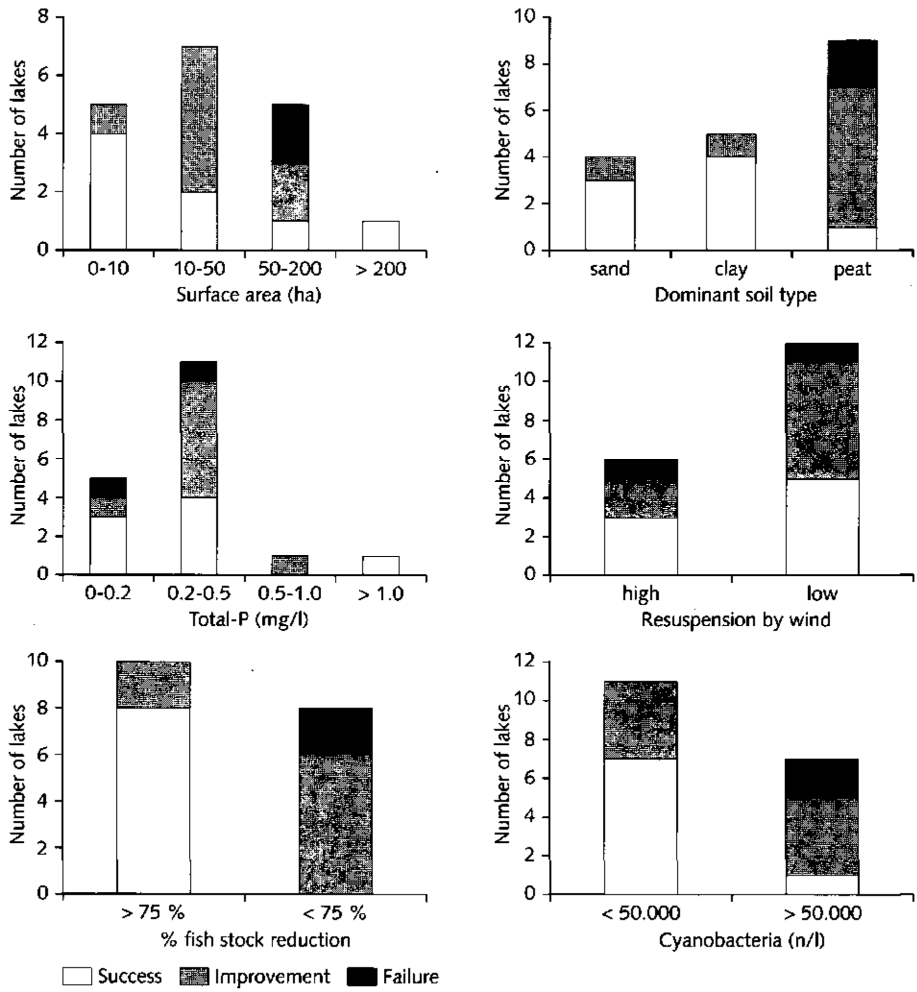

Figure 9.10: *Occurrence of bottom view in relation with surface area, phosphorus level, sediment type, cyanobacteria abundance, wind resuspension and fish reduction.*

Resuspension by wind did not prevent a high transparency in the lakes with > 75 % fish stock reduction (Figure 9.10, Table 9.4). Resuspension by wind occurred before the measure was taken in Zuidlaardermeer, Duinigermeer and to a lesser extent in lake Wolderwijd, but this did not prevent the lakes from becoming clear. In Zuidlaardermeer the construction of a large enclosure (75 ha) reduced the wind resuspension (Torenbeek & de Vries, 1997), whereas in lake Duinigermeer wind resuspension was decreased by an explosive growth of *Chara* (Van Berkum *et al.*, 1995).
However, because the criteria used for high wind resuspension are based only on wind fetch, lake

Table 9.4: *Factors which might prejudice successful biomanipulation (after the name of the lake the years which have been taken into consideration).*

	Transparency	Fish reduct.	Wind	Cyanobacteria	*Neomysis*
Zwemlust (86-97)	○	○	○	○	○
Waay (93-96)	○	○	○		
Noorddiep 3 (88-92)	○	○	○	○	○
Duinigermeer (93-96)	○	○	●	○	○
IJzeren Man (91-96)	○	○	○	○	○
Bleiswijkse Zoom; Galgje (87-94)	○	○	○	○	○
Zuidlaardermeer (96-97)	○	○	●		○
Wolderwijd (91, 97)	○	○	○	○	○
Wolderwijd (92)	◍	◍	○	○	○
Wolderwijd (93-95)	○	◍	○	◍	○
Boschkreek (92-96)	○	●	○	○	○
Hollands Ankeveense Plas (89-92)	◍	●	○	●	○
Nannewijd (94-96)	◍	●	●	●	○
Oude Venen; 40-Med (90-96)	◍	●	○	○	○
Oude Venen; Tusken Sleatten (90-96)	◍	●	○	○	○
Oude Venen; Izakswijd (90-95)	◍	●	○	○	○
Klein Vogelenzang (89-96)	◍	●	●	●	◍ L
Sondelerleien (91)	●	● *	○	●	○
Sondelerleien (92)	●	●	○	●	●
Sondelerleien (93)	●	●	○	●	○
Breukeleveense Plas (89-92)	●	●	○	● L	◍
Deelen (93-96)	●	●	○	●	○

Legend:

	○	◍	●
transparency (cm)	bottom	> 70	< 40
fish reduction (%)	> 75	65-75	< 65
wind resuspension	small	medium	large
Cyanobacteria (n/ml)	< 50,000	50,000-100,000	> 100,000
Neomysis	absent	present	> 100 ind m^{-2}

L: *Leptodora* instead of *Neomysis*

* reduction > 75 %, but fish immigration

depth and presence of sand, windresuspension is probably underestimated for lakes with very loose sediment. The characterization is probably too rough to conclude that wind resuspension can never prevent the clearing of the lake water. However, field observations gave the impression that the macrophytes consolidate the sediment (Duinigermeer). So once macrophytes appear, the wind resuspension decreases. Furthermore, in Denmark indications are found that zooplankton is able to increase the sedimentation of inorganic suspended matter (Jeppesen, pers. comm.).

A logistic regression showed no significant relation between the occurrence of bottom view and **the total-P concentration.** Jeppesen *et al.* (1990) stated that biomanipulation is best carried out in lakes with a phosphorus concentration of < 0.08-0.15 mg P l^{-1}. This may guarantee the stability of the clear water state, but it is probably not necessary for achieving clear water (Figure 9.10).
No relation was found between occurrence of bottom view and surface area of the treated lakes either (Figure 9.10). After analysing 33 biomanipulation cases all over Europe and the USA Reynolds (1994) concluded that the best chances for successful biomanipulation are in lakes covering an area of < 4 ha. This is not confirmed in this study.

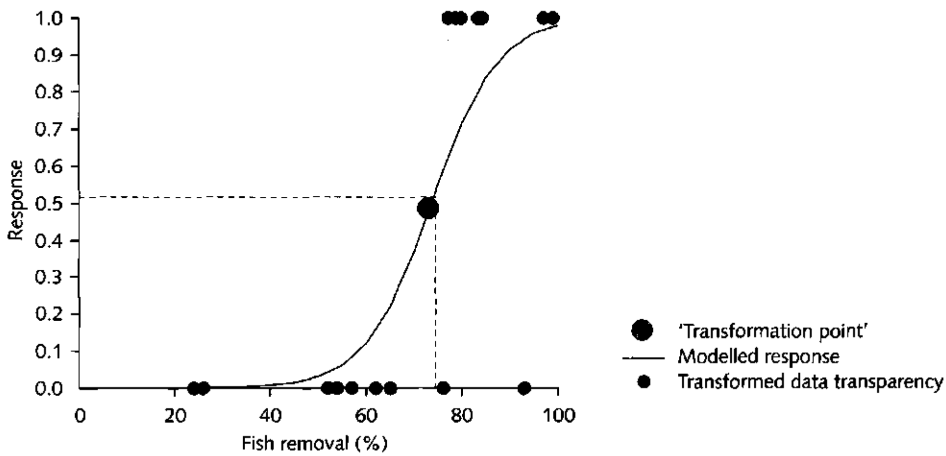

Figure 9.11: *Logistic regression on percentage of fish reduction and the occurrence of bottom view.*

A high density of cyanobacteria seems to reduce the chances of lake bottom view (Figure 9.10). However, in all lakes with a high density of cyanobacteria an insufficient fish reduction may also explain the lack of lake bottom view (Table 9.4). In Lake Breukeleveen not only insufficient fish stock reduction and a high density of cyanobacteria, but also the presence of *Leptodora*, and resuspension of the sediment by wind could have prevented the clearing of the water (Van Donk *et al.*, 1990b; Table 9.4). In Klein Vogelenzang the increase in transparency was probably due not only to the high density of cyanobacteria, but also to insufficient fish reduction. In winter 1990 when the young fish migrated from the lake, the blue-green algae disappeared (after a high peak of *Bosmina*) *Daphnia* came up and the water became clear. However, the clear water phase did not last long, and the water became turbid again during the growing season when the fish returned to the lake (Van der Vlugt *et al.*, 1992).

There are not enough data for conclusions to be drawn regarding the possible negative impact of ***Neomysis* or *Leptodora*** on the clearing of a lake in spring. A high density of *Neomysis* was found in 1992 in Lake Sondelerleien (Claassen & Clewits, 1995) and a high density of *Leptodora* was found in

1989 in Lake Breukeleveen (Van Donk *et al.*, 1990), but additional factors may have caused the relatively low transparency in both of these lakes.

In two lakes (Izakswijd and Sonderlerleijen) the water remained relatively turbid, despite a fairly substantial fish reduction. In Izakswijd the 75 % limit was only just met (76 %) and probably the lake did not clear completely, because the remaining fish consisted exclusively of small planktivorous fish. This case shows that it is best to reduce considerably more than 75 % of the original fish stock, (especially of planktivorous fish). In Sondelerleien the turbidity of the water was caused not by algae, but by resuspended matter, probably coming from the inflow of turbid water. The lake had a very short retention time (< 20 days) and the inflow water contained very high concentrations of suspended matter (Claassen & Maasdam, 1995). In this lake it is likely that biomanipulation will never lead to clear water. This is in line with the idea of Reynolds (1994), namely that success of biomanipulation is higher in lakes with a long residence time.

In the present set of cases bottom view was found more often in lakes where only biomanipulation had been carried out than in lakes where additional phosphorus reduction measures had been applied as well (Figure 9.12). This was probably caused by the relatively low fish reduction in the lakes where phosphorus reduction measures had been taken prior to the biomanipulation measures. Biomanipulation probably received less attention in these lakes than in lakes where it was applied as the only measure.

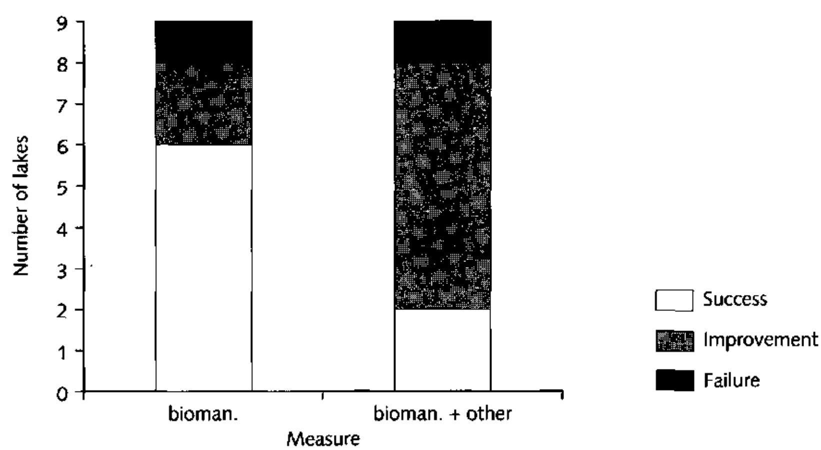

Figure 9.12: *Occurrence of bottom view in relation to additional measures.*

What factors determine-long term stability?

In chapter 6 the long-term responses (five-year results) in four biomanipulation cases in the Netherlands and Denmark were discussed (Chapter 6). In that paper, the following indicators for stability were chosen: (a) Secchi depth after 4-5 years is still high, (b) the fish biomass remains low, (c) biomass of 0+ fish is low, (d) percentage of piscivorous fish is high and (e) the length of *Daphnia* remains high during summer (Meijer *et al.*, 1994). These indicators were only qualitative and therefore difficult to test, but we will discuss these indicators with respect to long-term data (more than 8 years).

ad a) In the present study in almost all lakes with long term results the **Secchi depth** decreased over the years, but after 6 years the Secchi depth was still 5-8 times higher than before the measures were taken. In only one lake (Wolderwijd) did the Secchi depth gradually increase. This was related to the gradual increase in the abundance of Characeae in this lake (Chapter 8). In the first year the transparency was only high above the *Chara*, but in later years the area with *Chara* and clear water expanded dramatically and the whole system changed. The nutrient concentrations decreased dramatically, more mussels appeared and the fish composition changed (Lammens, Perrow & Meijer, unpubl. results).

ad b) In most lakes (Bleiswijkse Zoom/Galgje, Zwemlust, Noorddiep, Duinigermeer) the **fish biomass** increased after the measure. However, it seems to stabilise at a level of about half the original biomass (except lake Duinigermeer). This reduction in biomass may be caused by the reduction in benthivorous fish, resulting in less mobilization of nutrients from the bottom. In Zwemlust the productivity of the fish was lower because bream was replaced by rudd, which is a less efficient forager.

ad c) The biomass of **0+ fish** after the measures is high in most hypertrophic (total-P concentration > 0.25 mg P l^{-1}) lakes (> 100 kg ha^{-1}), but lower in lakes with lower nutrient concentrations (Waay, Duinigermeer and Wolderwijd, Table 9.1). Noorddiep is an exception in that it has a relatively high phosphorus concentration and a relatively low 0+ fish biomass, which may be caused by a relatively good foraging conditions for pike (Walker, 1994; Chapter 7).

ad d) In general in all Dutch lakes the percentage of **piscivorous fish** remains quite low after the fish stock reduction. Only in lake Zwemlust a high proportion of piscivorous fish was found in the first years after complete fish removal. Pike probably cannot develop because in all lakes hardly any vegetation were present in early spring, which is needed for pike to spawn and to create shelter for young pike against cannibalism (Grimm & Backx, 1990). No piscivorous perch are present, because the nutrient concentrations are too high for perch to win the competition with roach (Persson & Crowder, 1997).

ad e) Insufficient data were available to test the long-term development of the length of *Daphnia*.

According to the theory of alternative stable states long-term stability of the clear-water state can only be expected below certain critical nutrient levels. Critical total-P levels of 0.08-0.15 mg P l^{-1} have been mentioned (Jeppesen *et al.*, 1990), whereas higher concentrations are suggested for smaller lakes (Hosper, 1997). In most Dutch biomanipulation projects the total-P concentration before the measures were between 0.1 and 1.0 mg P l^{-1}. In six lakes the total-P concentrations became lower than 0.1 mg P l^{-1} after the measures. Only in the case of one of those lakes were long-term data available. The few lakes with low nutrient levels and the scarce data on fish make it impossible to test the hypothesis that long-term stability is found only at low nutrient concentrations. The current results, however, do point to a deterioration at higher nutrient concentrations.

The signs of stability chosen in the earlier work (Chapter 6) are related mainly to fish and Secchi depth. Later results have shown that the presence of macrophytes is probably even more important for stability than the presence of piscivorous fish. In our study we found that when more than 25 % of the lake surface is covered with submerged macrophytes the algal biomass is repressed by the macrophytes. In almost all succesfully biomanipulated lakes we found a strong decline in overall macrophyte abundance several years after the manipulation (Figure 9.7). However, the species composition of the macrophytes community may also be important. *Chara* can keep the water clear for a long period during the year, but for example *Potamogeton berchtoldii* may die off early in the summer, and will cause turbid water again in August (Van Donk & Gulati, 1995). The species composition of the macrophytes was not stable in all lakes (Figure 9.6). It seems that a higher instability is found in lakes with a high phosphorus concentration, but more research needs to be done on this aspect.

CONCLUSIONS

- Biomanipulation can be a very effective method for increasing the transparency of the water in a lake. In the Netherlands 90 % of the biomanipulation cases resulted in an improvement in water transparency.
- The greatest improvement was found in lakes with the highest fish stock reduction. All but two successes could be attributed to drastic fish stock reduction.
- The improvement in Secchi depth and chlorophyll-*a* concentrations in biomanipulated lakes is stronger than in lakes where only phosphorus reduction measures were taken.
- Clear water in spring is probably caused by *Daphnia* grazing, whereas in summer *Daphnia* grazing in open water is not important. Low nitrogen concentrations occurred, but nitrogen limitation of the algal growth could not be proved. Macrophytes that covered more than 25 % of the surface area coincided with low algal biomasses.
- Despite high nutrient levels, after more than five years the Secchi depth is still much higher than before the measures, although the transparency is decreasing.

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CHAPTER 10

EVOLUTION OF HYPOTHESES

EVOLUTION OF HYPOTHESES

This chapter describes in some detail the evolution of hypotheses that has occurred over a period of fourteen years. Whereas several ideas have been falsified, some are still valid but even more remain untested. Each of the following sections summarises, for a particular aspect, current thinking derived over a decade of intensive research and co-operation with groups in The Netherlands, Denmark, United Kingdom and elsewhere and how these ideas developed from the original set of hypotheses (Tabel 10.1 and Tabel 10.3).

HOW BIOMANIPULATION WORKS

The original hypothesis in short

In 1987 the idea of biomanipulation in The Netherlands was summarised by a simple figure showing what were assumed to be the most important parameters involved in reducing the algal biomass and clearing the water (Figure 10.1, Hosper *et al.*, 1987).
The piscivore, pike, was considered to be crucial for controlling the biomass of bream and to become abundant in the presence of macrophytes. In absence of bream, zooplankton could graze down the algae. At a low algal biomass the light climate would be suitable for the development of macrophytes, which in turn stimulate an increase in pike. This was regarded as the ideal clear water scenario.
Eutrophicaton had led to a high algal biomass and turbid water and therefore a scarcity of macrophytes and pike. Nutrient control alone was thought to be insufficient as long as bream remained abundant and able to feed on the zooplankton. In addition benthivorous bream (bream larger than 20 cm) was reckoned to exacerbate the situation by resuspending sediments, causing nutrient release in the water and disturbing the rooting of plants. Two alternative stable states were recognised: a clear water state with vegetation and pike and a turbid water state stabilised by bream (Scheffer, 1989). Therefore, removal of bream (known as biomanipulation) was considered to be essential for the recovery of the clear water state in the Netherlands (Hosper *et al.*, 1987; Hosper, 1989; Lammens, 1989). A low nutrient concentration was thought to increase the stability of the clear water state and therefore biomanipulation was suggested as a method additional to nutrient removal.

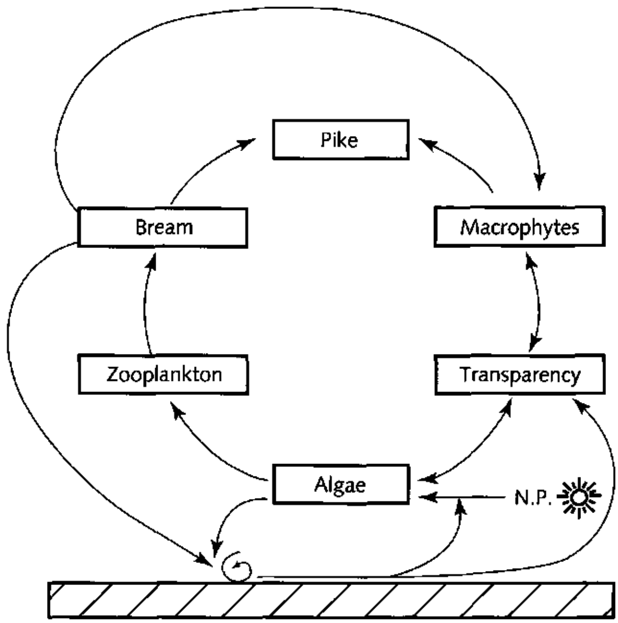

Figure 10.1: *Interactions in shallow lakes with a key role for the predatory fish pike (from Hosper et al., 1987).*

Following biomanipulation, attainment of a clear water macrophyte-dominated state induced changes in the whole ecosystem. In this chapter I focus on the changes in transparency, fish, zooplankton, phytoplankton, macrophytes and nutrients and their interactions (Table 10.1), but also other components of the ecosystem are affected. For example, an increase in macrophytes in several lakes causes an increase in bird numbers (Lauridsen *et al.*, 1993; Van Donk & Gulati, 1995; Noordhuis, 1997). Also an increase of Dreissena sp. may occur (Noordhuis, 1997) and a shift towards more snails have been observed (Kornijow *et al.*, 1990; Van den Berg *et al.*, 1997; Van Den Berg, 1999; Noordhuis, 1997).

Table 10.1: *Comparison of old hypotheses and observations on changes of the trophic levels after biomanipulation.*

Trophic level	Old hypothesis (Hosper *et al*, 1987)	Observations in Dutch lakes 1987-1996
Fish		
Piscivores	• Increase of pike resulting in	Pike does increase, but not enough to control 0+ cyprinids
	• Control of 0+ cyprinids	Increase of 0+ perch, but limited development of older perch
Planktivores	• Decrease of 0+ fish	In eutrophic lakes an increase rather than a decrease of 0+ cyprinids occurred
Benthivores	• Decrease of benthivores and • shift to macrophyte associated fish	hypotheses confirmed
Zooplankton	• Shift to large bodied Daphnia	Large Daphnia occur but are often limited to the Spring period
Phytoplankton	• Low algal biomass, • Risk of high algal biomass because of shift to inedible species	• low algal biomasses, • inedible algae only rarely present
Macrophytes	• Increase	Often but not always rapid colonisation of lakes with *Chara*
Nutrients	• No clear hypothesis formulated	Decrease of nitrogen and phosphorus in most lakes, not in all

TRANSPARENCY

Biomanipulation in the Netherlands has in all lakes been applied with the intention to cause a shift to the clear water state, manifested as a Secchi depth to the bottom of the lake.

In half of the biomanipulated Dutch lakes this shift has been obtained (Chapter 9). The increase in transparency was caused by a dramatic fall in algal biomass and in some lakes the concentration of inorganic suspended solids also decreased, indicating a reduction in the resuspension of bottom sediment. This shift towards the clear water state is only found in lakes where a substantial fish reduction has been carried out (Chapter 9). Numerous other studies confirm the effect of biomanipulation on transparency (Gulati *et al.*, 1990; Jeppesen, 1998; Jeppesen *et al.*, 1999; Hansson *et al.*, 1998; Drenner & Hambright, 1999; Table 10.2).
In The Netherlands, the shift towards the clear water state did not necessarily occur immediately after fish removal. In 40 % of the successfully biomanipulated lakes, it took more than 6 months to reach Secchi depth to the bottom. In lakes with immediate clearing, the water could become turbid again in the summer of the first year, where macrophytes had not colonised a substantial part of the lake in that year (as has been observed in Lake Wolderwijd and Lake de Waay).

The perception of success has changed over the past thirteen years. In the 1980's biomanipulation was only called successful when a complete shift towards the clear water state was obtained in the first year after the measure (Hosper & Meijer, 1993). The developments in Lake Wolderwijd (1991-1998) showed that a moderate or a temporary increase in transparency may first only lead to a local colonisation of macrophytes and local patches of clear water at shallow areas, but may eventually lead to a complete clearing of the lake several years after the measure (Chapters 8 and 9). Therefore, a significant increase in Secchi depth, but no Secchi depth to the bottom, is in this thesis not considered as a failure, but as partial success (Chapter 9). It depends on the depth profile of a lake if a moderate improvement of the Secchi depth may initiate a recovery of the clear water state.

In only 10% of biomanipulated Dutch lakes was there a failure to produce an improvement in the Secchi depth (Chapter 9). Other evaluations of biomanipulation projects also suggest a low percentage of real failures (< 20 %) (Hansson *et al.*, 1998; Drenner & Hambright, 1999). In accordance with our evaluation about 45 % of biomanipulation projects were thought to be completely successful, with the rest being partially successful.

Summarising, biomanipulation led to an increase of the Secchi depth in 90% of the projects, while in half of the biomanipulated lakes (but in 80 % of the lakes with a drastic fish removal) a shift towards the clear water state was observed.

FISH

In the early days of biomanipulation it was hypothesed that the return of clear water and macrophytes would lead to a shift from planktivorous and benthivorous cyprinids, mainly bream and carp, towards macrophyte-associated species such as pike, perch, tench and rudd (Lammens, 1986, 1989; de Nie, 1987; Grimm, 1989; Table 10.1). Pike was expected to be able to control the production of 0+ fish (Hosper, 1989, Figure 10.1).

Indeed, in all lakes where biomanipulation was conducted, the biomass of benthivorous fish remained low after fish removal (Meijer & de Boois, 1998). The most obvious explanation for the slow regrowth after fish removal seems to be that in vegetated lakes the foraging sites for benthivorous fish disappear. The biomass of macrophyte associated species such as tench, perch, roach and rudd increased (Table 10.2; Chapter 7; Perrow & Jowitt, 1996) as also has been found in some British lakes (Perrow *et al.*, 1999b). However, in a dense macrophyte community large fish will disappear. Indeed, a shift from large to small fish is found in lake Veluwe where only small sticklebacks and spined loach (Cobitis taenia) were caught within the dense vegetation of Charophytes (Perrow & Jowitt, 1996), whereas before the colonisation of the area with Charophytes the fish population was dominated by bream and roach (Backx & Grimm, 1994). Unfortunately, the lack of long time series (> 5 year) prevents a good analysis of the development of a new fish community.

In only two of the manipulated lakes the biomass of piscivores did increase compared to the situation before the fish stock reduction (Table 10.2), but due to limited data no significant changes between before and after the biomanipulation could be observed. In the small lakes Zwemlust and Bleiswijkse Zoom the introduced pike reached biomasses up to 30 kg ha^{-1} (Chapter 7), while biomasses up to 75 kg ha^{-1} were thought possible in those lakes (Grimm, 1989; Grimm & Backx, 1990). In both lakes small pike suffered from cannibalism and the individual length increased. The limited development of pike is now suggested to be due to lack of emergent vegetation, which would create better shelter for young pike after the period of spawning (March-April) when submersed macrophytes are still absent (Grimm & Backx, 1994). Especially in large lakes with a low shore line/surface area ratio small pike will never reach a high biomass. Six years after the fish removal and the pike introduction in Lake Wolderwijd, only large (> 0,8 m) specimens remained.

Perch did also not develop a substantial piscivorous population (perch > 0+) in manipulated lakes, although an increase of young of the year (Y-O-Y) perch frequently occurred (Chapter 7 and 9). In Noorddiep & Bleiswijkse Zoom a reasonable biomass (> 20 kg ha^{-1}) of piscivorous perch was present and the biomass had increased after the biomanipulation (Chapter 7). In other lakes the biomass of piscivorous perch remains below 7 kg ha^{-1}, despite biomasses of 20-30 kg ha^{-1} 0+ perch (Chapter 9). It is still unclear what causes the absence of large stocks of larger perch in Dutch shallow lakes. The most plausible explanation is food competition with the remaining bream and roach. In England perch only succeeded in becoming piscivorous in a biomanipulated lake where all bream and roach had been removed (Perrow, pers. communication). Furthermore perch is often shown to become dominant in lakes with low nutrient concentrations in combination with clear water and macrophytes (Persson & Crowder, 1997). Nonetheless, the nutrient concentrations in Lake Wolderwijd are lower than in Lake Bleiswijkse Zoom and Noorddiep, whereas the piscivorous perch biomasses are higher in the latter lakes. Perrow *et al.*, 1999 also suggest a too dense vegetation, changes in O_2 concentration or low ammonia concentrations as possible factors reducing the development of perch, but there are no indications that this maybe the case in the observed lakes. The patterns remain puzzling and unfortunately there is not yet enough long term information on the development of fish communities to analyse whether perch is able to win the competition from roach and bream in clear vegetated water with high nutrient concentrations (Persson, 1994).

Tabel 10.2: *Ratio of results after the biomanipulation/before the biomanipulation in the eight clear water lakes. For total P, total N, Secchi depth and Chlorophyll-a summer mean values have been used. Ratio's in bold means that the situation after the biomanipulation differed significantly from the situation before the biomanipulation (sign test p < 0,05).*

	ZL	BL	ND	IJM	DM	ZLM	WW	W
n before/after	1/8	1/8	1/7	1/8	2/4	2/2	3/8	2/2
n before/after fish data		1/5	1/5		1/2		1/6	1/2
0+ fish		**86**	2,57		2,4			1,12
piscivore biomass		0,95	1,4		1,6		0,8	0,6
biomass macrophyte ass. Fish		**68**	**1,8**		2,3		**8,1**	1,2
Daphnia biomass	+	0,59	**0,38**		3,3		0,92	0,2
Chlorophyll	**0,05**	**0,24**	**0,40**	**0,1**	**0,33**	**0,35**	**0,6**	0,32
% bluegreens	-	**0,46**	**0,25**		0,77		**0,46**	
macrophytes	+	+	+	+	+	+	+	+
tot P	**0,81**	**0,67**	**2,15**	**0,51**	**0,68**	**0,33**	**0,61**	**0,57**
tot N	**0,65**	**0,67**	**0,74**	0,33	**0,88**	0,52	**0,73**	0,75
Secchi depth	**9,4**	**3,5**	**2,6**	**16,8**	**2,2**	2,0	1,75	**2,4**

In contrast with the original hypothesis (Table 10.1) we observed no decrease of small planktivorous fish in the lakes after the biomanipulation (Table 10.2, Chapter 7 and 9). In Lake Bleiswijkse Zoom the total biomass of fish decreased after the measures, but the number of 0+ fish increased (Chapter 3). The increased production of Y-O-Y in Lake Bleiswijkse Zoom may be due to better foraging conditions for the adults, more spawning substrate, less silt-deposition over eggs, less food competition or less predation by piscivores (Chapter 7). However, in manipulated lakes with lower nutrient concentrations (Total P about 0,1 mg P/l) the biomass of 0+ fish seems lower (Chapter 9). Apparently in the hypertrophic lakes the development of piscivores was not strong enough to control fish recruitment (Chapter 9; Meijer & de Boois, 1998). Only in lake Noorddiep the original pike population developed well enough to keep the 0+ fish production low (Chapter 7). In Noorddiep the predation of perch and pike was stronger than in Lake Bleiswijkse Zoom, possibly because the vegetation was less dense in Noorddiep (Walker, 1994, Chapter 7). Also in some lakes in Denmark, Finland, Sweden and The UK it appeared difficult to realise control of 0+ production after biomanipulation in eutrophic lakes (Hansson *et al.*, 1998; Jeppesen, 1998; Sondergaard *et al.*, 1997; Bergman *et al.*, 1999; Perrow *et al.*, 1999a). Even after regular stocking with predators control of 0+ fish has not been achieved (Benndorf, 1995; Perrow *et al.*, 1997). Only when stocking with very high densities of pike some effect on the 0+ cyprinids can be obtained. In Denmark annual stocking of high densities of pike (500-3600 ha^{-1}) in lake Lyng resulted in a reduction of the 0+ cyprinids population particurlarly in the littoral zone (Berg *et al.*, 1997). The density of Y-O-Y roach was high in years with little stocking, and low in years with high stocking (Jeppesen *et al.*, 1999a). In Poland stocking of high densities (> 2000 per ha) of pike did reduce the small cyprinids (Prejs *et al.*, 1997). In order to keep the density of the 0+ cyprinids low the stocking have to be repeated every year (Jeppesen *et al.*, 1999a).

A review of fish control projects in North America (Meronek *et al.*, 1996) showed that only in 7 out

of 29 water bodies stocking with piscivores led to a reduction in the fish stock. From 1993 onwards no pike stocking has been carried out in biomanipulation experiments in the Netherlands.
However, in Denmark the role of piscivorous fish is still considered to be important for stabilising the clear water in summer, especially in less eutrophic lakes, as in those lakes perch do have age-structured populations with a number of age classes (Jeppesen *et al.*, 1990; Jeppesen, 1998).

Summarising, it can be stated that the original idea that the fish population would change towards more macrophyte associated fish has been confirmed in some lakes. In vegetated lakes the species composition does change and bream is no longer the dominant fish species. However, especially in lakes with relatively high nutrient levels, the planktivorous Y-O-Y fish density seems to increase and the possibilities for pike and perch are apparently not sufficient in the Dutch lakes to allow control of the production of 0+ cyprinids.

ZOOPLANKTON

In our original hypothesis zooplankton (mainly large *Daphnia*) played a crucial role in generating clear water after biomanipulation (Hosper, 1989). An absence of large *Daphnia* in lakes before manipulation and an increase of *Daphnia* length and biomass after the fish reduction, was expected (Table 10.1). *Daphnia* was supposed to control the algal biomass.

In contrast with the expectations, in Lakes Noorddiep and Lake Wolderwijd neither the *Daphnia* biomass or the length increased significantly after the biomanipulation (Chapter 6, Chapter 8 and unpublished results of Lake Noorddiep). In Lake Bleiswijkse Zoom and Lake Zwemlust *Daphnia* number increased, but the summer average *Daphnia* biomass was only high in the first years after the manipulation and decreased drastically in later years (Chapter 6; Hansson *et al.*, 1998). Only in Lake Duinigermeer the average summer biomass of *Daphnia* increased after biomanipulation (Table 10.2), but there were not enough data to make this increase a significant one.
Still *Daphnia* grazing is considered to be responsible for the low algal biomass in spring as the spring clearing always coincided with the highest densities of *Daphnia*.

In 6 out of 8 successfully biomanipulated lakes the *Daphnia* biomass was highest in spring and *Daphnia* was scarce in summer (Chapter 9). *Daphnia* may be limited by predation of 0+ fish in summer, as was suggested for some lakes by a reduction in body length (Meijer *et al.*,1994; Van Donk & Gulati, 1995, unpublished results of lake Bleiswijkse Zoom and Noorddiep). This equals experiences in UK and Sweden (Phillips *et al.*, 1999; Romare & Bergman, 1999).

Although *Daphnia* grazing is the likely cause of the clearing of the water in spring in most successfully biomanipulated lakes (Chapter 9, Jeppesen, 1998), the role of grazing in summer is considered to be important in some Danish lakes (Jeppesen, 1998), but is in the Dutch lakes still under discussion. Earlier it was concluded from the low *Daphnia* biomass in summer that *Daphnia* grazing was not responsible for the low algal biomass in that period (Chapter 4; Meijer *et al.*, 1994).

However, a low biomass of *Daphnia* may still be sufficient to suppres phytoplankton if algal biomass and therefore total algal productivity is low. Furthermore, it is possible that in the Dutch lakes the impact of zooplankton grazing in summer is underestimated due to the inadequate sampling methods since zooplankton was always sampled during daytime and often outside the vegetation (Chapter 9). Danish studies have shown that in clear water with macrophytes *Daphnia* may be highly underestimated from day time samples in the open water (Schriver *et al.*, 1995, Jeppesen et al., 1997; Lauridsen & Buenk, 1996). When planktivorous fish is present in the open water *Daphnia* often concentrates at the edge of the vegetation during the day and comes out of the vegetation only at night (Jeppesen *et al.*, 1997). The strength of diel horizontal migration (DHM) depends on the predation pressure of fish and on the density of the vegetation (Schriver *et al.*, 1995; Jeppesen *et al.*, 1997; Jeppesen, 1998, Lauridsen & Buenk, 1996; Perrow *et al.*, 1999a). In lake Volkerak Zoommeer *Daphnia* was found to take refuge in the macrophytes (Schutten *et al.*, 1992). In contrast, in Lake Veluwe day-night sampling in and outside the plants showed that *Daphnia* seemed to avoid dense *Chara* beds and sought refuge against 0+ fish within the stands of reed (*Phragmites australis*) in the margins (Lammens, unpublished data). Furthermore, the impact of zooplankton on algae among macrophytes may be high due to macrophyte associated species such as *Sida*, *Simocephalus*, *Eurycercus* and *Chydorus* (Stansfield *et al.*, 1997; Perrow *et al.*, 1999a), which are not found by standard Dutch sampling procedures.

Summarising, *Daphnia* is sometimes quite abundant even before the fish removal, but the grazing pressure of *Daphnia* on the algae generally increases after biomanipulation. *Daphnia* grazing seems crucial for reducing the algal biomass in spring. However, the importance of zooplankton grazing in summer remains difficult to asses. The different opinions of researchers on the role of zooplankton grazing in summer may be explained largely by different sampling methods and differences in the presence of fish and the density of the vegetation and the plant species. For a good understanding of the impact of zooplankton in the Dutch lakes, better sampling methods in clear vegetated lakes would be required.

PHYTOPLANKTON

The algal biomass was originally predicted to be strongly reduced by zooplankton grazing as a result of biomanipulation (Shapiro *et al.*, 1975; Hosper, 1989; Hosper & Jagtman,1990). However, the effect was thought to be hampered in the presence of inedible algae, especially in lakes with a high nutrient concentration (Table 10.1, Benndorf, 1988).

In accordance with these original ideas all substantial fish manipulations evaluated led to a significant decrease of the phytoplankton biomass (Chapter 6, 9, Table 10.2, Van Donk & Gulati, 1995; Chapter 6). This is in agreement with many other biomanipulation experiments (Gulati *et al.*, 1990; Jeppesen *et al.*, 1990; McQueen, 1998; Hansson *et al.*, 1998).

In the 1980's inhibition of zooplankton grazing by inedible cyanobacteria was thought to form a serious threat for successful biomanipulation (Benndorf, 1988; Lammens *et al.*, 1990).
There are two different situations to consider. Firstly, when filamentous cyanobacteria form an overwintering population and are present in early spring, *Daphnia* may not be able to create a spring clear water phase (Lammens *et al.*, 1990; McQueen *et al.*, 1986; Dawidowicz *et al.*, 1988). However, experiences in the Netherlands produced no conclusive evidence of the inhibition of *Daphnia* grazing by cyanobacteria. Admittedly, in three lakes with a high density of cyanobacteria the water did not become completely clear, but other factors could also explain the lack of success in these cases (Chapter 9).

Secondly, a clearing of the water by *Daphnia* grazing in spring, could be followed by a strong increase in inedible algae in summer as a response to selective *Daphnia* grazing on their more edible competitors (Benndorf, 1988; Boing *et al.*, 1998). From eighteen observed lakes only in three lakes inedible algae were occasionally found in summer, but the algal biomasses remained low (Talsma, 1997; Van Berkum *et al.*, 1995; Van Donk *et al.*, 1990; Meijer & de Boois, 1998). The percentage of bluegreens decreased in most lakes (Table 10.2). Also in other biomanipulation studies, an increase in inedible algae were hardly found (Phillips & Moss, 1994; Agrawal, 1998). Moreover, biomanipulation has often solved the problem of floating cyanobacteria (Van Donk *et al.*, 1990; Barten, 1998; Annadotter *et al.*, 1999; Kairesalo *et al.*, 1999), although they may return after some years when the fish stock increases (e.g. in Lake Zwemlust, Van Donk & Gulati, 1995; Romo *et al.*, 1996). In contrast with the expectations, often a shift towards small algae has been found (early years of lake Zwemlust, ponds in lake Wolderwijd, Zuid Laardermeer), which may be related to the competitive advantage of those small species at low nutrient levels (Van Donk *et al.*, 1990a; Reynolds, 1988), to their rapid growth rates compensating increased zooplankton grazing (Jeppesen, 1998) or to their capacity to avoid sedimentation within the macrophytes (Schriver *et al.*, 1995). A Danish analysis of the algal composition of a large number of enclosures revealed that in dense macrophyte beds without zooplankton grazing an increase in species resistant to sedimentation, such as cyanobacteria, was found (Schriver *et al.*, 1995). Indeed, in 1998 a bloom of *Aphanizomenon* sp. occurred above the macrophytes in lake Veluwe and lake Zuidlaardermeer (pers. comm. Van Schie , De Vries).

In conclusion, the hypothesis that biomanipulation leads to low algal biomass has been confirmed, whereas the idea that biomanipulation will lead to an increase in inedible algae has not been supported. The potential for failure of biomanipulation in lakes with a high density of filamentous cyanobacteriae has not yet been tested.

MACROPHYTES

Macrophytes were originally thought likely to start colonising the lakes as soon as the water cleared (Table 10.1), although in real terms the speed of recovery was not known. *Chara* was expected to develop as pioneer species, after which other macrophyte species would follow.

In most Dutch biomanipulated lakes macrophytes developed rapidly indeed. Especially in lakes with *Chara* the colonisation occurred within several weeks after the fish reduction (Van Berkum *et al.*, 1995; Chapter 4). In lakes without *Chara* dominance it could take one (Lake Zwemlust) to two years (Zuidlaardermeer) in order to achieve substantial macrophyte cover (Chapter 9). In general, macrophyte colonisation in the Netherlands occurred faster than in lakes in Denmark or England, where it could take more than three years (Lauridsen *et al.*, 1995; Perrow *et al.*, 1997: Madgewick, 1999). In peat lakes in England the physical sediment stability seems the principle constraint to macrophyte recovery (Schutten & Davy, submitted) or the lack of propagules after dredging (pers. comment M. Perrow), while in two Danish lakes grazing by birds was thought to be important in delaying the colonisation by plants (Lauridsen *et al.*, 1993). In large lakes (Wolderwijd/ Veluwemeer) the development of macrophytes was possibly restricted by the lack of propagules (Van den Berg *et al.*, 1996).

In our original ideas macrophytes were mainly considered to be important for creating a stable piscivorous pike population (Figure 10.1; Hosper, 1989), but later the role of macrophytes as refuges for zooplankton, producers of allelopathic substances, and as competitors with algae for nutrients, were also mentioned (Chapter 4; Hosper & Jagtman, 1990: Figure 5.10).

Ten years on we can conclude that in The Netherlands the macrophytes did not lead to a large piscivorous pike population (see earlier). However, macrophytes have become even more prominent in hypotheses about stabilisation of the clear water state. The impact of macrophytes on the transparency of the water is indicated, for instance, by the relatively high transparencies in presence of macrophytes at a particular phosphorus concentration compared to the transparencies found in lakes without macrophytes (Jeppesen *et al.*, 1990b; Portielje & Van der Molen, 1999). Even at a relatively low macrophyte coverage a substantial reduction of the algal biomass in the lake is likely (Sondergaard & Moss, 1997; Portielje & Van der Molen, 1999; Chapter 9). In Lake Wolderwijd in the first years after the biomanipulation the water remained only clear in the area with Charophytes; outside the *Chara*-meadows the water remained turbid, but after a gradual expansion of the *Chara* the water became clear in the whole lake (Chapter 9). Numerous other studies confirm the effect of macrophytes on water clarity (Jeppesen *et al.*, 1990b; Scheffer, 1998).

It is not easy to unravel the mechanisms responsible for the high transparency in presence of macrophytes. Many mechanisms potentially interact at the same time, and the relative contribution of the different mechanisms may differ from lake to lake.

Macrophytes seem to reduce the nitrogen concentration in some lakes (Chapter 7; Scheffer, 1998, Jeppesen, 1998). This might be due to better conditions for denitrification in the sediment or by uptake of nitrogen by the plants. In many lakes very low dissolved nitrogen concentrations occurred after this manipulation (Chapter 9) and in some lakes bioassays have shown nitrogen limitation of algal growth (Van Donk *et al.*, 1990a; Chapter 7; Chapter 3).

However, the strong decrease of chlorophyll-nutrient ratios at increasing macrophyte cover (Portielje & van der Molen, 1999; Chapter 9) suggests that nutrient limitation of the algal growth is not the only explanation for the low algal biomasses in presence of macrophytes in Dutch lakes. The low chlorophyll-nutrient ratio will partly be caused by changes in the algal species, but the decrease is so strong that also factors like zooplankton grazing, filtration by mussels, sedimentation or possibly allelopathy have to be considered.

Macrophytes as a refuge for zooplankton against planktivorous fish was suggested as being important over 15 years ago (Timms & Moss, 1984). Recent research on this subject has shown that the refuge mechanism appears to be more complex than previously thought, depending on the density and type of planktivorous fish, the density of the macrophytes (Jeppesen, 1998; Perrow *et al.*, 1999a) and perhaps other factors such as the concentration of humic substances (Lauridsen *et al.*, 1999).

As stated earlier in this chapter this refuge effect has been found in some Dutch lakes, but in most Dutch lakes the sampling of zooplankton is not adequate enough to find any refuge effect.

Dense *Chara* fields in lake Veluwe were shown to cause sedimentation of algae and inorganic suspended matter (Van den Berg *et al.*, 1997).

Release of allelopathic substances especially by *Chara* has been suggested to reduce algal biomass (Wium- Andersen *et al.*, 1982, Gross *et al.*, 1996). The importance of allelopathy is still under discussion (Forsberg *et al.*, 1990; Jasser, 1995; Sondergaard & Moss, 1997). Hootsmans & Breukelaar (1993) found 10% reduction of the algal growth in water taken between the macrophytes in Lake Wolderwijd and Lake Bleiswijkse Zoom.

Apart from these aspects the macrophytes induce many other changes in the system. They may indirectly stimulate the development of zebramussels as they provide substrate for the larvae and reduce the sedimentation on the mussels. Furthermore the presence of bottom algae increases after the macrophytes reduce the resuspension and the bream will disappear as the macrophytes reduce the foraging grounds for the bream (Figure 10.2).

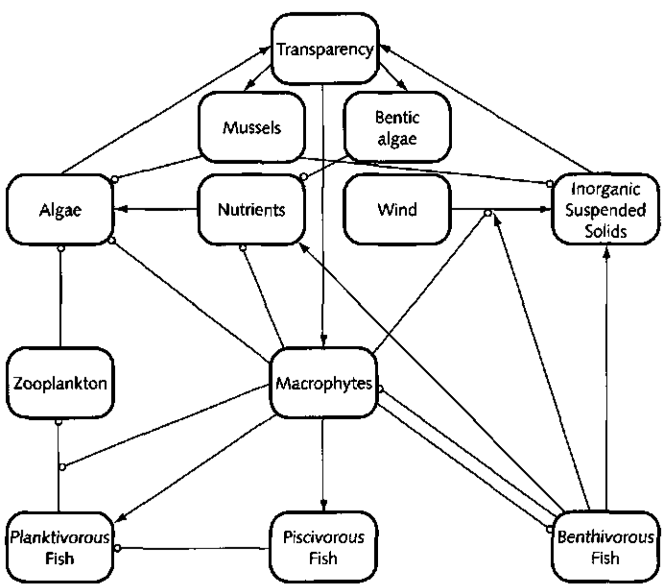

Figure 10.2: *The crucial role of macrophytes in increasing the transparency of the water* —→ *stimulation* —o *reduction.*

Summarising, the experiences of the past thirteen years indicate that in the Netherlands macrophytes colonise the lakes quite rapidly. Macrophytes are even more important for stabilising the clear water state than was thought ten years ago, although it is not pike that is stimulated by the plants and is responsible for stabilising the clear water state. There are various mechanisms that result in stabilising the clear water state.

NUTRIENTS

Effect of biomanipulation on nutrients

Although early papers demonstrated the impact of fish on phosphorus concentrations in enclosures (Tatrai & Istvanovics, 1986, Andersson *et al.*, 1978), initially in the Netherlands no explicit ideas about the change of the nutrient concentrations after biomanipulation were formulated (Table 10.1).

In the Dutch experiments the impact of biomanipulation on phosphorus was initially not so clear. For example in lake Noorddiep a drastic increase of the phosphorus concentration was found (Table 10.2, Meijer *et al.*, 1990) whereas in Lake Zwemlust phosphorus concentrations hardly decreased initially at all (Van Donk *et al.*, 1990; Chapter 6). In Danish lakes no significant changes in the phosphorus concentrations occurred in the first years of biomanipulation either (Jeppesen, 1998). However, experiments with benthivorous fish in small ponds in 1994 showed a strong increase of nutrients in the presence of benthivorous fish (Breukelaar *et al.*, 1994). Furthermore, a recent comparison of eight biomanipulated lakes in the Netherlands with non-manipulated lakes showed a significant decrease of total phosphorus after biomanipulation (Van der Molen & Portielje, 1998; Chapter 9; Table 10.2). This is mirrored by a recent evaluation of 20 cases in Denmark (Jeppesen, 1998). Consequently, it does seem that biomanipulation will usually lead to a decrease of phosphorus concentrations in the water (Carpenter *et al.*, 1992; Jeppesen, 1998; McQueen , 1998; Hansson *et al.*, 1998; Annadotter *et al.*, 1999; Bergman *et al.*, 1999). This may be due to several mechanisms such as the reduction of resuspension (Breukelaar *et al.*, 1994), sedimentation of faecal pellets produced by zoöplankton or mussels, the decrease of P-release from the sediment because of an increase in benthic algae (Delgrado *et al.*, 1991) or to the changes in benthic fauna after the removal of benthivorous fish (Bergman *et al.*, 1999).

Biomanipulation also appeared to affect nitrogen concentrations (Table 10.2). In Lake Bleiswijkse Zoom (1987) nitrogen limitation of the algal growth was shown in bioassays even in the first year (Chapter 6). Nitrogen limitation was also shown to be important in Lake Zwemlust (Van Donk *et al.*, 1989, 1990a, 1993). Low dissolved nitrogen concentrations were recorded in five lakes. A Danish study also showed a significant decrease of nitrogen after reduction of the cyprinids, including in lakes without vegetation (Jeppesen *et al.*, 1998). Moreover, the total nitrogen concentration was found to decrease with increasing macrophyte abundance (Chapter 7; Jeppesen *et al.*, 1998;

Scheffer, 1998), possibly because of increased denitrification in the anaerobic zones between the macrophytes (Van Luin, 1995). Although several cases are convincing, a comparison of biomanipulated and non-manipulated lakes in The Netherlands indicated only a non-significant decrease of the total nitrogen concentration in the biomanipulated lakes (Van der Molen & Portielje, 1998).

In summary, biomanipulation seemes to lead to a decrease in phosphorus as well as in nitrogen concentrations.

Effect of nutrients on the functioning of biomanipulation

The idea of Benndorf (1988) and McQueen (1989) that a high phosphorus concentration can prevent the clearing of the water, has been falsified (Perrow *et al.*, 1997; Chapter 9). Experiments in hypertrophic waters have shown that it is possible to generate clear water provided that the fish removal is drastic (Van Donk *et al.*, 1990; Chapter 9; Table 10.3).
On the other hand, it appears that the idea that biomanipulation can only lead to the long term stability of the clear water state at low nutrient concentrations is correct. The theory of alternative stable states suggests that at low nutrient levels the clear water state is always stable, whereas beyond a certain critical nutrient level lakes would always settle to the turbid state. Critical phosphorus concentrations for maintaining a stable clear water state are thought to range from < 0.1 mg P l^{-1} (Hosper & Jagtman, 1990; Moss *et al.*, 1996) to 0.08-0.15 mg P l^{-1} (Jeppesen *et al.*, 1990b) or 0.05-0.10 mg P l^{-1} (Jeppesen, 1998; Jeppesen *et al.*, 1999). Obviously, the critical phosphorus concentrations are less relevant if low nitrogen concentrations are present.

In contrast to expectations the transparency remained high for several consecutive years, even in hypertrophic Dutch lakes. After about 4-5 years the transparency did decrease in summer in most lakes, but even after 6-8 years the summer average Secchi depth was still 3-5 times higher than before the treatment (Chapter 9). The spring clear water phase which was absent before biomanipulation, re-occurred persistently even after the fish stock had returned to a high level.
The hypertrophic Lake Zwemlust has returned to the turbid state after 10 years (Van Donk, pers. comm). During those 10 years the ecosystem of the lake changed steadily. The composition of the macrophytes community shifted from year to year, also the fish community gradually changed. Although phytoplankton blooms in late summer became more pronounced, the lake remained vegetated and relatively clear in summer until nine years after the shift to the clear water situation induced by biomanipulation. The return to the turbid state is mainly attributed to the shift in the macrophyte community towards species that become senescent early in the season and to the high fish biomass and the low percentage of piscivores. The shift in macrophyte species and the reduction of the macrophyte biomass is considered to have been caused by herbivory of rudd and coots (Van Donk, 1997). The hypertrophic Lake IJzeren Man returned to the turbid state 8 years after the biomanipulation (pers. comm G. Bonhoff). For this lake the reasons behind this reversal are unknown. These case-studies suggest that the clear state is not stable at high nutrient

concentrations. However, they also show that the return time to the turbid equilibrium can be almost as long as a decade.

In a recent study on Lake Veluwe and Lake Wolderwijd historic data made it possible to define critical limits for a stable clear water state (Meijer *et al.*, 1999). In those lakes the clear water state ended in the 1960's when the *Chara* population collapsed at a total phosphorus concentration of about 0.15 mg P l^{-1}. Recovery of the clear state (first only locally, later in the whole lake) started at a total P-concentration below 0.10 mg P l^{-1} (Chapter 8). This hysteresis pattern indicates that in a range from 0.10 to 0.15 mg P/l two alternative stable states are present. In view of the theory one may thus expect that at a total P-concentration below 0.10 mg P/l a reduction of the fish stock in these lakes would only accelerate the natural recovery process, as has probably happened in lake Veluwe (Figure 10.3, Chapter 8). If biomanipulation is applied at a P-concentration higher than 0.15 mg P l^{-1}, the system may become clear but will eventually return to the turbid state. If biomanipulation is applied at an intermediate P-level (0.10-0.15 mg P l^{-1}) a stable clear water state may be reached provided that a high coverage of *Chara* is achieved. In 1991 after the biomanipulation of Lake Wolderwijd the colonisation of the macrophytes probably went too slow to obtain such a stable clear water state.
Unfortunately, we can not simply apply the critical nutrient levels found in the Veluwemeer studies to other lakes. For instance, shallow areas in Veluwemeer and Wolderwijd served as hot spots from which the colonization by Charophytes proceeded. In lakes without such shallow zones the natural

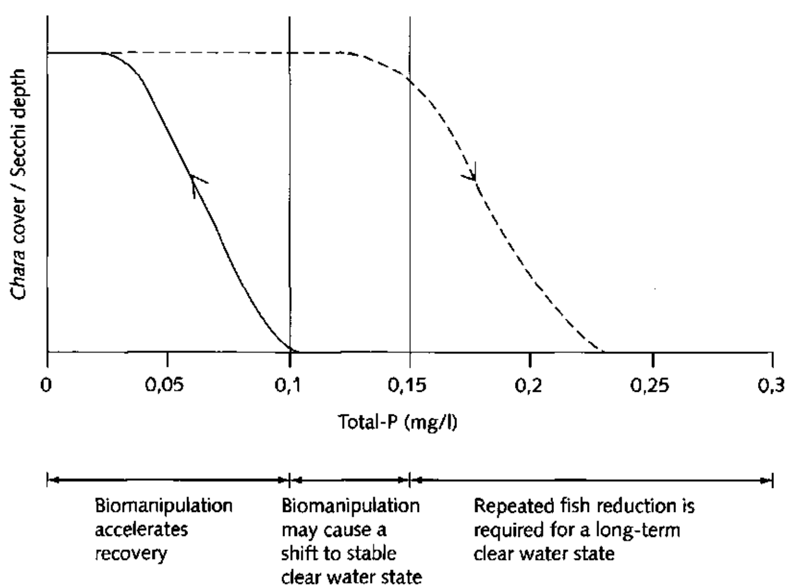

Figure 10.3: *The role of biomanipulation in the restoration process of Lake Veluwe and Lake Wolderwijd, based on the observed hysteresis pattern.*

restoration process will probably start at much lower P-concentrations. Also, for determining the critical P-levels for successful biomanipulation one should probably consider the size of the lake, the nitrogen levels, and the macrophyte seed bank.

In conclusion, clear water may result from biomanipulation even at very high nutrient concentrations. The chances of long term stability of the clear water state are lower at high nutrient levels, but critical levels may differ between lakes. Even hypertrophic biomanipulated lakes may remain clear for almost a decade after manipulation. This slow return rate to the turbid state implies that at high nutrient concentrations a clear water state may be maintained effectively through regular fish reductions.

CONCLUSIONS

How biomanipulation works

Of the evolution of ideas, described in this chapter, I think the most important change in thinking is that biomanipulation appears to be not only a top-down method, but a bottom up measure as well, as recently has been concluded by other authors too (Jeppesen, 1998; Hansson *et al.*, 1998; Bergman *et al.*, 1999). Biomanipulation appears to reduce the nutrient concentrations in lake water.

Hosper & Jagtman (1990) distinguished three steps in successful biomanipulation: a strong reduction of the fish stock, the getting of clear water and the keeping of clear water (Table 10.3). This general thought is still valid. This thesis shows that a strong reduction of the fish stock is essential for the success of biomanipulation. *Daphnia* grazing is still considered essential for initiating the clear water in spring, but the reduction of benthivores is of importance also. The reduction of benthivores is not only essential in reducing the resuspension of the bottom sediment in lakes with a high biomass of carp and large bream, it may also help to reduce the phosphorus concentration.
According to early views, colonisation of macrophytes seems crucial for maintaining the clear water in summer. Indeed, in lakes without macrophyte growth, the water frequently became turbid again in summer, if predation of 0+ fish on *Daphnia* was high. Our data indicate that a substantial coverage (more than 50%) of the lake with macrophytes is required to keep the water clear in the whole lake. At lower coverage only locally clear water above the macrophytes may be achieved.
It has become clear over the years that macrophytes induce many changes in the ecosystem, which help stabilising the clear water state. Surprisingly, the expected increase of piscivore control of 0+ fish has not been found in Dutch lakes. Rather, the macrophytes seem to stimulate the production of 0+ fish in eutrophic lakes. There is quite some evidence that macrophytes provide a refuge for zooplankton, but this effect may be small if high densities of 0+ fish are present within the vegetation. Importantly, in large, shallow lakes reduced resuspension between the macrophytes may significantly contribute to the water clarity. Furthermore, nitrogen limitation of the algal growth

biomanipulation were about 750,000 US dollar, while for P-reduction measures 5.000.000 US dollar are required each year (unpublished data). Although this thesis shows that in eutrophic lakes no long term success can be obtained, the long return time to the turbid state implies that even in highly eutrophic lakes, where the clear state is not stable, biomanipulation may be an cost-effective management strategy, as in some lakes it may suffice to reduce the fish stock drastically once every five years.

It should be stressed that biomanipulation may not work in all conditions. In open navigable systems, it may be difficult to remove a substantial part of the fish stock. In those lakes repeated fish reduction may still have effect (as shown in Finland and Sweden -Annadotter *et al.*, 1999; Kairesalo *et al.*, 1999), but in Holland there is little experience with this method. In Friesland a repeated fish reduction did result in a decrease of small cyprinids, but the bream did regrow very fast, probably due to still very eutrophic conditions in that time. The results in lake Veluwe showed that in the years with very turbid water bream could regrow very fast after a repeated fish reduction of 15 kg/ha each year, but in years with increasing *Chara* cover the bream could not recover from the yearly removals of the fish, because the foraging conditions for the bream had deteriorated.

Future application of the method

The water quality of Dutch lakes has in general gradually improved over the past ten years (Van der Molen & Portielje, 1999) due to the national and international policy of P-removal from detergents and P-reduction in effluents of sewage treatment plants. Nutrient and chlorophyll-*a* concentrations have decreased and the Secchi depth has slightly improved. In the Frisian lakes and in lakes in North West Overijssel short term spring clear water phases now occasionally occur and in some Frisian lakes even small areas with macrophytes have appeared, although in the past three years the results seem less promising. In such lakes biomanipulation may speed up the recovery process, although the water manager may be prudent and wait for further reductions in nutrients.

However, in the western part of Holland many shallow lakes are still turbid despite relatively low nutrient concentrations (< 0.08 mg P l^{-1}) (Hosper, 1997; Van der Molen & Portielje, 1999). In those lakes high densities of filamentous cyanobacteria are still present in early spring and the sediment is typically very loose and peaty. These lakes may be difficult to restore by biomanipulation as *Daphnia* spp. may have difficulty in consuming the cyanobacteria. However, there is a growing consensus of opinion that it should be possible to get clear water in those lakes too, provided that the fish reduction is very drastic (Perrow *et al.*, 1997). Recent studies have also shown the potential of *Daphnia* to reduce particles other than algae (Jeppesen *et al.*, 1999b). This is promising for applying biomanipulation in lakes with loose sediment .

In the deeper, more eutrophic, lakes in the western part of Holland the main problem is formed by nuisance from floating layers of naturally buoyant cyanobacteriae such as *Microcystis, Anabaena* and *Aphanizomenon.* It is worth trying to tackle this problem with biomanipulation, as results from many lakes and ponds show a decrease in such cyanobacteria after the reduction of the fish stock

(Van Donk *et al.*, 1990a; Christoffersen *et al.*, 1993; Annadotter *et al.*, 1999; Kairesalo *et al.*, 1999). Blooms of Microcystis have only been found after an increase in the fish stock (Breukers *et al.*, 1997; Romo *et al.*, 1996), which means that probably regular maintenance of the fish stock is required, especially as in those deeper lakes macrophytes will have difficulty to develop.

The results of our biomanipulation work so-far indicate that the magnitude of fish-stock reduction and the development of macrophytes should be the main points of attention in future biomanipulation applications. Specifically, special attention should be paid to removal of more than 75% of the fish stock, to removal or disturbance of spawning fish to reduce the production of 0+ fish and to reservation of money for additional fisheries. Furthermore, in view of the crucial role of macrophytes in stabilizing the clear water condition, the potential for macrophyte growth should be investigated beforehand, and if necessary macrophyte stimulating measures should be taken, like reducing the water depth or addition of oospores or seeds of plants.

Future research

Specific research on factors determining the changes in nutrient concentrations after fish reduction and factors controlling macrophyte colonization and the development of piscivorous perch in Dutch lakes is required to clarify some crucial remaining questions. Also, to develop a true understanding of stability, long term studies (> 10 years) of the response of different types of lakes to biomanipulation are urgently needed.

Certainly, much can be learned in the near future from comparing biomanipulation results in The Netherlands with whole lake experiments abroad. In many countries multi-case evaluations are now being made. Up until now most disappointing results seem attributable simply to insufficient fish removal. Therefore, much could be learned from failures in lakes where insufficient removal can be excluded as an explanation.

Perhaps the main challenge for further applied research on biomanipulation in the Netherlands would be to investigate the potential for restoring lakes with a high density of overwintering cyanobacteria and very loose sediment and lakes with floating cyanobacteria.

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Lake Bleiswijkse Zoom (Chapter 4)
Lake Bleiswijkse Zoom was biomanipulated by dividing the small lake into two parts, and removing more than 75 % of the original fish biomass from one part (Chapter 4). In the treated part the water cleared up spectacularly in spring offering a clear view of the bottom whereas in the control section the Secchi depth transparency remained 20 cm as it was before treatment. Analysis showed that algal biomass, but also inorganic suspended solids and nutrient concentrations were significantly lower than in the untreated part. This indicated the important role of sediment resuspension as a mechanism through which fish in such lakes affects water quality. Within two months the treated section became completely overgrown by Charophytes.

Impact of benthivorous fish (Chapter 5)
The role of benthivorous fish was analysed further using data from two biomanipulated small lakes (Bleiswijkse Zoom and Noorddiep). The biomass of benthivorous fish and the concentration of inorganic suspended solids were shown to be positively related. A model was used to calculate the impact of resuspended inorganic suspended solids on the turbidity. By combining these relations a direct effect of benthivorous fish on the Secchi depth was calculated. In addition, it was argued that the algal biomass was also indirectly influenced by removal of benthivorous fish, as the benthivorous fish prevented macrophytes from settling, whereas macrophytes were essential to keep the water clear.

Long term responses (Chapter 6)
Five year results from three biomanipulated Dutch lakes (Lake Zwemlust, Noorddiep and Bleiswijkse Zoom) were compared with those from a Danish biomanipulated lake (Lake Væng). In all lakes the fish stock reduction initially led to a low fish stock, low chlorophyll-*a* concentrations, increase in Secchi disk transparency and a high abundance of macrophytes. Large *Daphnia* also became abundant, but their density soon decreased due to food-limitation and predation by fish. The total nitrogen concentrations decreased in the lakes due to N-uptake by macrophytes and enhanced denitrification. In Lake Bleiswijkse Zoom the water transparency gradually decreased over the study period. The fish stock increased in this lake and the production of young fish in summer was high. Clear water became limited to spring as the macrophytes dissappeared. In the other lakes the water remained clear during the first five years. In the summer of the sixth year, however, transparency decreased in the hypertrophic Lake Zwemlust. Also in the less eutrophic Lake Væng, a brief turbid state (6 weeks) occurred in the summer of 1992. This summer deterioration of the water quality was related to a collapse in macrophytes in both lakes. Our comparison suggests that the relative short duration of the turbid state in Lake Væng was due to the low planktivorous fish stock as compared with the situation in Lake Zwemlust.

Development of fish communities after biomanipulation (Chapter 7)
The development of fish communities after biomanipulation has been studied in detail in three small lakes. In Lake Zwemlust fish were completely eliminated. Pike and rudd were introduced, but the predator pike appeared unable to control the explosive growth of rudd as was initially the intention. In Lake Noorddiep and Bleiswijkse Zoom fish was strongly reduced, but not completely eliminated. After the measure the fish population became more diverse. Bream and carp became

partly replaced by roach and perch. Pike-perch, the main predator before manipulation, was strongly reduced and replaced by pike and perch. The overall share of piscivorous fish increased at all sites. Contrary to the expectations, recruitment of young-of-the-year fish was similar or even higher in the manipulated clear lakes than in the turbid water before the measures, but the recruitement of young-of-the-year to older year classes differed between the species. Although predation by pike and perch could not control the young-of-the-year cyprinids, the predation may have contributed to the shift from bream to roach. Probably the most important explanation for the long-term changes in fish stock composition after biomanipulation is the fact that macrophytes provided new refugia and feeding conditions that favour roach and perch, but offer relatively poor survival conditions for bream and carp.

Biomanipulation on a large scale (Chapter 8)

Drastic fish removal in Lake Wolderwijd (2670 ha) showed that also in a very large lake biomanipulation can cause water clarity to increase. From this lake 425 tons of fish were removed, i.e. ca. 75% of the original fish stock. In addition 575.000 specimen of 0+ pike were introduced. The success of biomanipulation in the lake was transient. In spring 1991 the transparency of the water increased as a result of grazing by *Daphnia galeata*. However, the clear-water phase lasted for only six weeks. Macrophytes did not respond as fast as expected and most of the introduced young pike died. Nonetheless, from 1991 to 1993 the submerged vegetation gradually increased and Charophytes began to colonise the lake. Importantly, the water over the *Chara* meadows became spectacularly clear, probably as a result of increased net sedimentation in these areas, due to reduced resuspension.

A box with a summary of recent results has been added to the original text showing how Wolderwijd and the adjacent Lake Veluwe recovered in the following years to a clear water state with Charophyte meadows. Reconstruction of the history of Lake Veluwe provides the first evidence for the hypothesized hysteresis in response of shallow lake ecosystems to change in nutrient concentrations. The switch from clear to turbid water occurred at a total-P concentrations of 0.15 mg P l^{-1}, while recovery of the clear water state did not start until the total-P concentration dropped below 0.10 mg P l^{-1}.

Evaluation of Biomanipulation Projects (Chapter 9)

Evaluation of eighteen biomanipulation projects confirmed that biomanipulation can be a very effective method to increase the transparency of the water in lakes. In almost 50 % of the projects a return to the clear water state was obtained and in only ten per cent of the projects the biomanipulation failed to cause a significant increase in the Secchi depth. The increase in Secchi depth was stronger than the general recovery trend observed in Dutch lakes where no measures have been taken. The improvement in Secchi depth and chlorophyll-*a* was also more marked than in lakes where only the phosphorus loading had been reduced.

The critical factor for obtaining clear water appeared to be the extent of the fish reduction. Significant effects were observed only after > 75 % fish reduction. In such strongly biomanipulated lakes, wind resuspension of the sediment no longer affected water clarity.

Daphnia grazing seems the main factor responsible for spring clear water in practically all lakes. The factors that determine the clear water in summer are less obvious and more diverse, but a high macrophyte cover seems to play an important role.

The decrease in transparency over the years in almost all manipulated eutrophic lakes supports the idea that the clear, vegetation dominated state is not stable at high nutrient conditions. However, the typical return time to the turbid water state appears remarkably long (> 8 years). As we have not applied biomanipulation in mesotrophic lakes, we could not investigate if under those conditions the clear water state would be stable on the long term.

Evolution of ideas (Chapter 10)
The last chapter describes how our ideas on biomanipulation have evolved over the past fifteen years. In retrospect it can be concluded that biomanipulation seems a more effective tool than initially expected, especially the succes in eutrophic lakes was unforeseen. Expected negative effects such as an increase in inedible algae have hardly been found. The ideas about the mechanisms behind biomanipulation have evolved quite strongly. The initial idea that a spring increase in water clarity would be caused by *Daphnia* grazing has been supported by the experiments. However it was also shown that reduced resuspension after removal of benthivores could contribute to clarity in some lakes and that the fish removal tends to cause a pronounced reduction in nutrient concentrations.
The initial idea that colonisation by macrophytes would be crucial for maintaining the clear water in summer has been supported by the results. In lakes without macrophyte growth, the water frequently became turbid again in summer, if predation of 0+ fish on *Daphnia* was high. The results of the combined studies suggest that at least a coverage of 50->70% of the lake with macrophytes is required to keep the water clear in the whole lake. As shown earlier locally clear water could occur above dense fields of macrophytes. The expected increase of piscivore control of 0+ fish has not been found in Dutch lakes. Rather, the macrophytes seem to stimulate the production of 0+ fish in eutrophic lakes. Macrophytes can provide refuge for zooplankton, but this effect may be small if high densities of 0+ fish or Neomysis are present within the vegetation. In large, shallow lakes reduced resuspension and increased sedimentation between the macrophytes rather than the originally predicted food chain effects seem the main causes of water clarity. Furthermore, nitrogen limitation of the algal growth has proven to be important in some lakes, but in others a strong reduction of the chlorophyll-*a* nutrient ratio's suggest that other factors than nutrient limitation are responsable for the low algal biomasses in presence of plants. Those can be related to zooplankton grazing, allelopathic effects or increase of filtering zebramussels. An increase in benthic algae may have an effect too, but little is known about the role of this potentially important group yet.

Implication for the water quality manager

This thesis shows that biomanipulation can be a very effective way to induce a shift from turbid to clear water in shallow lakes. The results indicate that even in eutrophic lakes such a shift occurs

whenever more than 75% of the fish stock is removed. Also, wind resuspension seems unable to prevent clear water in such biomanipulated lakes.

Comparison of different restoration projects shows that biomanipulation has a larger effect on turbidity and algal biomass than measures aimed at reducing phosphorus loading of specific lakes. Surprisingly, biomanipulation even reduces the in-lake phosphorus concentrations to the same extent as specific phosphorus reduction measures.

The clear vegetated state achieved by biomanipulation is not stable in the long run in lakes with high nutrient levels. Nonetheless, the return time to the turbid state appears to be rather long (>8 years) even in highly eutrophic systems. In such cases biomanipulation needs to be repeated on a regular basis. Since the costs of a fish stock reduction are quite low compared to nutrient reduction measures, repeated biomanipulation can still be a highly cost-effective approach.

Major challenges for the future would be the restoration through biomanipulation of turbid lakes with a high density of cyanobacteria, exposed lakes with soft organic sediments, and lakes that are in open connection with other waters.

SAMENVATTING

Inleiding (Hoofdstuk 1)

In de eerste helft van de twintigste eeuw werden de Nederlandse meren gekenmerkt door helder water en een uitbundige groei van ondergedoken waterplanten. Door een grote aanvoer van voedingsstoffen (de nutriënten fosfaat en stikstof) begon deze situatie omstreeks 1960 te veranderen: de meeste meren en plassen werden troebel door een sterke groei van algen, potentieel toxische blauwalgen werden dominant en de water planten verdwenen. Herstel programma's waren gericht op het reduceren van de fosfaat belasting. Door deze maatregelen nam de fosfaatconcentratie en de hoeveelheid algen weliswaar af, maar de helderheid van het water nam slechts in geringe mate toe. De troebele toestand bleek zeer stabiel te zijn. Zij wordt gestabiliseerd door de aanwezigheid van oneetbare blauwalgen en de dominantie van brasem in de visstand. Brasem staat het herstel van de heldere toestand in de weg, doordat jonge vis de belangrijkste consument van algen, de watervlooien, eet en omdat grote brasem de bodem omwoelt op zoek naar bodemfauna. Verlaging van de fosfaat concentratie alleen is onvoldoende om het water weer helder te krijgen. Omstreeks 1985 is in Nederland een sterke uitdunning van de visstand geïntroduceerd als aanvullende herstelmethode, onder de naam Actief Biologisch Beheer (ABB). Dit proefschrift beschrijft het effect van deze methode op de waterkwaliteit en de mechanismen die een rol spelen bij het helder krijgen en helder houden van het water na de maatregel.

Alternatieve stabiele toestanden (Hoofdstuk 2)

In ondiepe meren zijn twee stabiele toestanden mogelijk: een helder water toestand die wordt gedomineerd door waterplanten en een troebele toestand die wordt gekenmerkt door een hoge algen biomassa en een dominantie van brasem. De troebele toestand is vooral aanwezig bij hoge nutriëntenconcentraties, de heldere toestand bij lage nutriëntenconcentraties. Uit modellen en praktijkervaringen is gebleken dat in een gebied met tussenliggende nutriëntenconcentraties beide situaties als alternatieve stabiele toestanden kunnen voorkomen. In dat traject van nutriënten kan een verstoring het systeem van de ene in de andere stabiele toestand brengen. Actief Biologische Beheer kan worden beschouwd als een verstoring die een meer kan doen omslaan in een heldere toestand. Als het water weer helder is geworden, zullen waterplanten zich weer kunnen gaan ontwikkelen en zullen de waterplanten het water ook helder houden. De waterplanten bieden schuilgelegenheid aan de watervlooien tegen predatie door vis, ze kunnen concurreren met algen om nutriënten, ze kunnen de opwerveling van bodemmateriaal verlagen en zij kunnen in sommige gevallen zelfs algenremmende stoffen uitscheiden. De waterplanten maken de heldere toestand stabiel, totdat een verstoring (zoals in het verleden bijvoorbeeld toepassing van planten-bestrijdingsmiddelen of uitzetten van bodemwoelende karper) of een sterke toename van de nutriëntenconcentraties het systeem weer doet omslaan naar de troebele toestand.

De eerste Actief Biologisch Beheers Experimenten (Hoofdstuk 3 en 4)

Het eerste Actief Biologisch Beheers experiment is uitgevoerd in kleine vijvers (Hoofdstuk 3). Tien vijvers van 0,1 ha werden in twee delen gesplitst: in het ene deel van iedere vijver werd kleine

brasem, blankvoorn en karper uitgezet, de andere helft diende als controle. Naar verwachting, veroorzaakte de aanwezigheid van de vis een afname van de helderheid en een toename van de algen biomassa.
In de Bleiswijkse Zoom werd Actief Biologisch Beheer toegepast door het meer te verdelen in twee delen (Hoofdstuk 4). In een deel (3.1 ha) werd meer dan 75 % van de oorspronkelijke visbiomassa verwijderd, het andere deel diende als referentie. Direct na de afvissing werd het water in het voorjaar helder door afname van de algenbiomassa en afname van de hoeveelheid opgewerveld bodemslib. Het doorzicht nam toe van 20 cm tot zicht tot de bodem en binnen 6 weken raakte de bodem begroeid met kranswieren. Zowel de stikstof als de fosfaatconcentraties namen aanzienlijk af na de uitdunning van de visstand.

Effect van benthivore vis op de helderheid van het water (Hoofdstuk 5)
De resultaten van de Bleiswijkse Zoom en het gelijk behandelde Noorddiep gaven aanleiding voor een nader onderzoek van de rol van de bodemwoelende (benthivore) vis. In beide meren was voorafgaande aan de uitdunning van de visstand een hoge biomassa benthivore vis (grote brasem en karper) aanwezig, die het water troebel maakte wanneer zij op zoek ging naar bodemfauna. Metingen in deze meren laten een positieve relatie zien tussen de hoeveelheid benthivore vis en de hoeveelheid opgewerveld slib. Met een model is de invloed van het opgewervelde materiaal op het doorzicht van het water berekend, waarna de invloed van benthivore vis op de helderheid van het water is gekwantificeerd. Het effect van de vis op de helderheid is afhankelijk van de diepte van het water en de bodemsamenstelling. In een meer met een zandbodem is troebeling door de vis minder omdat het opgewervelde sediment sneller weer bezinkt.

Lange termijn (5 jaar) effecten van de maatregel (Hoofdstuk 6)
Nadat duidelijk was geworden dat een sterke uitdunning van de visstand in kleine wateren tot helder water kon leiden, bleef de vraag over of deze bereikte toestand op de lange termijn stabiel kon zijn. Daarom zijn in dit hoofdstuk de resultaten van 5 jaar na ABB van Noorddiep, Bleiswijkse Zoom en Zwemlust vergeleken met de resultaten van een Deens meer (Væng). In alle meren leidde een uitdunning van de visstand tot een lage visbiomassa, een lage algenbiomassa, een toename van het doorzicht en een abundante plantengroei. De totaal stikstofconcentratie nam af door opname van stikstof door de waterplanten en mogelijke versterkte denitrificatie. In de Bleiswijkse Zoom begon de helderheid van het water binnen vijf jaar af te nemen, waarschijnlijk veroorzaakt door de sterke toename van de visbiomassa en verstoringen in de vorm van herhaalde inlaten van troebel water. Het water bleef wel helder in het voorjaar, maar in de zomer nam de hoeveelheid watervlooien (*Daphnia*) af, werd het water troebel en verdwenen de waterplanten. In de andere meren bleef het water gedurende vijf jaar helder. In de zomer van het zesde jaar nam het doorzicht tijdelijk af in Zwemlust, terwijl ook in het minder eutrofe Deense meer (Væng) het doorzicht tijdelijk wat minder was, na een plotselinge instorting van de waterplanten. Een verslechtering van het doorzicht lijkt vooral plaats te vinden in de zomer en lijkt verbonden te zijn met het instorten van de planten. Bij een hoog aandeel roofvis en relatief lage nutrienten concentraties (zoals in Væng) kon de helderheid zich sneller herstellen dan in Zwemlust, waar de nutriëntenconcentraties veel hoger zijn en het aandeel roofvis aan de totale populatie geringer was.

Ontwikkeling van de visstand na Actief Biologisch Beheer (Hoofdstuk 7)
Het idee dat de waterplanten een verschuiving in vissoorten teweeg zou brengen is getoetst aan de ontwikkeling van de visstand na ABB in de Bleiswijkse Zoom, het Noorddiep en Zwemlust. In Zwemlust is na totale verwijdering van de vis, alleen snoek en ruisvoorn uitgezet. In Zwemlust is de uitgezette snoek niet in staat gebleken om de ontwikkeling van ruisvoorn te onderdrukken. In Noorddiep en de Bleiswijkse Zoom is de vispopulatie na het Actief Biologisch Beheer volgens verwachtig meer divers geworden. Brasem en karper werden minder dominant en zijn gedeeltelijk vervangen door blankvoorn en baars. In tegenstelling tot de verwachting kon predatie door snoek en baars de ontwikkeling van visbroed niet onder controle houden, maar zij hebben waarschijnlijk wel bijgedragen aan de verschuiving van brasem naar blankvoorn en baars, door selectieve predatie op brasem in het open water, terwijl de blankvoorn en de baars zich verschool in de vegetatie.

Actief Biologisch Beheer in een groot meer (Hoofdstuk 8)
Ook in een groot meer kan een drastische uitdunning van de visstand leiden tot helder water, zoals is aangetoond in het Wolderwijd (2650 ha). Uit dit meer is 425,000 kg vis verwijderd. Na de uitdunning is het water 6 weken zeer helder geweest door consumptie van de algen door de watervlooien. Vanaf eind juni verdwenen de watervlooien waarschijnlijk door predatie door visbroed en het water werd weer troebel. De uitgezette snoek was niet in staat om de produktie van broed te onderdrukken. De snoek heeft zich niet goed ontwikkeld, waarschijnlijk door het ontbreken van oevervegetatie. De tijdelijke verhoging van het doorzicht heeft de ontwikkeling van kranswieren op gang gebracht. Vanaf 1991 hebben de kranswieren zich sterk uitgebreid. Boven de kranswieren bleef het water de gehele zomer helder, terwijl in de rest van het meer het water troebel werd in de zomermaanden.

Evaluatie van 18 Actief Biologisch Beheers projecten (Hoofdstuk 9)
Vanaf 1990-1994 nam het aantal ABB projecten sterk toe doordat in die periode een landelijke subsidie-regeling van kracht werd. Niet alle ABB projecten waren even succesvol. Een evaluatie van achttien Actief Biologisch Beheersprojecten is uitgevoerd om te onderzoeken wat de kritische factoren zijn voor succes en welke mechanismen hierbij een rol spelen.
In 8 van de 18 beschouwde projecten is een omslag naar de heldere toestand verkregen. De meest bepalende factor voor het verkrijgen van een omslag naar helder water blijkt de mate van uitdunning van de visstand te zijn. Alleen in meren waarbij meer dan 75 % van de visstand is verwijderd, is een omslag naar helder water verkregen. In meren waar een dergelijke sterke uitdunning is uitgevoerd, kan opwerveling van het sediment door wind de toename in helderheid niet tegenhouden.
In twee meren is ondanks een sterke uitdunning van de visstand geen omslag naar helder water verkregen, in het ene meer door een zeer sterke aanvoer van troebel water, in het andere meer was de 75% grens net gehaald en bestond de achtergebleven vis vrijwel geheel uit kleine planktivore vis. Uit de gegevens van de meren is niet duidelijk geworden of een hoge dichtheid blauwalgen of een hoge dichtheid predatoren van de watervlo *Daphnia* een herstel in de weg kunnen staan.

Slechts in twee van de 18 meren is geen verbetering van het doorzicht verkregen. In de rest van de meren is wel een verbetering van het doorzicht opgetreden, maar geen zicht tot de bodem. De toename van het doorzicht was na uitdunning van de visstand significant hoger dan in Nederlandse meren waar geen maatregelen zijn uitgevoerd. De verbetering van het doorzicht en de verlaging van de algen biomassa is ook significant hoger dan in meren waar alleen de fosfaatbelasting is verlaagd.

In de relatief voedselrijke Nederlandse wateren blijkt het doorzicht in de loop der jaren na de maatregel af te nemen, maar zes-acht jaar na de maatregel is het doorzicht nog steeds een factor 2 hoger dan voor de maatregel.

Historische ontwikkeling van hypothesen (Hoofdstuk 10)
Tot slot is in het laatste hoofdstuk aangegeven hoe in de laatste vijftien jaar de ideeën over het effect van Actief Biologisch Beheer en de mechanismen die hierbij een rol spelen zijn veranderd.
Na vijftien jaar kan geconcludeerd worden dat een uitdunning van de visstand een effectievere maatregel lijkt dan oorspronkelijk gedacht. Verwachte negatieve effecten, zoals een toename van oneetbare algen, zijn nauwelijks aangetroffen. Wel blijkt dat de uitvoering van Actief Biologisch Beheer moeilijker te zijn dan vooraf werd ingeschat. De streefwaarde van > 75 % uitdunning van de visstand is in een aantal wateren niet behaald door onvoldoende financiële middelen, ongeschikt materiaal of intrek van vis van buitenaf.

Ook de ideeën over de werking van actief biologisch beheer zijn enigszins veranderd.
Werd in het prille begin vooral aandacht besteed aan de toename van *Daphnia* graas om de algen te reduceren, al gauw werd duidelijk dat in de ondiepe meren ook de reductie van benthivore vis zeer belangrijk is. Dit is niet alleen belangrijk ter reductie van de hoeveelheid anorganisch materiaal. Waarschijnlijk zorgt de afname van de benthivore vis ook voor een afname van de hoeveelheid nutriënten in het water. Door de afname van de hoeveelheid benthivore vis kunnen waterplanten, maar ook bodemalgen zich waarschijnlijk beter ontwikkelen.
Het belang van watervlooien voor het initiëren van de helder water fase in het voorjaar is door de toepassingen bevestigd, maar er is discussie over het helder houden van het water in de zomer. In de zomer lijkt vooral de aanwezigheid van veel waterplanten essentieel voor het helder houden van het water. Bij een dichte vegetatie op een klein deel van het meer kan plaatselijk helder water boven de planten ontstaan. Ongeveer 50-70 % van het meer moet waarschijnlijk bedekt zijn met planten, om het water in de zomer in het hele meer helder te houden. In de afgelopen vijftien jaar is gebleken dat er veel mechanismen zijn die via de waterplanten het water helder houden en dat niet in ieder water dezelfde mechanismen van belang zijn. Het belang van waterplanten als schuilgelegenheid voor zoöplankton blijkt ingewikkelder dan gedacht: ze lijkt sterk af te hangen van de hoeveelheid vis en de dichtheid van de vegetatie. In de meeste Nederlandse wateren is de potentiële rol van zoöplankton voor de graas van algen in de zomer moeilijk aan te geven, omdat de bemonstermethode voor het zoöplankton veelal onvoldoende nauwkeurig is. De oorspronkelijke gedachte dat de waterplanten de ontwikkeling van roofvis stimuleren, waardoor de ontwikkeling van visbroed laag blijft, is niet juist gebleken. In Nederland lijkt het gebrek aan oevervegetatie een beperkende factor voor de ontwikkeling van snoek, terwijl de beperkte ontwikkeling van baars in de richting van oudere jaarklassen nog niet volledig is begrepen. Vooral in eutrofe wateren lijkt de hoeveelheid visbroed in aanwezigheid van planten juist toe te nemen, waardoor *Daphnia* in de zomer sterk afneemt. In wateren met lagere nutriëntengehalten neemt de hoeveelheid broed na de

afvissing minder sterk toe. De versterking van de sedimentatie en de afname van de resuspensie van bodemmateriaal door de planten lijkt vooral een rol te spelen in de grotere wateren. In de kleinere wateren is meestal een sterke verlaging van de stikstofconcentraties gevonden. In het Wolderwijd leidde de verbetering van de helderheid tot een terugkeer van de driehoeksmosselen die de helderheid weer verder in stand houden door filtratie van materiaal uit de waterkolom, maar dit lijkt in de andere meren geen belangrijke factor te zijn. De visstand lijkt in alle meren na de *uitdunningsvisserij in aanwezigheid van planten te leiden tot een verandering van de* soortensamenstelling en een afname van de groeisnelheid van de benthivore vis. De rol van bodemalgen in het stabiliseren van de heldere toestand is nog niet precies bekend.

Implicaties voor waterkwaliteitsbeheer

Hoewel in Nederlandse meren de waterkwaliteit de laatste tien jaar aan het verbeteren is, valt zonder aanvullende maatregelen een omslag naar een heldere toestand in de meeste gevallen voorlopig nog niet te verwachten. Dit proefschrift laat zien dat Actief Biologisch Beheer een zeer effectieve methode kan zijn om zo'n omslag te versnellen.

Een overzicht van uitgevoerde experimenten toont aan dat nagenoeg elk meer waar tenminste 75 % van de vis is weggevangen helder wordt.
Een vergelijking van verschillende herstelprojecten laat ook zien dat afvissing niet alleen een groter effect op helderheid en algenbiomassa heeft dan maatregelen gericht op reductie van het nutriënten gehalte, maar verrassend genoeg ook leidt tot een substantiële verlaging van de fosfaatconcentratie in het water.

De kosten van Actief Biologisch Beheer zijn relatief laag vergeleken bij die van fosfaatreducerende maatregelen. In veel gevallen is een eenmalige afvissing voldoende om het water permanent helder te maken. In fosfaatrijke wateren moet de maatregel waarschijnlijk om de vijf jaar worden herhaald. Door de lage kosten van afvissing is zo'n beheer echter toch nog relatief goedkoop vergeleken met andere beheersmethoden. Ervaringen in andere landen laten zien dat herhaalde uitdunningen ook een uitkomst kunnen zijn in meren waar een drastische uitdunning van de visstand moeilijk is uit te voeren, bijvoorbeeld omdat ze in open verbinding staan met andere wateren.

Om de kans op succes te maximaliseren valt het aan te raden om ook de hoeveelheid kleine vis en de paaivis te minimaliseren. Tevens is het verstandig om van te voren geld te reserveren voor aanvullende onderhoudsvisserijen en onderzoek te doen naar de kiemkracht van zaden in de bodem om zonodig maatregelen te kunnen nemen om de kolonisatie door planten te versnellen (verondieping, aanbrengen van voorplantingsorganen).

De belangrijkste uitdaging van de toekomst is het succesvol toepassen van Actief Biologisch Beheer in open systemen, in meren met veel blauwalgen en in meren met een makkelijk opwervelbare bodem.

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Marie Louise Meijer
maart 2000

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OVER DE AUTEUR

De eerste kennismaking met eutrofiëring kwam voor Marie-Louise (3 augustus 1957, Den Bosch) in haar kindtijd, toen zij met haar vader ging kijken naar vissterfte in de wateren van het Hoogheemraadschap van Rijnland.
Na het behalen van het Gymnasium B-diploma is zij in 1975 begonnen met haar studie biologie in Leiden. De hoofdstage van haar studie omvatte 9 maanden onderzoek naar de beschikbaarheid van sedimentfosfaten voor algen onder leiding van Sjoerd Klapwijk bij het Hoogheemraadschap van Rijnland. Ze heeft ook onder zoek gedaan naar denitrificatie in rijstvelden bij Professor H.L. Golterman in het Biologisch Station Tour de Valat in de Camarque. Na het afronden van haar studie in 1982 heeft ze een beurs van de EG gekregen voor de vergelijking van de chemie van de Rijn en de Rhone. Hierna heeft ze in totaal 2 jaar onderzoek gedaan aan drijflagen van de cyanobacterie *Microcystis aeruginosa* bij het Zuiveringsschap Hollandse Eilanden en Waarden en bij de toenmalige Deltadienst van Rijkswaterstaat.
In april 1985 is zij in dienst getreden bij het RIZA. Vanaf 1985 is zij bezig geweest met praktijkexperimenten met Actief Biologisch Beheer, eerst in proefvijvers, later in kleine plassen en vanaf 1989 in het Wolderwijd. In 1989 heeft zij samen met anderen het congres Biomanipulation, Tool for Watermanagement in Amsterdam georganiseerd. Samen met Harry Hosper en Paddy Walker heeft zij de Handleiding Actief Biologisch Beheer geschreven. Van 1995 tot 1998 is zij bezig geweest met een evaluatie van de Actief Biologisch Beheers experimenten in Nederland. In 1999 was zij projectleider van de studie Stabiliteit van de Veluwerandmeren, waarin specialisten van het programma Ecologie Meren van het RIZA gezamelijk zijn gekomen tot een visie op de weerstand en de veerkracht van deze meren. Zij heeft de begeleidingscommissie Actief Biologisch Beheer uitgebouwd tot het huidige Platform Ecologisch Herstel Meren, een groep van ongeveer 80 waterbeheerders, onderzoekers en adviseurs die ervaringen uitwisselen over herstelprojecten in meren en plassen. Met het Wolderwijd-project heeft zij deelgenomen aan het EG-project ERIFER en ze is momenteel contactpersoon voor het EG project BIOMAN. Zij heeft op meerdere congressen lezingen gegeven en workshops geleid.
Zij is getrouwd met Eric Bergshoeff en heeft twee dochters:
Floor van 7 jaar en Pien van 5 jaar.
Vanaf 1992 werkt zij part-time.