Clearing Lakes

an ecosystem approach to the restoration and management of shallow lakes in the Netherlands

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Stellingen

1. Hoewel discussies rond het Nederlandse mestbeleid wellicht anders doen geloven, is de strijd tegen de 'groene soep' in de Nederlandse meren en plassen nog niet verloren.

2. Bloei van draadvormige cyanobacteriën (zoals *Oscillatoria agardhii)* en overmaat aan planktivore en benthivore vis, zijn de grootste blokkades voor ecologisch herstel van meren en plassen, nadat de externe fosfaatbelasting eenmaal is gereduceerd.

3. Het sterk uitdunnen van de visstand in een eenmalige wintervisserij, is voor kleinere, afgesloten plassen een effectieve en efficiënte maatregel voor bestrijding van algenbloei, zelfs bij relatief hoge fosfaatgehalten.

4. In grote meren- en plassengebieden kunnen reguliere wintervisserijen, gericht op het verlagen van de stand aan planktivore en benthivore vis, een bijdrage leveren aan de bestrijding van algenbloei.

5. De Ecologische Hoofdstructuur (EHS) verdient tenminste dezelfde publieke en politieke aandacht als andere grote infrastructurele projecten, zoals de Betuwelijn, de Hoge Snelheidslijn (HSL) en een tweede Schiphol.

6. De leus 'Lelystad, een dijk van een stad' zou sterk aan geloofwaardigheid winnen, en waarschijnlijk zelfs overbodig zijn geweest, als deze stad aan de dijk was gebouwd.

7. In een 'open plan proces' maakt 'Jutlandisering' een goede kans het te winnen van 'Nederland-Distributieland'.

8. Voor kennismanagement geldt dat het feitelijke leiderschap zal liggen bij diegene die de relaties in een netwerk van mensen op de meest aantrekkelijke wijze weet te voeden.
   Joseph W.M. Kessels, Het Corporate Curriculum, Inaugurele Rede 23 februari 1996, Rijks Universiteit Leiden.

9. Voor de ontwikkeling van de Europese gedachte is een 'eurotaal' belangrijker dan een 'euromunt'.

10. Symptoombestrijding wordt aantrekkelijker, als de oorzaken al zijn weggenomen.

Stellingen bij het proefschrift 'Clearing lakes, an ecosystem approach to the restoration and management of shallow lakes in the Netherlands'.

Harry Hosper, Wageningen, 13 mei 1997

Contents

Abstract

Eutrophication of lakes is a major problem for water management in the Netherlands. Lake restoration has been focused on the control of external P loading from point sources. However, this approach did not result in the water quality desired. The algae-dominated turbid water state may be extremely stable, and then additional measures are necessary to remove certain 'blockages', such as: the persistent bloom of *Oscillatoria* algae, the bloom-mediated P release from the sediments, and the abundance of fish, preventing zooplankton and submerged macrophytes from developing. This thesis addresses: (1) the lake conditions prior to disturbance, (2) the relationships between nutrient loading and lake response, (3) the control of P release from the sediments and *Oscillatoria* blooms by lake flushing and (4) the perspectives of fish stock management for the restoration of shallow lakes.

.. we have presented a version of eutrophication and of ecosystem behavior devoid of all assumptions but one, that phosphorus is important. Well, what is the answer? The answer is that we too must plug our ears and sail past the Sirens. We must learn to juggle all of the balls, if not at once, then a few at a time...

Joseph Shapiro (1979)

General introduction

Identification of the problem

Lake restoration is one of the major issues in water management in the Netherlands. Hundreds of millions of guilders are being spent yearly for nutrient control and additional lake restoration measures (Anonymous, 1995). In the first half of this century, the majority of shallow lakes was clear and the lake bottom was covered with vegetation. Now, most lakes look murky and green because of an excessive algal growth and the resuspension of sediments by fish and wind. Wildlife and recreational values have been severely negatively affected. Submerged plants have disappeared and the fish stock is characterized by large numbers of only a few species of prey fish, like bream and roach, and relatively low numbers of predatory fish, such as pike, pike-perch and perch. Eutrophication, i.e. increased nutrient loading, is the main cause for the deterioration of the lake ecosystems. Other perturbations, such as chemical pollution toxic to zooplankton, and the loss of lake-marginal wetlands, will have reinforced the effects of nutrient enrichment. The lake restoration strategy in the Netherlands has been focused on reduction of the external phosphorus loading. However, so far the control of external loading has not resulted in the water quality desired (Van Liere & Gulati, 1992; De Deckere *et al.*, 1996). The turbid lake ecosystem tends to be resistant to recovery and solely reducing of external nutrient loading seemed to be insufficient for attaining clear water conditions. A comprehensive approach to lake ecosystem functioning may provide additional tools for lake restoration.

General concepts and scope of this thesis

The development of the lake restoration strategy started with the 'Vollenweider approach', which aimed at criteria for external nutrient loading from the analysis of large numbers of different lakes (multi-lake studies) (Vollenweider, 1968). It then became clear that lake sediments, where most of the phosphorus (P) had accumulated, could act as a source of P, once the external loading had been reduced (Golterman, 1977). So, the reduction in external loading may be counteracted by (enhanced) internal loading, giving a marginal response in water quality. Additionally, ecologists argued that the biotic structure of the turbid water ecosystem (e.g. large numbers of zooplankton-eating and benthos-eating fish and no submerged macrophytes) also contributes to the resistance of the lake to recovery (Shapiro, 1980; Moss, 1983). Shapiro *et al.* (1975) had already emphasized the necessity of treating lakes as ecosystems, rather than 'containers of algae and phosphorus'. For understanding the algal dynamics and the mechanisms causing resistance in lake recovery, an ecosystem approach is needed. Fig. 1.1 shows a simple model of phytoplankton biomass, as a result of production and loss processes. Production by photosynthesis is controlled by external and internal nutrient loading and the availability of sunlight. Loss processes are consumption by filter-feeders (such as zooplankton and mussels), mortality (due to factors such as limiting resources or parasites), and sinking of algae to the sediments. Inflow and outflow are omitted in this model.

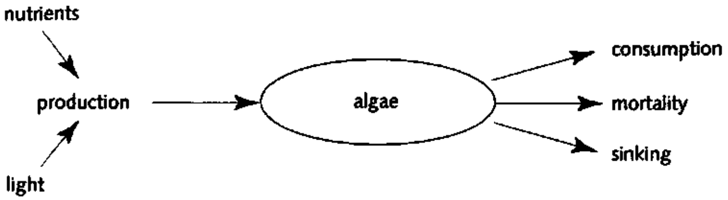

Fig. 1.1 *Algal biomass is the net result of production and loss processes.*

The algae are part of the lake ecosystem and the feedback from this ecosystem to the algae is lacking in the above model. Algae affect the physical (e.g. water turbidity), chemical (e.g. pH and oxygen levels) and biological lake conditions (e.g. food web structure, abundance of submerged macrophytes) and this effect is dependant on both the species composition and biomass of the algae. The changed lake conditions may, in turn, promote the algae, leading to a self-perpetuating process of increasing algal blooms (Fig. 1.2).

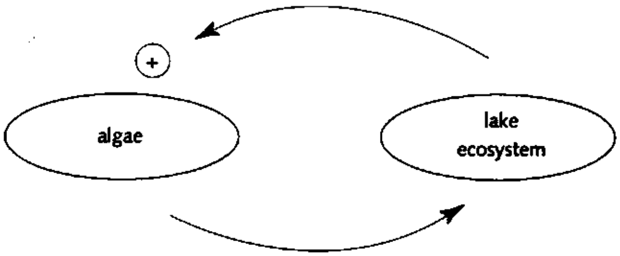

Fig. 1.2 *Interaction of algae and the physical, chemical and biological conditions of the lake ecosystem.*

Finally, light availability, which depends on lake depth (or mixing depth for stratified lakes) and non-algal turbidity, determines the upper limit of algal biomass. Understanding these feedback mechanisms is of primary importance for restoration and management of shallow lakes, as can be illustrated by the following examples:

Physical conditions

Algae make the water turbid. Beyond a certain threshold of lake turbidity, populations of submerged macrophytes in shallow lakes collapse, and with that the 'clearing effects' of the submerged vegetation. Providing refuge to grazing zooplankton, competition for nutrients between macrophytes and algae, and protecting the sediments against wind- or fish-induced resuspension, are among the major mechanisms by which vegetation makes the water clearer.

Chemical conditions

Algal production leads to a high sediment oxygen demand (by decomposition of sinking algae) and high pH (by net consumption of CO_2). Both factors, low redox potential and high pH at the water-sediment interface, enhance P release from the sediments (internal loading), thus fueling algal growth.

Biological conditions

Highly productive lake systems favor the development of blue-green algae (cyanobacteria). Cyanobacteria may show conspicuously low rates of loss, due to low maintenance energy requirements (low mortality rates), reduced edibility for zooplankton (low consumption rates), and buoyancy control by gas vacuoles (low sinking rates). Turbid lakes, devoid of vegetation, are low in piscivorous (fish-eating) fish, and high in planktivorous (zooplankton-eating) and benthivorous (benthos-eating) fish. Abundant planktivores control the zooplankton, resulting in low grazing of algae. Large numbers of benthivores, unhindered by plants, stir up the mud, thus contributing to turbidity and P release.

In addition to nutrient enrichment, several other perturbations affecting the lake ecosystem may indirectly result in a further deterioration of lake water quality (Fig. 1.3). Examples are the loss of shallow lake-marginal wetlands, intentional destruction of aquatic vegetation, heavy stocking of benthivorous fish, the inlet into lakes of external water with a significantly different macro-ionic composition, or pollution with toxic chemicals. The loss of lake-marginal wetlands, by strictly stabilizing the water levels (Coops, 1996) or by drainage, can enhance algal blooms. Wetland areas provide spawning and nursery habitat for the predatory fish pike, thus contributing to top-down control of algal biomass (Klinge *et al.*, 1995). Furthermore, vegetated areas act as a sink for nutrients, fine resuspended sediments and algae. High stocks of benthivores, like common carp and bream, may destroy existing stands of submerged vegetation. Altering the macro-chemistry by letting in river water (rich in macro-ions such as bicarbonate, sulfate and chloride) to peat lakes which were previously isolated, may enhance the internal loading of P from the sediments (Roelofs & Smolders, 1993; Beltman & Van der Krift, 1997). Pollution with chemicals toxic to zooplankton, may result in reduced grazing of algae (Hurlbert, 1975; Scholten *et al.*, 1994). In the 1970s, the Rhine river was acutely toxic to *Daphnia magna* (Sloof *et al.*, 1985), making it most likely that toxic chemicals reinforced the effects of eutrophication in Rhine-fed lakes at that time.

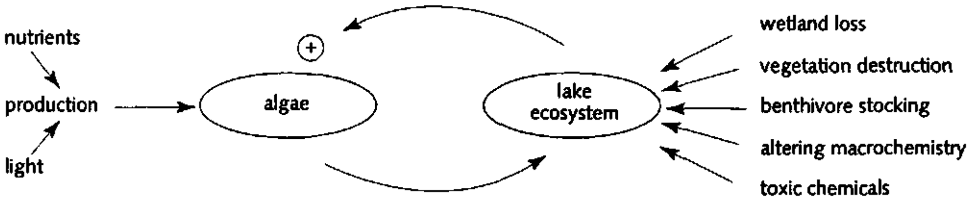

Fig. 1.3 *Perturbations other than increased nutrient loading may also indirectly promote algal blooms.*

A number of processes and factors regulating algal biomass, can be utilized for lake management purposes. Light and nutrients (and temperature) control the algal production. Light availability for algae may be reduced, for instance by deepening of the lake. Deepening and turning a shallow, vertically mixed lake into a deep stratified lake can also be effective for increasing the sedimentation of algae and non-algal suspended solids. The latter type of measures (changing the morphometry of the lakes) is beyond the scope of this thesis. Here, attention is focused on the control of external and internal nutrient loading and on biomanipulation, i.e. the manipulation of fish stocks aiming at increased consumption of algae and reduced resuspension of algae and sediments. It should be noted, however, that in lake restoration and management, negative influences such as pollution with toxic chemicals, and the loss of wetlands and littoral vegetation, should also be reversed. The lakes under study are shallow (mean depth 1-4 m) and vertically mixed throughout the year.

Structure of this thesis

Development of the lake restoration strategy (chapter 1)

In the lake restoration strategy the scope gradually broadened from solely controlling point sources of P, towards a more comprehensive and ecosystem-based approach. At present, P removal from sewage is common practice in the Netherlands, and phosphates in household detergents have been replaced by less harmful compounds. P levels in rivers and lakes are going down, but algal blooms tend to be persistent. Additional in-lake measures are being explored now.

Historical lake conditions (chapter 2)

A good picture of the undisturbed situation provides the basis for defining the goals and objectives for lake restoration. One natural lake (Naardermeer) and two lake areas resulting from peat mining (Reeuwijk lakes and Oude Venen) were selected for a reference study.

External nutrient loading and lake response (chapter 3)

From multiple lake studies in North America and Europe, Vollenweider (1968, 1975) derived relationships for external nutrient loading and in-lake variables, such as total-P (TP), total-N (TN), chlorophyll *a* and transparency. A first national eutrophication survey was conducted in 1976-1977, covering about 65 lakes, in response to Vollenweider's work. More extensive surveys were carried out during 1983-1985 (Lijklema *et al.*, 1988, 1989) and 1980-1988 (STOWA, 1993). From these data sets, criteria for nutrient loading and nutrient and chlorophyll *a* concentrations could be derived.

Internal phosphorus loading (chapter 4)
Sediments act as a source of P and so lake managers, investing in the control of the external P loading, are interested in the extent and duration of the internal loading and possible additional measures to reduce the internal loading. In the lake sediments in the Netherlands, iron plays a key role in the binding of P (Van der Molen & Boers, 1994). The solubility of P is determined by pH and redox conditions. Raised pH and low redox result in P release (Lijklema, 1977, 1980). So increased algal abundance, by photosynthesis and decay, may stimulate P release. This hypothesis was tested in Veluwemeer, a large shallow lake (3,356 ha, mean depth (z) = 1.25 m), which suffered from persistent cyanobacterial blooms. The lake has been flushed during winter in order to interrupt the algal bloom and to break the vicious cycle of high algal biomass, raised pH and related P release from the sediments.

Biomanipulation (chapters 5 and 6)
In biomanipulation, food web interactions are manipulated to increase lake clarity. By removing planktivorous fish during winter, the spring zooplankton is favored, resulting in increased grazing, low algal biomass, clear water and consequently more submerged macrophytes. Strong 'clearing effects' of submerged vegetation lead to a stabilization of the clear water state. By removing benthivorous fish, sediment resuspension is reduced, thus contributing to reduced turbidity of the lake water. After a number of successful, small-scale case studies (chapter 5), a biomanipulation experiment was conducted in the large and shallow Wolderwijd (2,555 ha, z = 1.60 m) (chapter 6).

Guiding restoration and management (chapter 7)
In the final chapter an integration is attempted, resulting in practical guidelines for restoration and management. The lake condition is described in relation to the process of eutrophication and the reverse process of oligotrophication. The concept of 'stable states, buffers and switches' explains the resistance of shallow lake ecosystems to changing nutrient loading. Lessons for lake restoration could be learned from the biomanipulation case studies and from the stepwise restoration process of Veluwemeer.

Development of the lake restoration strategy

From the late 1960s to the 1990s, the strategy for lake restoration gradually evolved from solely phosphorus stripping at sewage treatment plants towards a more comprehensive and ecosystem-based approach, including the control of non-point nutrient sources and in-lake measures such as dredging, flushing and biomanipulation. In his report for the OECD, Vollenweider (1968) brought the problem of eutrophication to the notice of administrators and water management authorities. Although the key role of P was not yet generally recognized (Legge & Dingeldein, 1970), the OECD report triggered a great deal of political and scientific activity, which focused on P control. The proceedings of the symposium 'Eutrophication; causes, consequences, correctives' (NAS/US, 1969) is another excellent reference from the early days. Vallentyne (1974) addressed the non-specialist audience with his book The Algal Bowl, the title of which refers to the great American Dust Bowl of the 1930s. Sweden was a pioneer in lake restoration. As early as 1975, P removal from sewage was common practice and the effects on water quality were extensively monitored (Forsberg *et al.*, 1975; Hosper, 1975; Ryding & Rast, 1989). In 1970-1971, dredging of sediment was carried out successfully to control internal nutrient loading in the Swedish lake Trummen (200 ha) (Björk, 1972; Eiseltová, 1994). Andersson *et al.* (1978) and Andersson (1988) had already experimented with biomanipulation in Trummen in the 1970s.

The importance of P release from sediments and particularly the relation of mobilization to redox conditions, was already recognized by Einsele (1936, 1938) and Mortimer (1941, 1942). Golterman *et al.* (1969) pointed out the relevance of P release for lake restoration and in 1976 the first international conference on the interactions between sediments and freshwater was organized in Amsterdam (Golterman, 1977). It became clear that significant P release also occurred under aerobic conditions, during the growing season (Golterman, 1977). Andersen (1975) and Lijklema (1977, 1980) emphasized the effect of raised pH in shallow lakes, as a result of photosynthesis, on P release. Altering the alkalinity or sulfate content (Roelofs & Smolders, 1993; Smolders & Roelofs, 1995) or the salinity (Barendrecht, 1993; Beltman & Van der Krift, 1997) of the lake, by the inlet of river water into formerly isolated peat lakes, has been suggested to be a cause of P release from peaty sediments.

Hrbáček *et al.* (1961), Brooks & Dodson (1965) and Brooks (1969) emphasized the role of fish and zooplankton in controlling phytoplankton. Later, other researchers stressed the importance of this top-down control for lake management and restoration (Hurlbert *et al.*, 1972; Shapiro *et al.*, 1975; Shapiro, 1980; Andersson *et al.*, 1978; Fott *et al.*, 1980; Moss, 1983, 1987; Lampert, 1983; Benndorf *et al.*, 1981, 1984; Carpenter *et al.*, 1985). An inadvertent biomanipulation in Lake Washington (USA) showed very clearly the relevance of food web interactions for algal biomass and transparency (Edmondson, 1979, 1991). Some fish species invaded Lake Washington, and this resulted in a decline of the planktivorous *Neomysis*, an increase in large, algae-grazing zooplankton and consequently, an increase in clarity of the lake. Practical experience with biomanipulation in whole lakes, however, was still very limited at that time and mostly directed to manipulation of predatory fish (Benndorf, 1988; Gulati *et al.*, 1990).

In the Netherlands, the problem of eutrophication was first described by Golterman (1965, 1970) and Leentvaar (1970), and later by the 'task force on phosphates' (KNCV, 1976). Numerous research reports and government policy documents followed (CUWVO, 1976, 1978, 1980; Hosper, 1978a, 1978b, 1980a; Schmidt-Van Dorp, 1978; Anonymous, 1979).

The state of the art then was presented at the symposium Eutrophication in the Netherlands (Dorgelo & Bakker, 1980) and later at the KNCV symposium (KNCV, 1984). In the 1980s, it was increasingly recognized that in addition to a general (inter-)national nutrient control policy, a lake-specific approach is necessary for successful restoration (CUWVO, 1983; Anonymous, 1989). The general policy of reduction of the P loading from sewage and industrial waste water in the Netherlands and in the international Rhine river basin, was very successful. The P discharge from point sources within the Netherlands (sewage, industry), decreased by around 65%, during the period 1985 to 1995 (Fig. 1.4). Presently, the major contribution comes from non-point sources (mainly agriculture) and reduction of these sources can be anticipated in the long term only (WSV, 1996). The P flow in the river Rhine, the main source of freshwater for the Netherlands, has also shown a significant decline (Fig. 1.5). In the years to come, N elimination from sewage will be phased in (Anonymous, 1995).

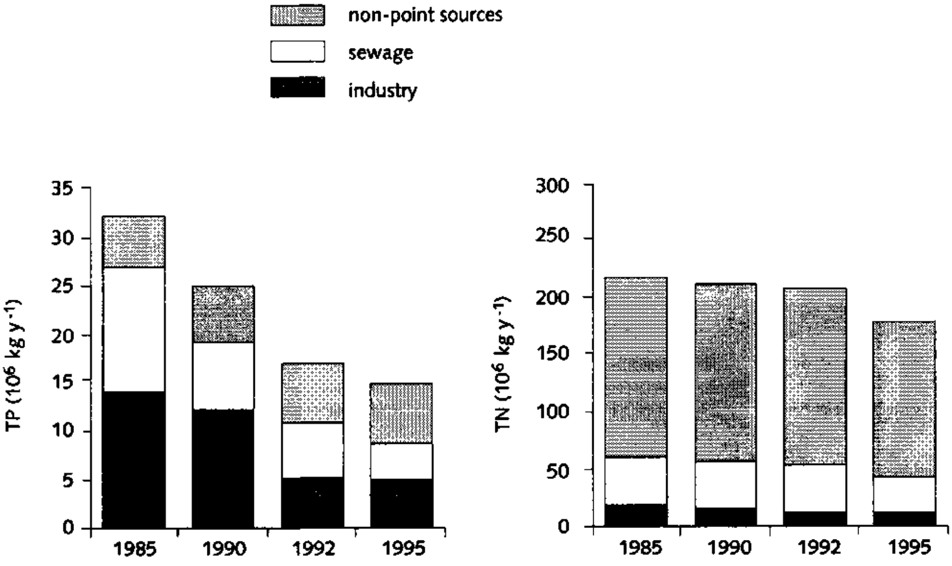

Fig. 1.4 *Discharges of TP and TN into surface waters from different sources in the Netherlands (from Anonymous, 1995).*

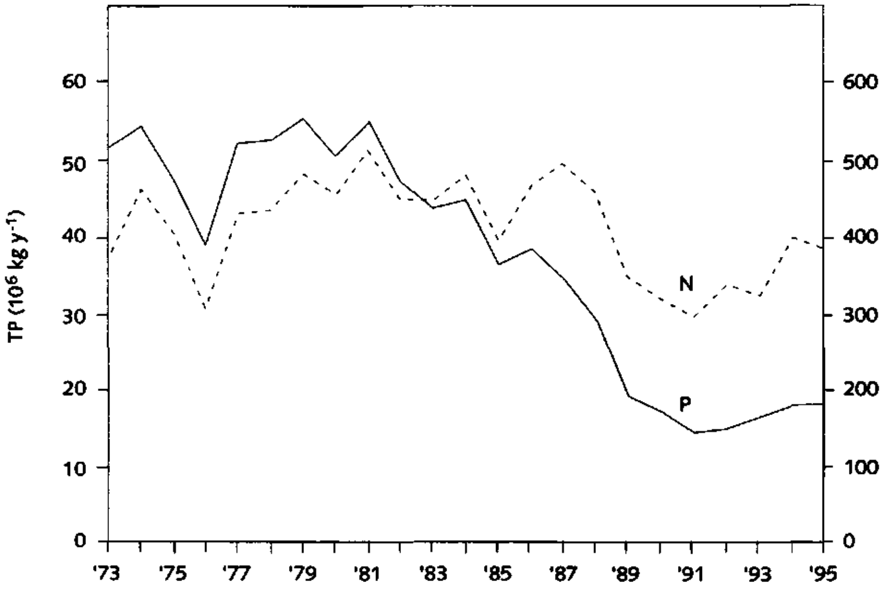

Fig. 1.5 *Flows of TP and TN in the Rhine river at Lobith (German-Netherlands border), 1973-1995 (from Anonymous, 1995 and RIZA).*

Examples of a lake-specific approach include diversion or treatment of nutrient-rich inflows, manipulation or dredging of sediments and biomanipulation. Cooke *et al.* (1993) provide an excellent review of the available restoration procedures. Other handbooks for the control of eutrophication have been written by Ryding & Rast (1989), Eiseltová (1994) and Moss *et al.* (1996). In the Netherlands, a temporary government grant for lake restoration (the REGIWA grant, 1991-1994), stimulated new large-scale pilot projects. Recently, biomanipulation, particularly fish stock reduction, has shown promise as a powerful tool for restoration of shallow lakes in the Netherlands (Hosper *et al.*, 1987; Van Donk & Gulati, 1989; Gulati *et al.*, 1990; Hosper *et al.*, 1992).

Chapter 2

Shallow lakes in the Netherlands: searching for lake restoration objectives

Introduction

Sustainable use, conservation of biodiversity and self-regulation are the leading principles for water management in the Netherlands (Anonymous, 1989). It is obvious, that for decision making in water management planning, these broad goals have to be translated into more specific objectives. What kind of ecosystems, in relation to water uses, provide guarantees for the fundamental values of sustainable use, biodiversity and self-regulation? Ten Brink *et al.* (1991) presented a semi-quantitative method for description and assessment of aquatic ecosystems, the so-called AMOEBA-approach. The assumption is made by the authors, that the ecosystem prior to disturbance, the 'reference system', offers the best guarantee for the desired ecological sustainability. Such an approach is in agreement with the recommendations of the National Research Council U.S. (1992), which stated that the goals of aquatic ecosystem restoration are 'to emulate a natural functioning, self-regulating system that is integrated with the ecological landscape in which it occurs'. An ecosystem which has not, or has been only slightly influenced by human activities, may provide clues to define key variables and processes, expressing ecological sustainability. The closer one comes to the reference system the larger the guarantee for ecological sustainability and vice versa. Society will choose its objectives somewhere between 'zero' and the point of reference. The search for a concrete ecological objective can therefore be reduced to the question: what is the maximum acceptable deviation from the reference system? Accepting this approach, lake restoration can now be defined as all efforts which bring the lake closer to the historical reference system. For recent manmade lakes an historical reference does not exist and in these cases goals and objectives for lake management could be derived from knowledge of comparable natural lake systems elsewhere, or from ecological theory (Ten Brink *et al.*, 1991).

Most shallow (1-4 m) lakes in the Netherlands are located in the low-lying peat areas of the northern and western part of the country (Fig. 2.1). These relatively 'old' lakes (at least by Dutch standards) originate either from flooding and erosion of the peat, or from peat mining. Some of the peat lakes were excavated for sand production down to a depth of 10 to 50 m. In the 20th century, other large manmade lakes have been constructed by (partly) damming off estuaries from the sea. Lakes bordering the large rivers result from flooding or from sand, clay and gravel mining. Numerous small and mostly low alkalinity lakes are found in the sandy eastern and southern part of the Netherlands. Some of these lakes are also the result of sand extraction for construction purposes.

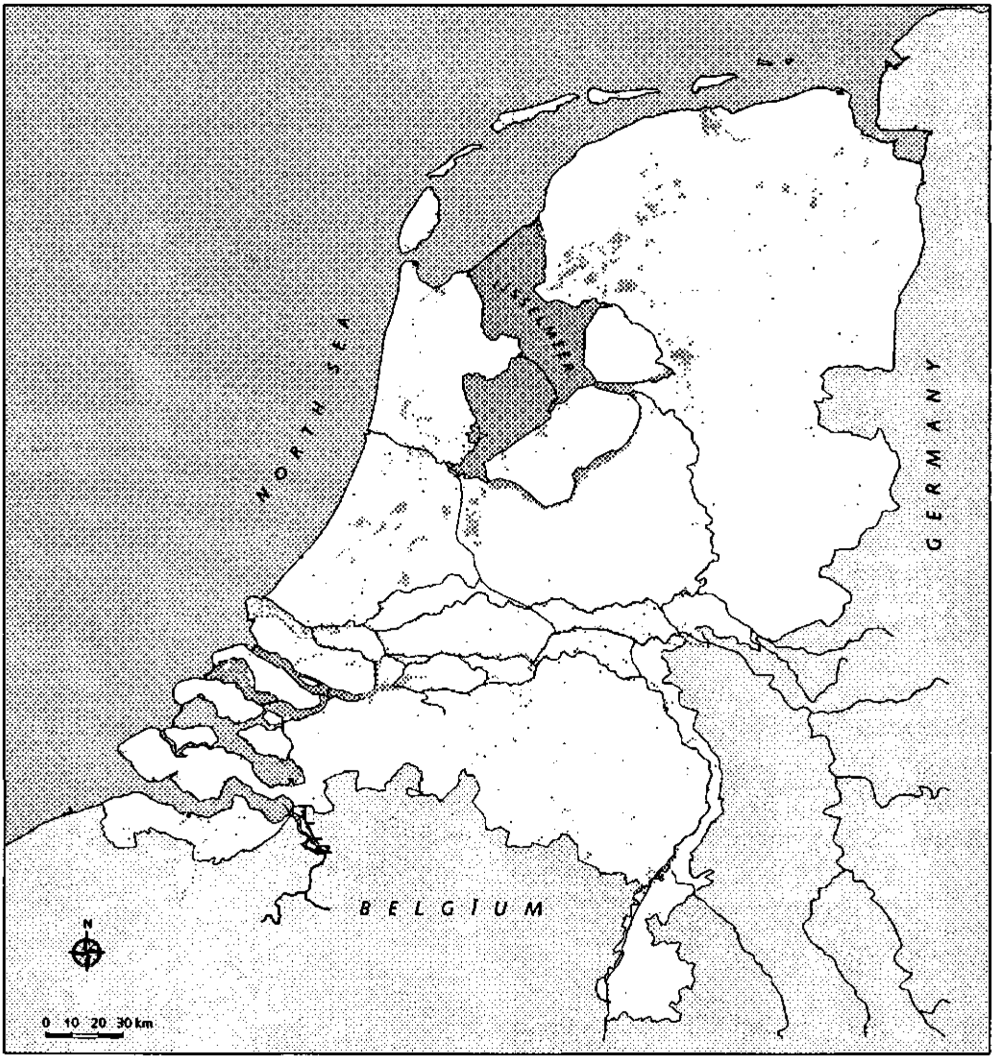

Fig. 2.1 *Lakes and large rivers in the Netherlands.*

In this chapter, an attempt is made to reconstruct the historical reference system for three peat lakes in different parts of the Netherlands: Naardermeer (North-Holland province), Reeuwijk lakes (South-Holland province) and Oude Venen (Friesland province). The reference system will be described in terms of target variables, such as transparency, macrophyte cover and fish stocks and related steering variables, such as nutrient loading, water level manipulations and fish stock management. For a better understanding of the characteristics and the functioning of shallow peat lakes, this chapter begins with an overview of the origin of this type of lakes.

Origin of peat lakes in the Netherlands

Schultz (1992) and Van de Ven (1994) give excellent overviews of the history of water management and land reclamation in the Netherlands. The following is derived from these references, supplemented by information from local water management authorities.

By 800 AD, man had, as yet, little influence on the landscape. The main processes forming the landscape were the formation of peat and the sedimentation and erosion by the sea and the rivers. Extensive peat areas covered large parts of the Netherlands and the surface level of most of the peatland was well over mean sea level. After 800, man became more and more the decisive factor in the formation and degradation of the landscape. The peat areas behind the coastal dunes were reclaimed for agricultural purposes by artificial drainage (with ditches and canals). Consequently, the surface level of the reclaimed peat areas dropped considerably, in some areas by several meters. These lowlands became extremely vulnerable to flooding and erosion. Between 800 and 1250 there was an enormous loss of land. Around 1250 numerous freshwater lakes had come into being in the western Netherlands (e.g. West Friesland lakes, Beemster, Schermer, Purmer, Spieringmeer and the large Haarlemmermeer, 18,000 ha) and in the northern part of the country (in Friesland, the swamps of the Lage Midden with among others Tjeukemeer, Slotermeer, Fluessen and Sneekermeer). Due to continuing land subsidence, drainage of the peat areas became more and more difficult. Sometimes it was impossible to drain during prolonged periods of time, as the water level outside was higher than in the ditches. This problem was solved by the introduction of the windmill in the early 15th century.

The period of 1600-1850 was very dynamic in landscape forming. On the one hand numerous new lakes were created by peat mining, on the other many natural lakes and peat mining lakes were drained and turned into arable land. Peat was the main source of energy before coal, oil and natural gas were available on a large scale and at a reasonable price. For centuries, the population dug or dredged and subsequently burned up this 'burnable land'. Two techniques can be distinguished for the digging of peat. The oldest technique is peat cutting above the groundwater level, which is also called dry peat cutting. The other technique involves peat dredging below the groundwater level, which is also called wet peat cutting. The method became popular in Holland and Utrecht around 1550. The dry technique was used in Overijssel, Friesland and Groningen, but from the mid 18th century onwards, the wet peat digging was used in these provinces as well. In the technique of wet peat digging the peat was pulled out of the water by a hand drag from a barge or a plank and thrown into the barge. After that it was spread evenly across a so-called 'legakker', a strip of ground conserved for this purpose. When the peat had dried sufficiently, it was cut into the required shape and piled up in stacks for further drying. The land that had been dredged turned into water, the so-called broad meres, and the remaining strips of ground were used as hay meadows. Under the influence of wind and the wash of waves the strips of ground eroded and gradually disappeared in many places, and the broad meres expanded. Many lakes of today in the

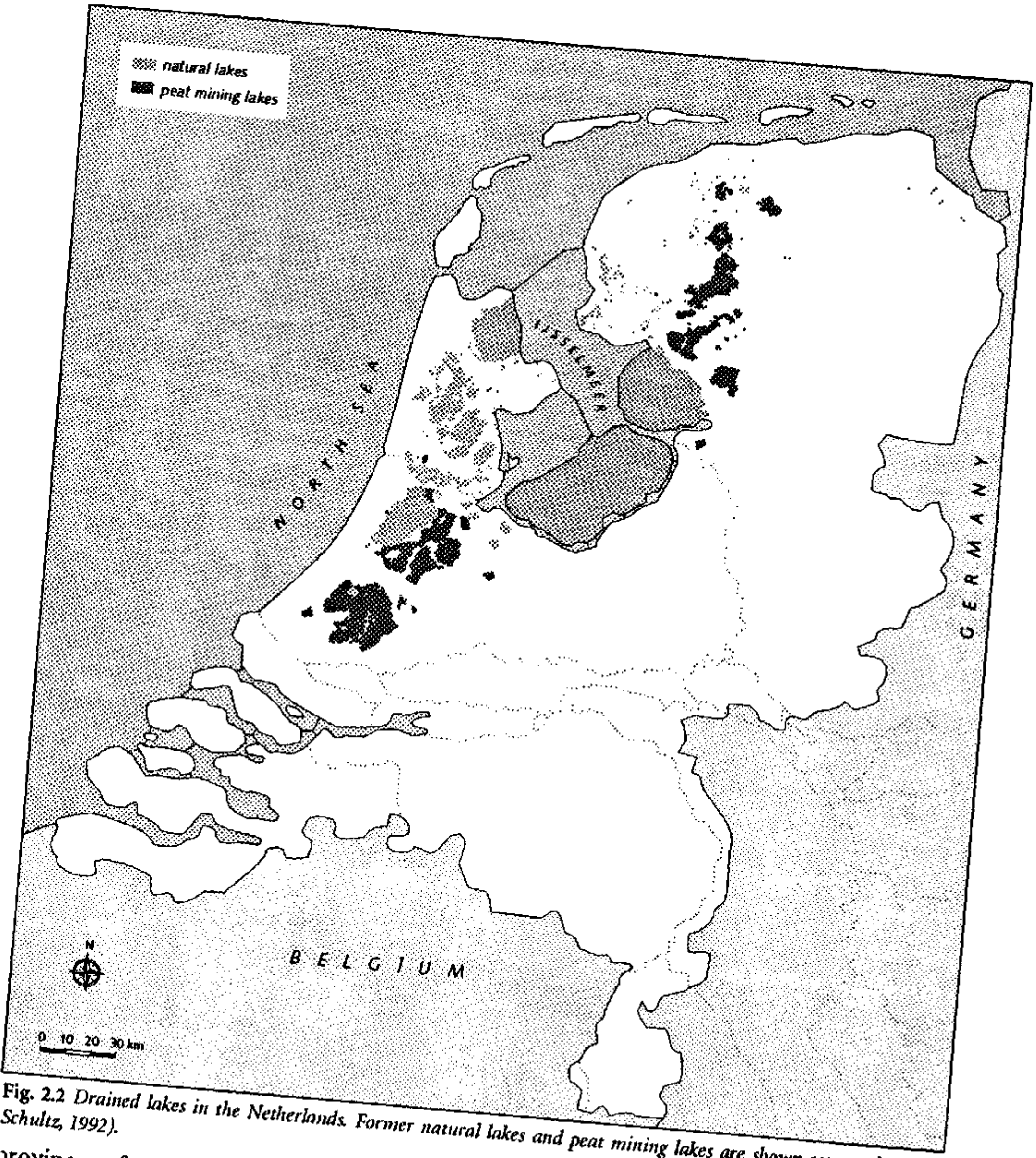

Fig. 2.2 *Drained lakes in the Netherlands. Former natural lakes and peat mining lakes are shown separately (from Schultz, 1992).*

provinces of South-Holland (Nieuwkoop lakes, Reeuwijk lakes) and Utrecht (Loosdrecht lakes, Vinkeveen lakes) and later also in Overijssel (Weerribben, De Wieden), Friesland (De Leijen, Oude Venen, Nannewijd) originated from the wet peat digging.

Hundreds of lakes, varying largely in area, have been drained by windmills and later steam power (Fig. 2.2). The main reason for draining, particularly of the large lakes, was the prevention of flooding. Additionally, there was the advantage of obtaining arable land. The most spectacular land reclamation in the 19th century was the Haarlemmermeer in 1852. The present-day Kagerplassen, Westeinderplassen and Braassemermeer are the remains of the former Haarlemmermeer and other large lakes in the area. The large lake Zuidplas (4,000 ha), between Rotterdam and Gouda, was reclaimed in 1839 and the danger that the whole of midden-Holland would turn into one big expanse of water had been averted. The Zevenhuizerplas and the Rotte Meren are remains of the former Zuidplas. The reclamation of the broad mere Alexanderpolder (2,700 ha), adjacent to the Zuidplas, followed in 1873. The Kralingse plas remained out of this reclamation project. The present-day Alkmaardermeer and Uitgeestermeer are remains of former large lakes in North-Holland.

In search of a reference system for peat lakes

"In our shallow lakes generally sunlight reaches the bottom. Macrophytes can grow down to a depth of 4 to 5 meters and usually cover the whole lake bottom". This quote from Redeke (1948) indicates that in the 1940s, the shallow lakes in the Netherlands used to be clear and rich in submerged macrophytes. So, at that time the lakes differed largely from the present-day turbid lakes and for that reason the years before 1950 have been focused on in this study. After a broad survey of the literature, which gave insight in the availability of data, three lake areas were selected for further study: the natural peat lake Naardermeer and two lake areas resulting from peat mining, the Reeuwijk lakes and the Oude Venen.

Naardermeer

Description of the lake

The present-day Naardermeer of about 200 ha of open water (mean depth 1 m) and 800 ha of marshland is one of the oldest 'natural' lakes in the Netherlands. The lake has a predominantly sandy sediment, with peat, clay and soft organic mud locally. The lake was formed in the middle ages by flooding, followed by erosion of the peatland. Around 1500, the lake was dammed off from the river Vecht and the Zuiderzee. Because of insufficient return on the necessary investments, the lake 'survived' several attempts of drainage and reclamation (in 1628 and in 1884). A railway track across the lake was completed in 1874. Since 1906, the lake has been a nature reserve. Until the beginning of the 17th century, the Naardermeer was one large lake. Later on, extended marshlands developed in and around the lake and the area of open water fragmented into some smaller lakes. The lake is fed by nutrient-poor groundwater from the adjacent, elevated sandy area ('t Gooi). Groundwater extraction in 't Gooi for drinking water supply, and the continuing drainage of the surrounding grasslands, resulted in a decreased inflow of groundwater to the lake. Therefore, in the summer season more and more nutrient-rich water from outside has had to be supplied, leading to eutrophication. In 1960 the lake manager decided to stop this inflow and parts of the lake desiccated in summer, as a result. From 1984 onwards, the water supply has been resumed, but now phosphorus is removed from the inflow by chemical treatment. In 1985 the location of the large cormorant colony (> 2,000 pairs), was hydrologically isolated from the lake (Barendrecht *et al.*, 1989).

Target variables

Van Zinderen Bakker (1942) wrote: *"Looking overboard, in the middle of the lake, I am searching the lake bottom. An endless meadow of light green stonewort stretches out before me ... These stoneworts are seen in all parts of the lake."* In 1943 at least the following Charophytes were found: *Chara aspera*, *Chara vulgaris*, *Nitella flexilis* and *Nitella obtusa* (Nat *et al.*, 1994). A few years later, Van Zinderen Bakker (1948) gave his observations about the littoral vegetation: *"Nowhere else in the western Netherlands, do we find such a broad belt of emergent vegetation, providing habitat for numerous plants and animals. The lakes of the Naardermeer may be small and shallow, the reedbelts and woodlands however, are very extensive ... It is a great advantage that these littoral zones are not split up into narrow strips of land, as is the case in all the lakes formed by peat digging."* The same author in discussion with the local fisherman, states that eel is most important for commercial fishery, but that other species such as tench, perch, pike, rudd and bitterling are abundant as well. The first observations of algal blooms in the lake were made in 1959 (Bakker *et al.*, 1976). Otters were observed in the area until 1963.

Steering variables

There are no data on nutrient levels before 1950. It can, however, be assumed that nutrient loading was extremely low, during the years that groundwater and rainwater were the only possible external nutrient sources. The water level of the Naardermeer was fairly constant over the year. Fluctuations were less than 10 cm and the peaty, littoral zones follow these movements of the water level (Van Zinderen Bakker, 1942). Fishing is of minor importance to the functioning of the Naardermeer ecosystem. For many generations, only one family (the Hoetmer family) fished in the lake, mainly for eel. It is obvious that the changed hydrology (a negative water budget, due to decreasing inflow of groundwater and ongoing drainage of the surrounding polders), necessitating the inlet of nutrient-rich water from outside, is the fundamental cause of deterioration of the lake.

Reeuwijk lakes

Description of the lake

The Reeuwijk lake area consists of eleven, interconnected shallow lakes, in all 714 ha of open water with a mean depth of about 2 m. The lakes have a varied sediment of sand, peat and clay and originate from peat mining in the 16th and 17th century. Small-scale peat digging continued up to the 1950s. Adjacent to, but completely isolated from the shallow lake area, is the deep lake Broekvelden-Vettenbroek. This lake has a maximum depth of 30 m, as a result of sand extraction in the 1960s. The shallow and peaty Reeuwijk lakes have become highly eutrophic during the last decades. Lake shore residents remember the early 1960s as the period of transition from a clear water state towards a turbid water state (Van Gemeren, 1993). The main sources of nutrients are the inlet of water from the Rhine river (for water level management) and the effluent from the sewage treatment plant for the city of Reeuwijk. Phosphorus was removed from the sewage by chemical treatment from 1986 onwards (Van der Vlugt & Klapwijk, 1990). No improvement in algal biomass and transparency has been observed so far (Van der Vlugt & Klapwijk, 1990; Van der Vlugt & Van der Veer, in press).

Target variables
Van Gemeren (1987, 1993) analyzed the historical development of the lakes and described the conditions in 1930: *"In those days the water was unimaginably clear. While removing their egg shells, peat diggers could watch them fall down to the bottom of the lake"*. Nat *et al.* (1994) in their extensive historical review of the abundance of Charophytes, report that in 1938-1944, *Chara contraria*, *Chara globularis* and *Nitellopsis obtusa*, were observed in one of the lakes. Van Gemeren (1993) concluded that the Reeuwijk lakes, and particularly the southern part, were dominated by submerged macrophytes in the 1930s. In the northern part the water was more turbid and brownish and the macrophytes were less abundant. Aerial photographs in Van Gemeren (1993), show an extensive littoral vegetation of reed (*Phragmites*) and cattails (*Typha*). In 1930, 95% of the shores of the lakes Groot Vogelenzang and Klein Vogelenzang were vegetated, while 28% was left by 1989. Scheygrond (1933) reported about the fish stock: *"In the past years, valuable fish species were successfully introduced, such as pike-perch, houting, common carp, tench and eel... By seine fishing large numbers of pike, bream, white bream, roach and perch are being caught. Every year some thousands of pounds of white bream are removed and stocked elsewhere"*. Oskam (1973) interviewed the fishermen about the abundance of fish in the 1940s, compared to the 1970s. All species showed a decrease or were stable. A major decrease in abundance was reported for smelt, bleak and burbot. Some other species decreased as well: pike, tench, bitterling, roach, rudd and perch. In both periods bream was abundant and pike-perch was a common species. Finally, otters were observed in the area up to the mid 1970s.

Steering variables
Unfortunately, long-term trends in nutrient loading from the different sources are not available. It is most likely that the inlet during dry periods of increasingly polluted river water, together with the sewage discharge, caused the collapse of the clear water state around 1960. A large number of fishermen were active in these lakes, compared to the Naardermeer. Scheygrond (1933) reported that about 30 to 50 families earned a living by fishing. Pike-perch has been introduced in the lakes, since the end of the 19th century. Oskam (1973) mentioned that, especially in the 1920s, the lakes were stocked with pike-perch. It was noted before that every year some thousands of pounds of white bream were removed from the lake (Scheygrond, 1933). It might be speculated that the commercial fishery in these lakes contributed to the stability of the clear water state. Regular fishing on planktivorous fish may promote the zooplankton and consequently the grazing on algae. Because of intra-specific predation in populations of predatory fish (e.g. pike and pike-perch), the removal of the larger specimen of predatory fish indirectly leads to an enhanced predation on planktivorous fish. Additionally, the removal of benthivorous fish leads to reduced resuspension of sediments (see chapter 5).

Oude Venen

Description of the lake

The Oude Venen is a varied wetland area of lakes and marshland, 2,500 ha in all. The six largest lakes have a mean depth of 1.7 m. The sediment of the lake is peat and sand, with some clay locally. Around 1700, the greater part of this area was still peatland. Shortly after then peat digging started. The peat was removed down to the sandy subsoil, leaving open water. Large broad meres came into being, reinforced by wind and waves. The peat digging continued up to the 19th century. Some of the lakes were drained and turned into grasslands. On the west side, the lakes were in open connection with the Friesland lake system. On the east side, nutrient-poor groundwater from the sandy hills of Drenthe and the Garijp-Oudega area seeps into the lake (Klink, 1987). Continuing drainage of the surrounding polders to ever lower water levels, resulted in a loss of water from the lakes to the polders. Consequently, the influence of the more and more eutrophic Friesland lakes on the Oude Venen has increased.

Target variables

In his book on the Oude Venen, Zandstra (1948) reported algal blooms: *"One of those algae, a so-called blue-green alga, can be frequently found in our lakes. During calm weather these algae may rise and accumulate at the lake surface, causing 'algal bloom'"*. Several species of submerged macrophytes were observed in the lakes: *Ceratophyllum demersum, Elodea canadensis, Potamogeton lucens, P. pectinatus* and *Fontinalis antipyretica*. Charophytes were not reported. Most lakes in the Oude Venen showed a western zone (to the leeward) with a well-developed littoral vegetation, mainly with reed and cattails, and an eastern zone (on the windward side), with an eroded shoreline. Common fish species were pike, rudd, tench, perch, roach, eel, ruffe and common carp. It is striking that pike-perch was a rare species and bream was not mentioned as a common species. Zandstra (1948) also described the spawning conditions for the fish: *"Those shallow, macrophyte-dominated lakes which can be found in the Oude Venen, provide excellent spawning conditions for the fish ... When the water level is high, the pike leave the lake and we can see them spawning over the grassy shorelands"*. In the 1930s the otter was the most characteristic mammal of the Oude Venen. The last otter was killed in a car accident in 1988.

Steering variables

As for both other case studies, data on nutrient levels of the period before 1950, are not available. The nutrient levels in the Oude Venen are the net result of the inflow of nutrient-poor groundwater and the exchange with the relatively nutrient-rich water of the Friesland lakes. Due to this exchange, it may be assumed that the nutrient levels in the Oude Venen were higher than in the hydrologically more isolated and groundwater-fed peat lakes such as the Naardermeer and the Loosdrecht lakes. Water level dynamics have changed dramatically over the past 100 years (Ligtvoet & Grimm, 1992). During winter and spring, extended grassland areas used to be flooded and as noted before (Zandstra, 1948), the predatory fish pike makes use of these shallow vegetated areas for spawning. Commercial fishing was of great importance in the Oude Venen (Zandstra, 1948). About 20 fishermen earned a living in these lakes, fishing for eel, tench, pike and bream.

Discussion

This study attempted to reconstruct the reference system for three shallow peat lakes in the Netherlands: Naardermeer (mean depth 1.0 m), Reeuwijk lakes (mean depth 2.0 m) and Oude Venen (mean depth 1.7 m). The reference system is defined as the state of the lake prior to disturbance, and should be described in terms of target variables (such as transparency, macrophyte cover, fish stocks) and related steering variables (such as nutrient loading, water level manipulations, fish stock management). Information was derived from (grey) literature and from interviews with regional lake experts.

Circumstantial evidence (Redeke, 1948; interviews) suggested that many shallow lakes showed a major deterioration in transparency during the 1950s and 1960s. Therefore, this reference study focused on the period before 1950. The information collected refers mainly to the 1930s and the 1940s. It may be concluded that during that time, all three lakes were in a clear water state with a more or less dense submerged vegetation. However, there is some evidence that the trophic state increases from the Naardermeer, through the Reeuwijk lakes to the Oude Venen. Charophytes (i.e. indicators for clear water) were abundant in the Naardermeer, less abundant in the Reeuwijk lakes, and were not reported from the Oude Venen. Occasional cyanobacterial blooms of scum-forming species were observed in the Oude Venen. The littoral vegetation of mainly reed and cattails, was very well-developed in the Naardermeer and the Reeuwijk lakes. The Oude Venen showed a vegetated littoral zone in the west, but an eroded littoral zone in the east. Pike, rudd and tench, fish species indicating clear and vegetated waters (Willemsen, 1980), were common in all three lakes. However, the indicators for turbid waters, bream and pike-perch (Willemsen, 1980), were also common in the Reeuwijk lakes. Unfortunately, there are no data on nutrient concentrations or nutrient loading for that period. In the Oude Venen the strong natural fluctuations of the water level may have favored the pike reproduction. The Oude Venen and particularly the Reeuwijk lakes were intensively used for commercial fishing. The role of the fishing in maintaining the clear water state remains uncertain and should be evaluated in more detail.

In conclusion, the stability of the clear water state appears to be different for the three lakes (Table 2.1). Stability is defined here as the resistance in lake ecosystems to perturbations, such as increased nutrient loading (see also chapter 5). The extremely low nutrient loading seems to be the major factor favoring the clear water state of Naardermeer. For both other lakes, it could be speculated that the commercial fishery (Reeuwijk lakes) and the natural water level dynamics, providing excellent pike habitat (Oude Venen), played a significant role in maintaining the clear water state (Table 2.1).

	Naardermeer	Reeuwijk lakes	Oude Venen
stability of the clear water state	high	lower	lowest
factors favoring the clear water state:			
low nutrient loading	* * *	* *	*
high fishing on planktivores/benthivores	*	* * *	* *
natural water level dynamics	* *	* *	* * *

Table 2.1 *Stability of the clear water state and possible factors favoring the clear water state of Naardermeer, Reeuwijk lakes and Oude Venen in the 1930s and 1940s (*** major role; ** moderate role; * minor role).*

For another group of well-studied peat lakes, the Loosdrecht lakes, Hofstra & Van Liere (1992) have described the historical development of eutrophication as a series of stages: (1) oligotrophy from 1800-1920, (2) mesotrophy from 1930-1955, (3) eutrophy from 1960-1980 and finally (4) 1980-present, a stable turbid water state in spite of reduced nutrient loading. The findings for the three peat lakes fully agree with their stage (2). Unfortunately, our study did not produce any data to support the phenomenon of an oligotrophic stage (1). Klinge *et al.* (1995) suggested that perch is the dominant predator in stage (1), pike in stage (2) and pike-perch in stage (3). The reference study in this chapter focused on stage (2) lakes, and indeed pike appears to be a common fish species in these lakes. The results, however, do not allow conclusions about the steering role of pike in the food chain. Although stage (1) lakes may have existed before the 1930s, that stage (2) is a more realistic reference system for our shallow peat lakes and a challenge to lake restoration (Hofstra & Van Liere, 1992).

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Multi-lake studies: external nutrient loading and lake response

Introduction

Increased nutrient loading to lakes is the main cause of algal blooms, turbid water and concomitant biotic changes in the aquatic ecosystem, such as the decline of submerged vegetation and related fish species. In planning and assessment of lake restoration, criteria are needed for nutrient loading and nutrient concentration. Comparative studies of a multitude of lakes showed to be helpful in developing these criteria. Vollenweider (1968, 1969, 1975, 1976) was one of the first to conduct multi-lake studies in order to get insight in relationships between nutrient loading and the effects of eutrophication, considering some important lake characteristics, such as mean depth and flushing rate. Vollenweider focused on deep, mostly P-limited lakes. A 'eutrophication survey' in the Netherlands was conducted in 1976-1977, in response to Vollenweider's work. The Dutch lakes differ from Vollenweider's data set in that most lakes are shallow (< 3 m) and not necessarily P-limited. In today's hypertrophic condition, algal biomass may be limited by P, but also by N, light or other factors. P loading, however, is widely considered to be the most important steering variable in lake restoration in the Netherlands (Anonymous, 1993, 1995).

The purpose of this study was to develop quantitative relationships between nutrient loading, nutrient concentrations, algal biomass and transparency for shallow Dutch lakes. The empirical relationships became known in the Netherlands as the CUWVO models, after the committee that initiated this research, and have been extensively used in lake management studies (Claassen, 1982; Werkgroep Eutrofiëring, 1983; De Ruiter, 1984; Oosterloo, 1984; Van Eck *et al.*, 1986; Meijer & Uunk, 1988; Klapwijk 1988; Klapwijk *et al.*, 1988; Klink & Claassen, 1988; Roijackers & Verstraelen, 1989; Anonymous, 1993). The national water quality standards for TP, TN, chlorophyll *a* and Secchi depth are also based on the CUWVO models (Anonymous, 1981, 1986, 1989). More up-to-date relationships for lake management are derived by including the results of recent developments in multi-lake studies and modeling (OECD, 1982; Lijklema *et al.*, 1988, 1989; STOWA, 1993).

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Data compilation

Lake data on hydrology, nutrient loading and concentrations (TP, TN), chlorophyll *a*, phytoplankton species and transparency were compiled for the years 1976-1977. Information on morphometry and sediment characteristics was collected as well. The information was gathered for 65 lakes. Most of the lakes are of moderate surface area (< 500 ha) and shallow (< 3 m), with sediments of (a mix of) sand, clay or peat. Reliable water and nutrient budget data were only available for 14 lakes. All lake managers used standard methods for sampling and chemical analysis. Chlorophyll *a* data before 1985 from RIZA appeared to be incorrect and have been corrected by multiplying the original data with a factor of 0.67 (Griffioen, pers. comm.). See CUWVO (1980) for the complete data set.

Conceptual and empirical models

The lake response to changes in external nutrient loading can be described by the following cause-effect chain:

phosphorus		phosphorus		chlorophyll		Secchi depth
loading	→	concentration	→	concentration	→	transparency

The conceptual and empirical relationships loading-concentration and chlorophyll-Secchi depth are elaborated below.

P loading and P concentration

Steady-state mass balance modeling has been used since the 1960s for studying the relationship between P loading and P concentration. A particularly comprehensive analysis of this kind of models was made by Vollenweider (1969). Steady-state in this context means that during a long period the input, output, and sedimentation conditions are assumed to remain the same, although there is variation within the period. Thus, in the empirical tests of the models the average values of certain long periods (e.g. years) must be used and correspondingly the model outputs represent average concentrations. Another important assumption in the models is the assumption of total mixing in all directions; the lake behaves as a 'continually stirred tank reactor' (Vollenweider, 1969, 1975). P is not a conservative substance, but involved in many physico-chemical (sorption, sedimentation, resuspension, diffusion from the sediments) or biological (uptake by algae, mineralization) processes, usually resulting in a net annual removal of P to the lake sediments. When a first order removal of P is assumed, i.e. the removal of P is proportional to the in-lake concentration, the mass balance for the simplified system becomes:

$$\frac{dP}{dt} = \frac{1}{\tau}.P_i - \frac{1}{\tau}.P - \sigma.P \qquad (1)$$

where:

P = TP in the lake (g m^{-3})
τ = hydraulic residence time (y)
P_i = TP in the inflow (g m^{-3})
σ = net removal rate (y^{-1})

At steady-state, temporal changes are zero, and Eq. (1) can be rewritten as:

$$\frac{P}{P_i} = \frac{1}{1 + \sigma\tau} \tag{2}$$

The major difficulty in using Eq. (2) for prediction purposes arises from the inability to specify appropriate values of σ, the removal rate, for different lakes. Thus, attempts have been made to estimate values of σ based on other lake parameters that are known. Vollenweider (1976) developed a statistical relationship between the removal rate σ and the hydraulic residence time τ (τ = volume/outflow) of lakes:

$$\sigma \simeq \sqrt{\frac{1}{\tau}} \tag{3}$$

Apparently, highly flushed lakes (low τ) show a relatively high net removal rate. Such a relationship may be explained by the higher settling velocities of suspended solids, originating from inflowing streams.

Eq. (2) can now be written as:

$$\frac{P}{P_i} \simeq \frac{1}{1 + \sqrt{\tau}} \tag{4}$$

Note that the equation is dimensionally incorrect, due to the statistical nature of the relationship. Eq. (4) is derived primarily from data on deep, stratified and nutrient-poor lakes in Europe and North America. Clasen & Bernhardt (1980) applied Vollenweider's empirical approach to shallow lakes and reservoirs and presented a slightly modified version of the model:

$$\frac{P}{P_i} \simeq \frac{1}{1 + 2\sqrt{\tau}} \tag{5}$$

The above equations are the result of conceptual and empirical modeling, and can be used for evaluating the possible effects of changes in P loading and hydraulic loading. Note that according to Eqs. (4) and (5), the effect of loading reduction is independent of P_i. This implies that the response of in-lake TP is proportional to the change in TP loading. OECD

(1982) developed more advanced relationships, showing a weaker response at lower loading levels (see below).

Chlorophyll and Secchi depth

The Secchi disc is a circular white (or black and white) disc that is lowered into a water body until it disappears from the sight of the observer. The depth of disappearance is a visual measure of the clarity of water (Cialdi & Secchi, 1865; Tyler, 1968; Preisendorfer, 1986; Kirk, 1994). The Secchi disc was named after the Italian scientist Pietro Angelo Secchi, but it was Faraday, best known for his work on electricity, who used similar methods in the Thames river, ten years earlier (Cadée, 1996). As a result of absorption and scattering of the solar flux, the downward irradiance E of the light field diminishes with depth. Irradiance decreases exponentially according to:

$$E(z) = E(0) \cdot e^{-K.z} \quad \text{or} \quad \ln E(z)/E(0) = -K.z \tag{6}$$

where E(z) and E(0) are the values of downward irradiance at depth *z* and just below the surface and K is the wavelength specific vertical attenuation coefficient for downward irradiance (m^{-1}). Scattering as such does not influence irradiance, but only contributes to the light attenuation because it increases the pathlength of light through the medium and therefore the chance that photons are absorbed. Thus, K largely depends on the absorption and less on the scattering of light (Kirk, 1994). The relative rates of attenuation in the different wavebands are determined by the absorption spectrum of the aquatic medium. In inland waters blue and red light are strongly absorbed by the algae and the remaining green light penetrates most. The fraction of the light spectrum that can be used by the algae for photosynthesis is known as photosynthetically active radiation (PAR) and covers the range of 400-700 nm. The attenuation coefficient K_{PAR}, integrated over depth and called K hereafter, can also be expressed as:

$$K = K_w + K_d + K_s + K_a \tag{7}$$

where:

K_w = attenuation due to water molecules (m^{-1})
K_d = attenuation due to dissolved substances (m^{-1})
K_s = attenuation due to non-algal suspended solids (m^{-1})
K_a = attenuation due to algae (m^{-1})

According to Beer's law, which expresses the relationship between light attenuation and concentration of light attenuating components, $K_a = \alpha \cdot CHL$, where a is the specific light attenuation coefficient ($m^{-1}/mg\ m^{-3}$ or $m^2\ mg^{-1}$) and CHL the chlorophyll *a* concentration ($mg\ m^{-3}$). If all non-algal light attenuation is pooled to a background light attenuation coefficient K_0, Eq. (7) can be rewritten as:

$$K = K_0 + \alpha \cdot CHL \tag{8}$$

The next step is to relate K to the Secchi depth. A Secchi disc disappears from sight if no contrast can be observed between the disc and the surrounding water. This threshold contrast depends on (1) the downward irradiance on the disc and (2) the attenuation of the light beam returning from the disc to the observer. In this reflected radiation, all scattered light that does not reach the eye of the observer, is lost. Therefore, the apparent light extinction for the returning light is equal to the beam attenuation as measured in a spectro-photometer. Thus, a Secchi disc measurement combines K with the beam attenuation coefficient (Preisendorfer, 1986):

$$SD = \frac{\Gamma}{K + c} \tag{9}$$

where:
SD = Secchi depth (m)
Γ = constant between 8 and 9
c = beam attenuation coefficient (m^{-1}), being the sum of the beam absorption coefficient (a) and the beam scattering coefficient (b)

Since in natural waters, c is substantially greater than K, the Secchi depth is determined more by c than by K (Preisendorfer, 1986; Buiteveld, 1995). Therefore, scattering will have a relatively strong influence on Secchi depth. A general inverse relationship between SD and K can be expected only if K and c covary. This is true if the ratio between the light attenuating components, and thus the ratio between scattering and absorption, remains constant. For such a simplified system it can be assumed that:

$$SD = \frac{constant}{K} \tag{10}$$

where the constant is the so-called Poole-Atkins coefficient (PA) (Kirk, 1994). According to Eq. (6), this coefficient can be written as:

$$PA = -\ \ln\ E\,(SD)\,/\,E\,(0) \tag{11}$$

where E(SD) is the downward irradiance at Secchi depth

Some characteristic PA values for shallow lakes are given in Table 3.1. Low PA lakes, such as Markermeer, are relatively rich in light-scattering suspended solids (e.g. clay particles).

		Poole-Atkins coefficient	E(SD) in % of E(0)	Reference
Danube Delta lakes	($z = 1\text{-}2$ m)	1.5-1.9	22-15%	Cristofor *et al.* (1994)
Loosdrecht lakes	($z = 1\text{-}2$ m)	1.5-2.1	22-12%	Dekker *et al.* (1992)
IJsselmeer	($z = 4.5$ m)	1.7	18%	Buiteveld (pers. comm.)
Markermeer	($z = 3.2$ m)	1.0	37%	"
Wolderwijd	($z = 1.6$ m)	1.3	27%	"
Veluwemeer	($z = 1.2$ m)	1.3	27%	"

Table 3.1 *Some characteristic values for the Poole-Atkins coefficient (PA = K. SD) and corresponding downward irradiance at Secchi depth, relative to downward irradiance just below the surface (E(SD)/E(0) in %).*

Combining of Eqs. (8) and (10) gives the following linear relationship (assuming α and PA are constant between lakes):

$$\frac{1}{SD} = \frac{1}{SD_0} + \frac{\alpha}{PA} \cdot CHL \qquad (12)$$

or

$$CHL = \frac{PA}{\alpha} \cdot \frac{1}{SD} - \frac{PA}{\alpha} \cdot \frac{1}{SD_0} \qquad (13)$$

where SD_0 is the Secchi depth in the absence of algae.

It should be noted that the Eqs. (10-13) are rough approximations. In natural lakes the ratio of SD and 1/K is not a constant, but varies in space and time because of the varying contribution of absorption and scattering to the attenuation of light (Kirk, 1994; Buiteveld, 1995). The specific light attenuation coefficient for phytoplankton α depends on cell size, geometry and pigment contents and may vary from 0.007-0.029 $m^2 mg^{-1}$ (Kirk, 1994).

Results

P loading and P concentration

Most lakes in the Netherlands are extremely shallow, completely mixed by wind and relatively rich in nutrients, and thus deviate strongly from Vollenweider's data set. For that reason we evaluated our own data set to find a statistical relationship between P/Pi and areal hydraulic loading q_s (and $q_s = z/\tau$) (cf. Larsen and Mercier, 1976). This resulted in:

$$\frac{P}{P_i} = 0.201 \log q_s + 0.322 \quad (n = 14,\ r = 0.85,\ s = 0.12) \qquad (14)$$

where:

n = number of cases

r = correlation coefficient

s = residual standard error in P/P_i

The Vollenweider Eqs. (4) and (5) and Eq. (14) can be used for calculating TP in relation to P loading and areal hydraulic loading. By comparison of calculated and measured TP, the Eqs. (4), (5) and Eq. (14) were tested on the Dutch lakes data set. The resulting correlation coefficients are 0.87, 0.86 and 0.97, respectively ($n = 14$, $p > 0.99$). From these equations the admissible loading (i.e. the loading that will give the TP that is required) can be calculated from a standard for in-lake TP, although with wide confidence limits.

As $P_i = L/qs$, Eq. (14) can be rewritten as:

$$L = \frac{P\, q_s}{0.201 \log q_s + 0.322} \qquad (15)$$

or after substitution of $q_s = z/\tau$:

$$L = \frac{P\ .\ z/\tau}{0.201 \log z/\tau + 0.322} \qquad (16)$$

For a standard of TP of 0.10 g m^{-3} in a lake with $z = 2$ m and $\tau = 1$ y, the admissible loading would be 0.5 g P m^{-2} y^{-1}. Including the residual standard error s in P/P_i (Eq. 14), gives a range of L of 0.3-1.1 g P m^{-2} y^{-1} ($p = 90\%$). More sophisticated methods for estimating prediction confidence limits, combining the errors in model parameters and input variables with the standard error in the model, were developed by Reckhow (1979). As noted before, in the loading-response models presented here, the ratio P/P_i is a function of areal hydraulic loading (or z and τ) only.

Nutrients and chlorophyll

For P-limited lakes a positive correlation may be expected between the total concentration of the limiting nutrient and the algal biomass, expressed as chlorophyll *a* (Sakamoto, 1966; Vollenweider, 1968; Dillon & Rigler, 1974; Jones & Bachmann, 1976; Nicholls & Dillon, 1978). However, during the growing season the algal production in shallow Dutch lakes in their current hypertrophic condition, is not permanently P-limited. Other factors such as N or light may limit also algal biomass. Fig. 3.1 shows that there is no simple correlation between TP and chlorophyll *a*, but that the upper limit of the cloud of points can be visually delineated reasonably well. The line indicated can be taken as the upper limit of the algal biomass at a certain nutrient concentration. For lakes close to the line it can be assumed that the algal biomass is largely P-limited. Obviously, lakes deviating from this line suggest an excess of P, and algal biomass is controlled by other factors. Fig. 3.2 shows a similar relationship for TN and chlorophyll *a* and the line representing the set of N-limited lakes. The limitation lines are described by the Eqs. (17) and (18):

$$CHL = -16 + 0.78 \, . \, TP \tag{17}$$

$$CHL = -89.6 + 0.09 \, . \, TN \tag{18}$$

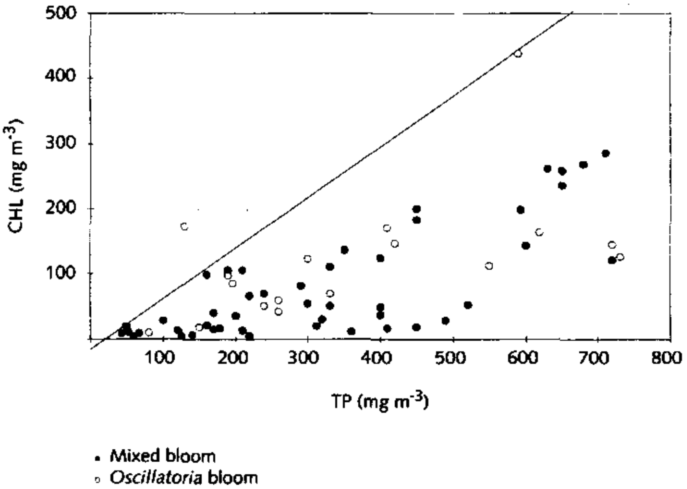

Fig. 3.1 *Chlorophyll a and TP for 63 lakes in the Netherlands, mean values April-September. The line (Eq. 17) approximates the maximum value for chlorophyll a in relation to TP.*

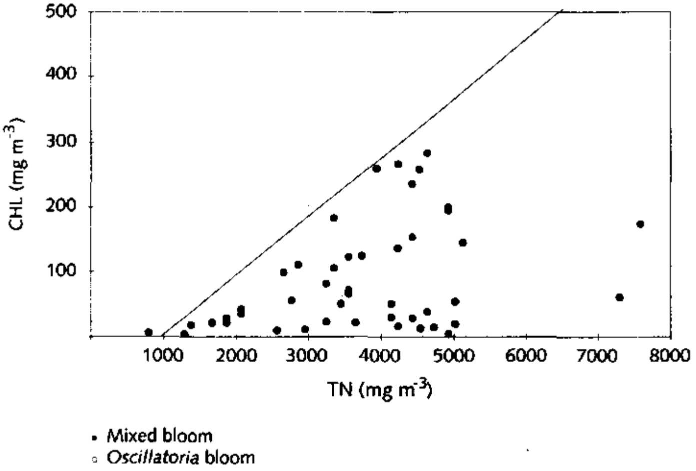

Fig. 3.2 *Chlorophyll a and TN for 65 lakes in the Netherlands, mean values April-September. The line (Eq. 18) approximates the maximum value for chlorophyll a in relation to TN.*

Chlorophyll and Secchi depth

Fig. 3.3 shows chlorophyll *a* *vs.* inverse Secchi depth. Following the Eqs. (12) and (13), regression lines are calculated for CHL on 1/SD and for the reverse 1/SD on CHL:

$$\frac{1}{SD} = 0.828 + 0.188 \,.\, CHL \quad (n = 63,\ r = 0.85,\ s = 1.04) \tag{19}$$

$$CHL = 38.1 \ \frac{1}{SD} - 3.2 \quad (n = 63,\ r = 0.85,\ s = 47.0) \tag{20}$$

It appears that CHL can be calculated from 1/SD, with very wide confidence limits only. For an objective of SD = 1 m, CHL = 35 (0-112) mg m^{-3} (p = 90%).

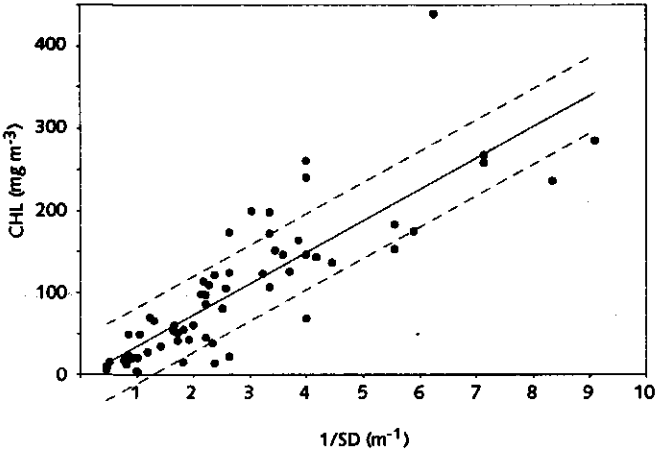

Fig. 3.3 Chlorophyll a and inverse Secchi depth for 63 lakes in the Netherlands, mean values April-September. The dashed lines indicate the residual standard error in CHL.

Light-limited algal growth

The above nutrient limitation lines were derived from field data. The question is whether a similar empirical approach can be applied for finding the chlorophyll *a* maximum for light-limited algal growth. A set of limitation lines for TP, TN and light would be helpful in finding the limiting factor for algal biomass for specific lakes. Van Straten (1986) presented an empirical steady-state model for the maximum standing crop of algae, based upon the conceptual model of Lorenzen & Mitchell (1973). It is assumed that the light availability and thus the algal growth rate decreases with increasing algal biomass, because of self-shading. Besides self-shading, the light climate for the algae is influenced by non-algal turbidity. At steady-state the gross growth rate is balanced by mortality and respiration and the maximum standing crop is:

$$CHL_{max} \cdot z = \frac{2f \cdot \mu_{max}}{\alpha \cdot r} - \frac{K_0 \cdot z}{\alpha} \tag{21}$$

where:

CHL_{max} = maximum algal biomass (chlorophyll *a*) (mg m^{-3})
z = mean depth (for mixed shallow lakes) (m)
α = the specific algal light attenuation coefficient (m^2 mg^{-1})
f = relative daylight length (-)
μ_{max} = maximum gross growth rate (t^{-1})
r = mortality and respiration rate (t^{-1})
K_0 = non-algal light attenuation coefficient (m^{-1})

The first term in the equation represents the theoretical maximum standing crop, when non-algal turbidity (K_0) is zero and self-shading determines the upper limit of algal biomass. Note that this theoretical maximum is independent of the depth of the lake. The second term accounts for the shading effect of non-algal turbidity. As $K_0 = PA/SD_0$, Eq. (21) can be rewritten as:

$$CHL_{max} \cdot z = \text{constant} - \frac{PA}{\alpha} \cdot \frac{z}{SD_0} \tag{22}$$

The slope of the line is defined by PA/α. This coefficient can be derived from the regression line of 1/SD to CHL for Dutch lakes, presented above (Eqs. 12 and 19), giving:

$$CHL_{max} \cdot z = constant - 53 \frac{z}{SD_0} \tag{23}$$

Eq. (23) describes the light-limited standing crop of algae in relation to the 'non-algal' light climate, expressed as z/SD_0. SD_0 for individual lakes can be estimated with Eq. (12), substituting $\alpha/PA = 0.0188$ m^2 mg^{-1}. The constant in Eq. (23) can be found empirically by delineating the upper limit of a cloud of points. Fig. 3.4 shows the relationships both for mean summer standing crop and maximum standing crop. Arbitrarily the following limitation lines can be indicated.

For the upper limit of summer mean CHL:

$$CHL_{max} \cdot z = 530 - 53 \frac{z}{SD_0} \tag{24}$$

For the upper limit of summer peak CHL:

$$CHL_{max} \cdot z = 656 - 53 \frac{z}{SD_0} \tag{25}$$

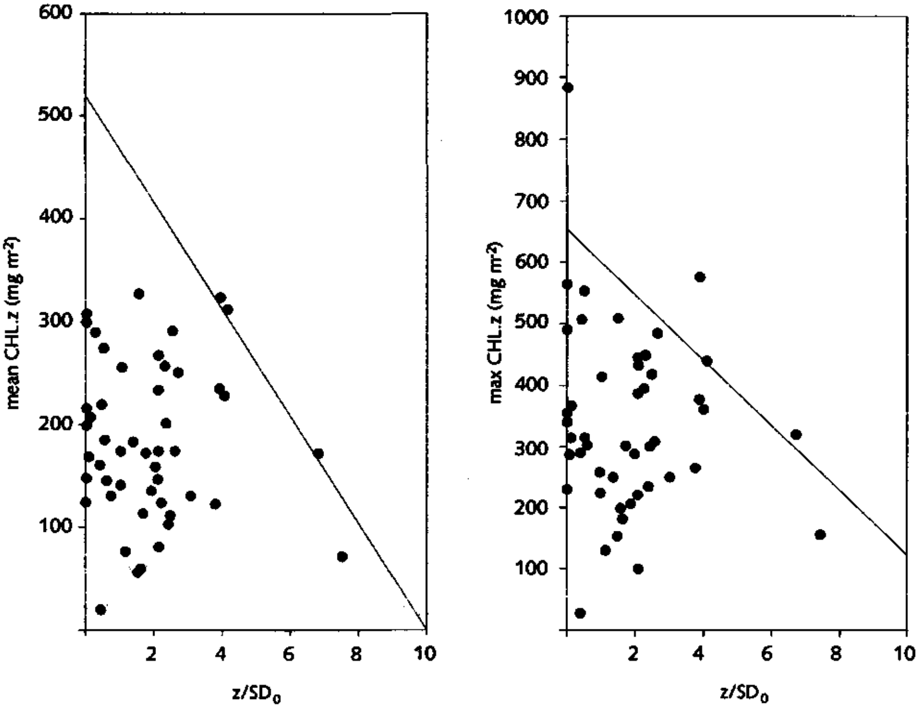

Fig. 3.4 *Chlorophyll a (CHL) per m^2 vs. mean depth/Secchi without algae (z/SD_0), mean values April-September (left-hand panel) and maximum values April-September (right-hand panel). SD_0 is calculated with Eq. (12) and the regression coefficient (= α/PA), derived from the Dutch lakes (Eq. 19). The indicated lines approximate the maximum value for the standing crop of algae. The position of the line is found by delineating the cloud of points with a given slope of 53 mg m^{-2}.*

It should be noted here that the values for the shade factor z/SD_0 are biased, because of the assumed constancy of the coefficient α/PA. For low PA lakes (high scattering, such as Markermeer), the shade factor z/SD_0 is overestimated, leading to a rightward shift of the data points in Fig. 3.4. The shade factor is underestimated for high PA lakes (low scattering, such as IJsselmeer). As noted before, the specific light attenuation coefficient for phytoplankton α, varies with the type of algae. The set of Eqs. (17, 18) and (24, 25) can be used as a rough tool for evaluating the role of TP, TN and light as limiting factors for algal growth.

Comparison with more recent surveys and discussion

In this multi-lake study quantitative relationships were derived among nutrient loading, nutrient concentration, algal biomass and transparency for shallow Dutch lakes. The analysis was based upon data from about 65 lakes, of which only 14 lakes had both water and nutrient budgets, for the 1976-1977 years. Here the results are discussed in relation to later studies of OECD (1982) and more extensive eutrophication surveys of Lijklema *et al.* (1988, 1989) for 1983-1985 and of STOWA (1993) for 1980-1988.

P loading and P concentration

Hydraulic residence time and mean depth were suggested by Vollenweider (1976) to be key variables controlling the relationship between P loading and P concentration (Eqs. 4 and 5). A reduction of P loading would therefore result in a proportional decrease of the P concentration in the lake. A similar empirical model, relating P/P_i and areal hydraulic loading, could be derived for shallow lakes in the Netherlands (Eq. 14). This model then can be used for calculating the acceptable loading levels, although it has wide confidence limits. In later studies, OECD (1982) presented a modified version of the Vollenweider model (with P in mg m^{-3}):

$$P = 1.02 \left[\frac{P_i}{1+\sqrt{\tau}}\right]^{0.88} \tag{26}$$

The exponent, which is significantly lower than 1.0, shows that at reduced loading P retention decreases, so the response of P becomes weaker. OECD (1982) stressed that this result of the study should be considered as an essential modification compared with the former models. However, the deviation from a linear response is small, as can be shown by a simple example. Assuming $\tau = 1$ y, $z = 2$ m and a decrease in P_i from 1,000 to 100 mg m^{-3}, then the load reduction of 90% will result in an in-lake P reduction of 87%.

For the 1976-1977 data set, no significant correlation between P retention R ($R = 1 - P/P_i$) and P_i was found ($r = 0.1053$). Lijklema *et al.* (1989) found a weak correlation between R and P_i ($r = 0.44$, $n = 20$) and presented a modified version of the OECD model (Eq. 27):

$$P = 0.698 \left[\frac{P_i}{1+\sqrt{\tau}}\right]^{0.88} \tag{27}$$

Application of the OECD model and the Lijklema model to the 1976-1977 data set did not result in a better correlation between measured and calculated TP (Eqs. 26 and 27: $r = 0.85$, $n = 14$, compared to Eq. 14: $r = 0.97$, $n = 14$). Although the Vollenweider type models suggest a proportional or 'somewhat' less than proportional effect of loading reduction, case studies in lake restoration showed a major resistance to recovery (Cullen & Forsberg, 1988; Sas, 1989; Jeppesen *et al.*, 1991; Van der Molen & Boers, 1994). It should be noted that the Vollenweider models assume the lakes to be in steady-state, i.e. equilibrium between loading and in-lake concentration, and do not account for adaptation processes. The delay in recovery may be explained by internal P loading from the sediments and homeostasis in the biotic community (Jeppesen *et al.*, 1990a, 1990b, 1991). For a better understanding of the dynamic behavior of loading-response relationships, attention should be focused on the evaluation of lake restoration case studies.

Nutrients and chlorophyll

For lakes dominated by filamentous cyanobacteria (*Oscillatoria*), both more recent surveys showed a significantly higher yield of chlorophyll *a* per unit P (Table 3.2, Fig. 3.5). As the chlorophyll/algal dryweight ratio for *Oscillatoria* does not differ from the ratio for other algal species (Reynolds, 1984), this higher yield of chlorophyll *a* indicates a higher yield of algal biomass per unit P. Also for lakes with a mixed phytoplankton community, the 1980-1988 data set showed a higher CHL/TP ratio. The CHL/TP ratios found for the Dutch lakes with mixed phytoplankton populations, fall within the range of 0.4-1.1 (at TP = 100 mg m^{-3}) for North American and European P-limited lakes, presented by Nicholls & Dillon (1978) and Ahlgren *et al.* (1988). Reynolds (1984) gives a range of 0.5-2.0 for the CHL/TP ratio of freshwater algae (assuming P content is 1% of algal dryweight). The regression lines for chlorophyll *vs.* TN are almost similar for the different data sets and the *Oscillatoria* lakes do not significantly deviate from the other lakes (Table 3.2, Fig. 3.6).

Lake data set	**Chlorophyll-TP**		**Chlorophyll-TN**
	mixed phytoplankton	***Oscillatoria* dominance**	
1976-1977	CHL = -16 + 0.78 TP		CHL = -89.6 + 0.09 TN
1983-1985	CHL = 0.62 TP	CHL = 1.43 TP	CHL = -89.6 + 0.09 TN
1980-1988	CHL = -24 + 1.04 TP	CHL = 1.54 TP	CHL = -95.2 + 0.09 TN

Table 3.2 *Relationships of chlorophyll-TP and chlorophyll-TN, for P- and N-limited lakes respectively. Mean values April-September. Data 1983-1985 from Lijklema et al. (1989) and data 1980-1988 from STOWA (1993). All lines are found by visually delineating the upper limit of the cloud of points. Oscillatoria dominance is defined as Oscillatoria > 50% of algal biovolume. CHL, TP and TN in mg* m^{-3}.

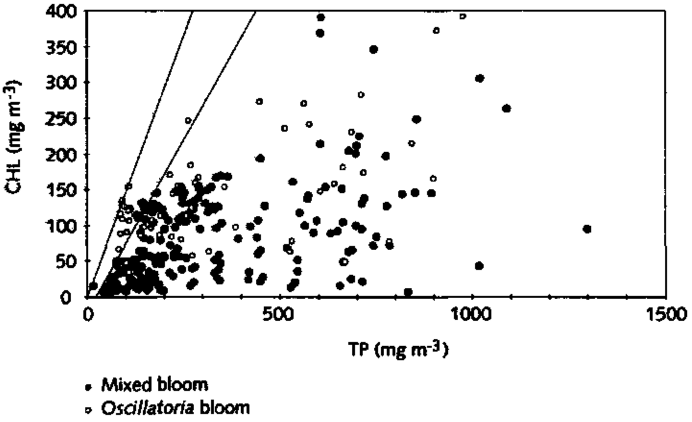

Fig. 3.5 *Chlorophyll a and TP for 284 lake-years in the Netherlands, mean values April-September (1980-1988). Data set from STOWA (1993). The lines approximate the maximum value for chlorophyll a in relation to TP. The upper line is for Oscillatoria-dominated lakes.*

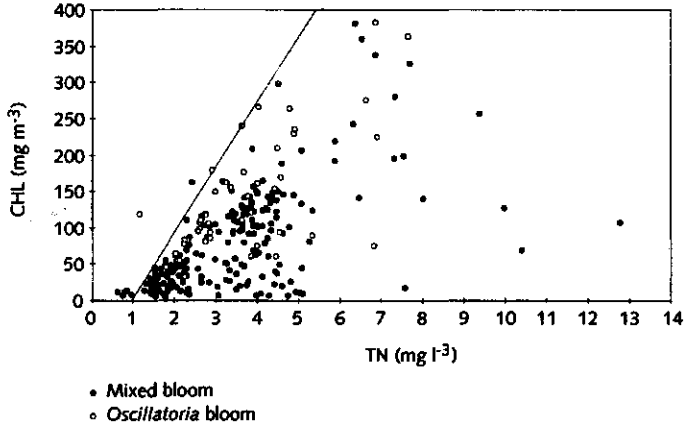

Fig. 3.6 *Chlorophyll a and TN for 270 lake-years in the Netherlands, mean values April-September (1980-1988). Data set from STOWA (1993). The line approximates the maximum value for chlorophyll a in relation to TN.*

In restoring lakes with an excess of P, a 'threshold response' may be expected: algal biomass will not go down until a certain threshold TP concentration, indicated by the P-limitation line, is attained (Fig. 3.7). However, the P-limitation line should not be used rigidly. Individual lakes may show substantial variation in their response to decreasing TP levels. Smith & Shapiro (1981) analyzed several lake restoration case studies and demonstrated that CHL and TP decreased according to CHL/TP ratios varying from 0.270 to 0.940. Additional factors such as the partitioning of P between algal and non-algal components, the variation in

CHL/TP ratios for different types of algae, and strong grazing effects (see chapter 5) may explain the variation in response.

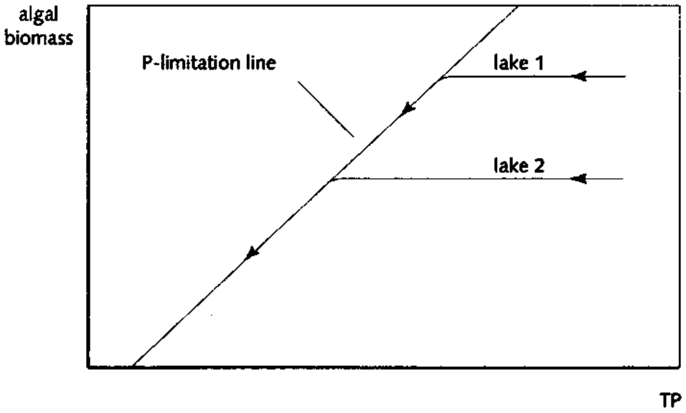

Fig. 3.7 *Threshold response of algal biomass to TP reduction. For lakes deviating from the P-limitation line, the maximum algal biomass is determined by other factors than P, e.g. light or N.*

Chlorophyll and Secchi depth

Table 3.3 gives the regression lines for the three different data sets, distinguished by various classes of lake depth. Scatterplots for the STOWA data set are shown in Fig. 3.8. The lower correlation coefficient between 1/SD and CHL in the shallow lakes, can be explained by the effects of a highly variable non-algal turbidity, related to wind-induced resuspension. However, even for the deeper lakes the residual standard error is large and estimates for CHL from given values of SD are subject to very wide confidence limits. According to the equations from the 1980-1988 data set, a desired SD of 1 m corresponds to a CHL level of 35 mg m^{-3} (0-133 mg m^{-3}, p = 90%) in shallow lakes and 43 mg m^{-3} (0-91 mg m^{-3}, p = 90%) in deeper lakes. It will be clear that relationships with such wide confidence limits have limited practical value for lake management. For more insight in the light climate of specific lakes, it is necessary to analyze the contribution of all optical active components to the attenuation of light. Buiteveld (1995) developed a model to calculate SD and K from data on CHL, inorganic suspended matter, detritus and yellow substance (dissolved humic matter). The problem then is shifted to the question how to predict these variables and changes thereof, resulting from lake restoration efforts.

Lake data set	Regression lines acc. to $CHL = a.1/SD - b$ or $1/SD = a.CHL + b$	
1976-1977	all lakes, $z = 0.7\text{-}30$ m	
	$CHL = 38.1\ 1/SD - 3.2$	($n = 63, r = 0.85, s = 47.0$)
1983-1985	$z < 6$ m	
	$1/SD = 0.0126\ CHL + 1{,}267$	($n = 82, r = 0.81, s = 0.65$)
	$z > 6$ m	
	$1/SD = 0.0174\ CHL + 0.385$	($n = 35, r = 0.87, s = 0.31$)
1980-1988	all lakes, $z < 6$ m	
	$CHL = 29.3\ 1/SD - 4.5$	($n = 375, r = 0.67, s = 53.6$)
	$z < 2$ m	
	$CHL = 28.4\ 1/SD + 6.9$	($n = 280, r = 0.60, s = 59.6$)
	$z = 2\text{-}6$ m	
	$CHL = 36.4\ 1/SD + 6.6$	($n = 95, r = 0.81, s = 28.9$)

Table 3.3 *Regression lines for the relationship chlorophyll a-inverse Secchi depth. Mean values for April-September. Data set 1983-1985 from Lijklema et al. (1988) and data set 1980-1988 from STOWA (1993) (n = number of lake-years, r = correlation coefficient, s = residual standard error). CHL in mg* m^{-3}, *1/SD in* m^{-1}.

Secchi depth in *Oscillatoria* lakes

Because of their high yield of CHL per unit P (Fig. 3.5), *Oscillatoria*-dominated lakes pose a special problem to lake management. It can be seen from the position of the *Oscillatoria* lakes in Figs. 3.8 and 3.9, that dominance is found particularly in shallow turbid lakes with a Secchi depth of 0.20-0.50 m. As *Oscillatoria* is sensitive to high light conditions (Berger, 1987), the dominance of these cyanobacteria disappears at low biomass (see Figs. 3.5 and 3.8). Linking 1/SD and TP directly (Fig. 3.10), also shows that the *Oscillatoria* lakes tend to be more turbid than the other lakes at the same TP level. Consequently, in lake restoration by P loading reduction, *Oscillatoria* lakes will show more resistance to recovery, indicating the phenomenon of hysteresis (see also chapter 5). Berger (1987), Schreurs (1992) and Scheffer *et al.* (in press) also suggested that *Oscillatoria* populations behave that way. Once the *Oscillatoria* dominance is broken, an increase in Secchi depth may be expected (see chapter 4).

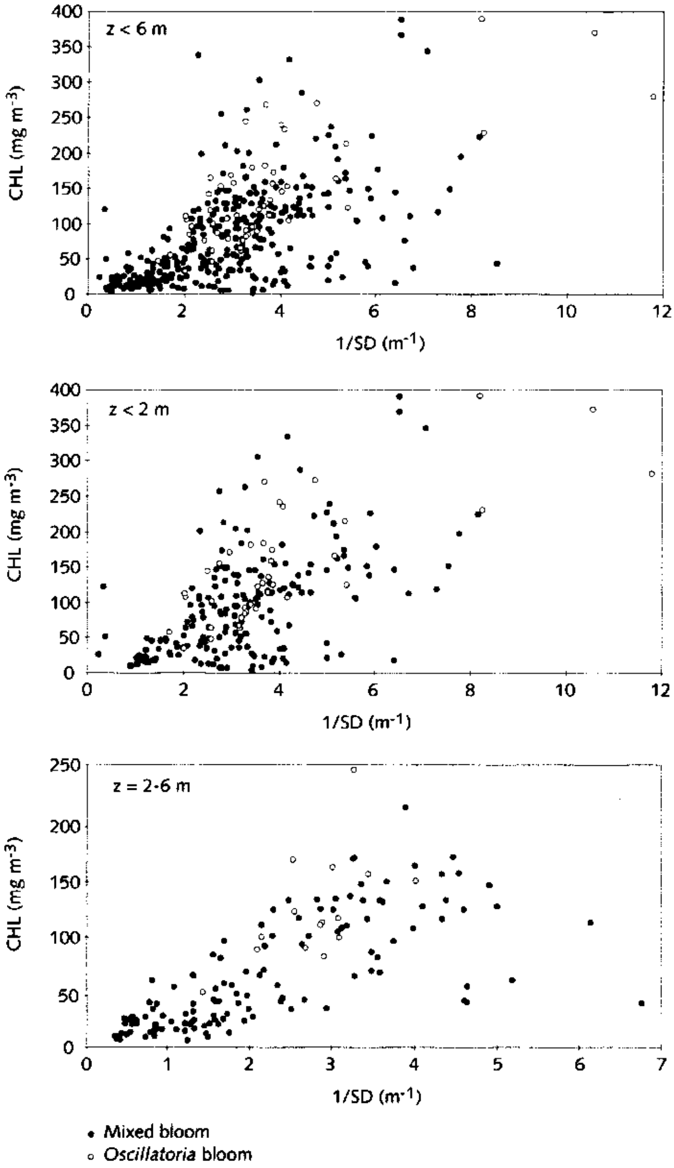

Fig. 3.8 *Chlorophyll a and inverse Secchi depth from the 1980-1988 data set (STOWA, 1993). Lake-years with Oscillatoria dominance (> 50% of biovolume) are indicated with (o). Upper panel: z < 6 m. Middle panel: z < 2 m. Lower panel: z = 2-6 m. The line in the upper panel represents the approximated maximum value for chlorophyll a in relation to 1/SD (CHL = 58.1/SD - 13).*

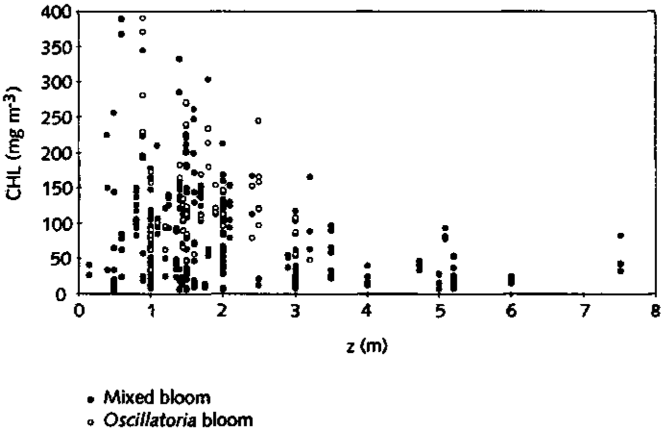

Fig. 3.9 *Chlorophyll a and mean depth from the 1980-1988 data set (STOWA, 1993). Lake-years with Oscillatoria dominance (> 50% of biovolume) are indicated with (o).*

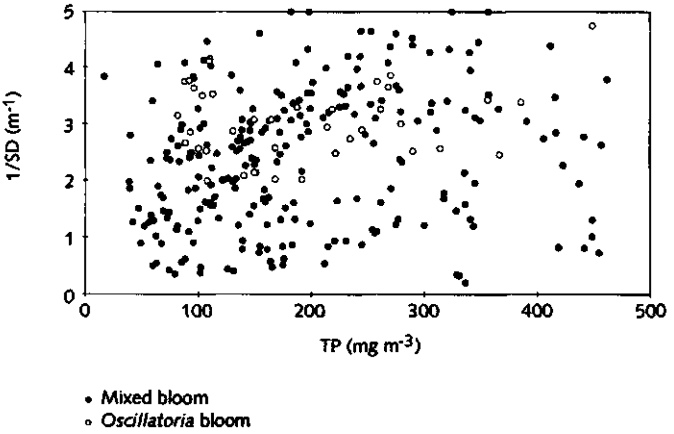

Fig. 3.10 *Inverse Secchi depth and TP from the 1980-1988 data set (STOWA, 1993). Lake-years with Oscillatoria dominance (> 50% of biovolume) are indicated with (o).*

Objectives for Secchi depth

Lake managers are interested in the Secchi depth (SD), which is necessary to restore the proper conditions for submerged vegetation. A tentative relationship between SD and the chances for establishment and survival of submerged vegetation can be derived as follows. Net photosynthesis by freshwater phytoplankton at depth z, can be expected if the downward irradiance is at least 1% of the irradiance just below the surface: $E(z) > 0.01\ E(0)$ (Reynolds, 1984). However, submerged macrophytes and macro-algae, such as charophytes, require higher light levels for net photosynthesis. Chambers & Kalff (1985) give values of 21% of surface light for rooted macrophytes and 10% for charophytes. In clear oligotrophic lakes, charophytes can grow down to light levels of 2-3% of surface light (Sand-Jensen, 1989). As in the shallow Dutch lakes, charophytes were common species (see chapter 2), it is assumed here that reestablishment of the submerged vegetation will start at light levels of 10%. Then, according to Eq. (6), K.z = 2.3 and K can be converted to SD by Eq. (10), giving SD/z = PA/2.3. The Poole-Atkins coefficient (PA) varies from 1.0 in Markermeer (z = 3.2 m, clay sediments) to 1.5-2.1 in the Loosdrecht lakes (z = 1-2 m, sand and peat sediments) (Table 3.1). Therefore, for Markermeer, if SD > 1.4 m, it could be expected that sufficient light reaches the bottom, promoting the growth of submerged vegetation at the mean lake depth. For the Loosdrecht lakes the critical SD for the development of vegetation would be 0.6-0.9 m for the shallow parts (z = 1 m) and 1.3-1.8 m for the deeper parts (z = 2 m). The Veluwemeer experiences lend support to the applicability of this simple tool. The critical SD for this lake (z = 1.2 m, PA = 1.3) can be calculated as 0.57 x 1.2 m = 0.7 m. In summer 1975, with a mean SD of 0.20 m only, the vegetated area was less than 10% (Scheffer *et al.*, 1993a). After the collapse of the *Oscillatoria* bloom in 1985 (see chapter 4), the reestablishment of the submerged vegetation got started, at a mean summer SD of 0.40 m (Noordhuis, 1996). In summer 1995, with a mean SD of 0.50 m, the shallow part of the lake (< 1 m) was largely covered with vegetation (mainly *Chara*), although in widely varying densities (see also chapter 7). As soon as submerged vegetation colonizes the lake bed a positive feed back mechanism may be triggered, leading to a further increase in transparency of the overlying water (Jeppesen *et al.*, 1990b; Scheffer *et al.*, 1994; see chapter 5). It should be mentioned that in addition to light availability, other factors may interfere with the restoration of a sustainable submerged vegetation (e.g. periphyton growth in nutrient-rich lakes, soft sediments susceptible to wind-induced resuspension, bird grazing, etc.).

Objectives for chlorophyll and TP in relation to Secchi depth

For lake management purposes, Secchi depth objectives should be converted to TP concentrations, via chlorophyll *a*. Obviously, the relationships show wide confidence limits, and thus only tentative guidelines can be derived. Because of this uncertainty the regression lines for 1/SD and CHL (Table 3.3) have no practical value. However, Fig. 3.8 shows that the upper limit of the cloud of points can be delineated reasonably well, and that the *Oscillatoria* lakes do not deviate from the other lakes in this respect. So, for a Secchi depth > 0.5 m, CHL should not exceed 120 mg m^{-3} (Fig. 3.8). The converse, however, does not hold true. Due to the highly variable contribution of non-algal turbidity, a CHL value < 120 mg m^{-3} as such, does not guarantee a Secchi depth of > 0.5 m. So, for a Secchi depth of > 0.50 m, a necessary (but not exclusive) condition is CHL < 120 mg m^{-3}. The next step is to convert this upper limit for CHL into limits for TP (Fig. 3.5, Table 3.2) and here a distinction should be made between *Oscillatoria* lakes and the other lakes with a mixed phytoplankton community. Additionally, as *Oscillatoria* is sensitive to high light conditions (Berger, 1987), the fact has to be considered that at increasing transparency of the water, *Oscillatoria* will be replaced by other phytoplankton species. Firstly, the critical light climate for such a shift in species will be defined. In the shallow Veluwemeer (z = 1.2 m, see chapter 4) the *Oscillatoria* dominance was broken twice, temporarily in spring 1982 and for a longer period in spring 1985. In both years, in the period just before the species shift the water was relatively clear, with Secchi depth values around 0.50 m. The light climate in a mixed lake is a function of transparency and mean depth, and can be expressed in the ratio z_{eu}/z, where z_{eu} represents the depth of the upper water layer with net photosynthesis ($E(z_{eu}) = 0.01\ E(0)$; Reynolds, 1984). With Eqs. (6) and (10) and a Poole-Atkins coefficient (PA) for Veluwemeer of 1.3 (Table 3.1), it can be shown that $z_{eu} = 3.5SD$ and thus the critical ratio for the species shift $z_{eu}/z = 1.5$. Using the data on the species shift in Veluwemeer at $z_{eu}/z = 1.5$ as a prototype, critical Secchi depth, CHL and TP values can be derived. Instead of using the Veluwemeer PA of 1.3, for Dutch lakes in general it is better to use a PA of 1.8, derived from the more representative Loosdrecht lakes (Table 3.1). The following examples show the critical values for a species shift in a 1 and 2 m deep lake (PA = 1.8):

example 1:
if $z = 1$ m, the species shift can be expected at $SD > 0.6$ m, corresponding with
$CHL < 84$ mg m^{-3} and $TP < 55$ mg m^{-3}
example 2:
if $z = 2$ m, the species shift can be expected at $SD > 1.2$ m, corresponding with
$CHL < 35$ mg m^{-3} and $TP < 23$ mg m^{-3}

Remember that the CHL levels are upper limits and depending on the impact of non-algal turbidity, lower CHL and TP levels may be necessary to realize the species shift. Once the *Oscillatoria* has disappeared, the CHL/TP regression line for mixed phytoplankton comes into force, leading to lower CHL and higher SD at the same TP level. Table 3.4 gives relationships for Secchi depth and corresponding CHL and TP levels for shallow lakes of 1 and 2 m.

Secchi depth	**Chlorophyll *a***	**TP**		
		mixed phytoplankton	***Oscillatoria* lake** $z = 1$ m	***Oscillatoria* lake** $z = 2$ m
> 0.25	0-219	234	142	142
> 0.50	0-103	122	67	67
> 1.00	0-45	66	species shifted	43

Table 3.4 *Criteria for chlorophyll a and TP (mg m^{-3}), calculated from Secchi depth (m) objectives. See text for explanation. The denotation 'species shifted' means that Oscillatoria cannot survive under the corresponding light conditions and a shift to mixed phytoplankton will occurr. Note that the indicated chlorophyll levels are upper limits; if non-algal turbidity is high, lower chlorophyll and TP levels will be required.*

Finally

Vollenweider type models are based on a multitude of lakes differing in hydrology, morphometry, trophic status etc. By comparative analysis of a limited number of lake characteristics, we try to understand how a specific lake ecosystem may respond to changing external conditions, such as nutrient loading reduction. So far, biological aspects (e.g. vegetation, fish stocks) and chemical aspects (e.g. (im-)mobilization of P in sediments) were not considered in the multi-lake studies. However, the biotic and geochemical structure of a lake may play a key role in the lake response to fertilization or restoration. Carpenter *et al.* (1995) clearly showed the effects of the actual fish stock on the lake response to fertilization. Jeppesen *et al.* (1990b) demonstrated the impact of submerged macrophytes on algal biomass and transparency. In shallow lakes non-linear shifts may occur from algae-dominated turbid waters to macrophyte-dominated clear waters and vice versa (Scheffer *et al.*, 1993b). Chemical characteristics of the lake sediments (Boström *et al.*, 1982; Van der Molen & Boers, 1994) and the inflowing water (see chapter 4) may highly influence the lake response to P loading reduction. It will be clear that comparative multi-lake studies can be helpful in finding quantitative objectives for lake management. However, for better understanding the mechanisms in loading-response relationships, single-lake restoration studies over longer periods of time are most promising.

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Whole-lake study of Veluwemeer: lake flushing for control of *Oscillatoria* blooms and internal phosphorus loading

Introduction

Lake restoration strategies are primarily aimed at reduction of the external P loading. However, once the external loading has been reduced, recovery of the lake may be delayed by an internal loading from the sediments, where most of the P has accumulated (Golterman, 1977; Boström *et al.*, 1982; Cullen & Forsberg, 1988; Marsden, 1989; Jeppesen *et al.*, 1991; Van der Molen & Boers, 1994). Lake managers, investing large sums of money in the control of the external loading, are interested in the extent and duration of the internal loading and possible additional measures to control the internal loading. The importance of the release of P from lake sediments, particularly under anaerobic conditions, was already recognized by Einsele (1936, 1938) and Mortimer (1941, 1942). Later it became clear that a significant P release may also occur under aerobic conditions, during the growing season (Golterman, 1977). Andersen (1975), Lijklema (1977, 1980) and Boers (1991) pointed out the effect of raised pH, as a result of photosynthesis, on the release of P from shallow lake sediments. Björk (1972) reported on cases where no recovery had taken place during a period of ten years after loading reduction. In 1970-1971 dredging of sediments was carried out successfully to control internal loading in Lake Trummen, Sweden (200 ha) (Björk, 1972; Eiseltová, 1994). Other methods for reduction of P release are directed to chemical treatment of the sediments or the overlying water. See Cooke *et al.* (1993) for a review of in-lake techniques. Oglesby (1968) and Welch & Patmont (1980) introduced the idea of lake water dilution, by flushing with water low in nutrients. Their efforts were not directed at control of internal loading, but simply at lowering the nutrient levels in the lake by means of dilution.

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Hosper, S.H. (1983). H_2O 16: 172-177.
Hosper, S.H. (1984). Wat. Sci. Tech. 17: 757-768.
Hosper, S.H. and M-L. Meijer (1986). Hydrobiol. Bull. 20: 183-194.
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Veluwemeer has suffered from a persistent algal bloom because of eutrophication. External P loading was reduced in the beginning of 1979. Monthly TP budgets indicated a substantial net P release from the sediments during summer and therefore the prospects for recovery were really bad. Kouwe & Golterman (1976) suggested to flush Veluwemeer during summer with the excess water from the adjacent polder of Flevoland, which is low in TP. Their idea was to gradually deplete the P pool in the sediment, by washing out P-rich algae. Enclosure experiments, however, showed that even after six flushings a significant decrease in the P pool could not be observed (Kouwe & Golterman, 1976; Golterman, 1980). Instead of flushing during summer, we proposed winter flushing, with the aim not to deplete the P pool, but rather to prevent P being released by the sediments. This idea was primarily based on the observation that TP in the lake shows a dramatic increase during periods of high pH (pH 9-10). Raised pH, as an effect of the uptake of CO_2 by the algae, increases the solubility of iron-bound phosphates (Andersen, 1975; Lijklema, 1977, 1980), which is one of the main forms in which P is generally found in lake sediments, including Veluwemeer (Brinkman & Van Raaphorst, 1986; Danen-Louwerse *et al.*, 1993). The hypothesis was that (resuspended) sediments desorb P during periods of high pH, and this can give rise to a self-perpetuating process of algal growth, even higher pH, P release, further algal growth, etc. (Hosper, 1980b). Moreover, the extremely high algal biomass in summer and the related increased sediment oxygen demand (SOD), may result in anaerobic conditions (low redox potential) at the sediment-water interface, followed by P release (Fig. 4.1).

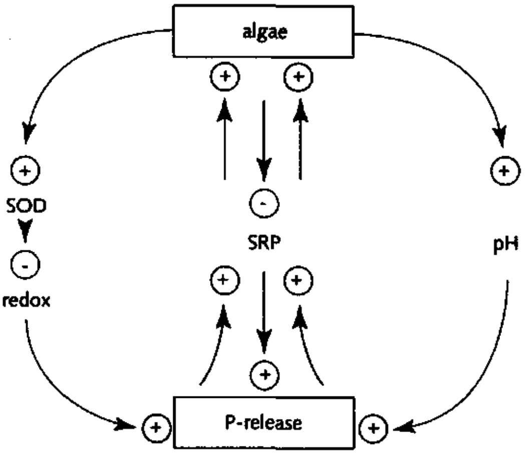

Fig. 4.1 *Algae-mediated P release from lake sediments. High pH and low redox increase solubility of P; algae take up soluble reactive phosphorus (SRP), leading to an increasing 'driving force' for diffusive P transport from the sediments.*

The original idea was that intensified flushing during winter with water poor in TP and algae, could interrupt this self-perpetuating process. Flushing may lead to clear water, P-limited algal growth, reduced pH and therefore lowered P release from the sediments. After the first flushing period, it was suggested that the high levels of Ca^{2+} and HCO_3^- in the flushing water may also contribute to pH reduction (Hosper, 1980b; Uunk, 1980). In most natural waters HCO_3^- is responsible for the pH buffering. In lakes containing substantial amounts of Ca^{2+}, the uptake of CO_2 by the algae may lead to the precipitation of $CaCO_3$ (calcite), and that places a ceiling over the pH values obtainable. Finally, due to the higher transparency in spring, green algae and diatoms would become more competitive as compared to the cyanobacterium *Oscillatoria agardhii*, which prefers dim light conditions (Mur *et al.*, 1978).

The purpose of this whole-lake study was to test the idea of winter flushing in order to reduce P release and to trigger a shift from an *Oscillatoria*-dominated, turbid water state towards a clear water state with a more diverse phytoplankton community. The relevant mechanisms for P release and the consequences for lake management will be discussed.

Study site

Veluwemeer (3,356 ha, mean depth 1.25 m, volume 42.10^6 m^3) was created in 1956, along with the construction of the polder of Flevoland in IJsselmeer. The lake is connected to the smaller Drontermeer (592 ha, mean depth 1.05 m, volume 6.10^6 m^3) and located between the dykes of the new polder and the former coast line of IJsselmeer (Fig. 4.2). A navigation channel (width 100 m, depth 3-4 m) runs the length of the lake. Veluwemeer was well-known for its clear water and rich submerged vegetation (Leentvaar, 1961, 1966). In the late 1960s, eutrophication resulted in a rapid deterioration of water quality. From 1971 onwards, there was a massive bloom of cyanobacteria (*Oscillatoria agardhii*), persisting year-round (Berger, 1975, 1987), with Secchi depth varying from 0.20 m in summer to 0.50 m in winter. The water managers responsible for Veluwemeer were pioneers in lake restoration. In 1972, the problem of eutrophication was recognized by the authorities (WCKR, 1972) and in the same year the first phosphorus elimination facility in the Netherlands at the sewage treatment plant of Elburg (75,000 population equivalents) came into operation. Phosphorus stripping at the second and larger treatment plant of Harderwijk (175,000 population equivalents) followed in February 1979, leading to a reduction of the external P loading of Veluwemeer-Drontermeer from 2.7 g P m^{-2} y^{-1} in 1978 to 1.5 g P m^{-2} y^{-1} in 1980-1983 (PER, 1986) and subsequent years (Snijdelaar, 1995). The lake has a characteristic hydrology, due to its location between the elevated 'old' land and the new polders, five meter below mean sea level. On one side of the lake there is an inflow of groundwater and several streams, whereas on the other side water is lost by infiltration into the polders (Fig. 4.3). The excess water of the lake is drained off through shiplocks into the adjacent lakes. The average hydraulic retention time, calculated on the basis of outflow (evaporation, infiltration and intensified flushing not included), is 0.7 y. Several pumping engines usually discharge the excess water of the polder of Flevoland into the large IJsselmeer, but it is also possible to pump this water into Veluwemeer. Large quantities of excess polder water are available, especially during winter.

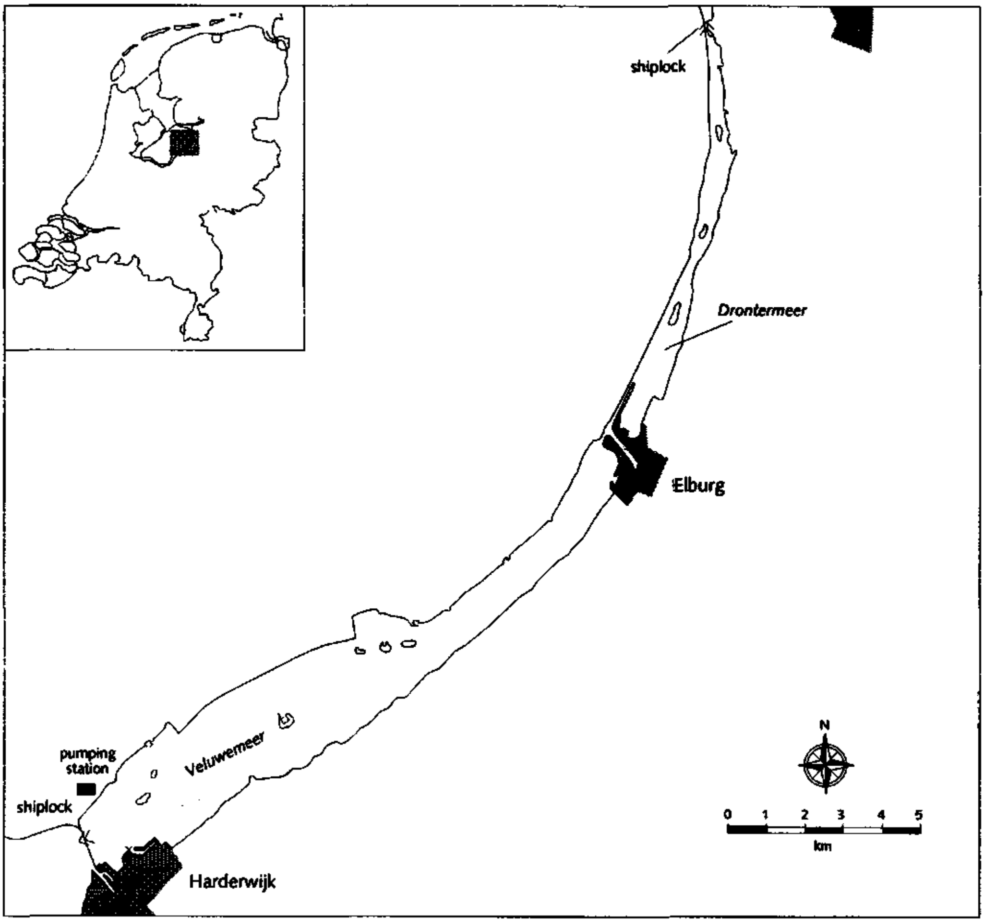

Fig. 4.2 *The lakes Veluwemeer and Drontermeer in the Netherlands.*

Materials and methods

Lake flushing

Intensified flushing of the lake has been carried out by feeding in excess water from the polder of Flevoland by the Lovink pumping station (max. capacity 19 $m^3 s^{-1}$) at the southern end of the lake, and discharging it through the shiplock in the north (Fig. 4.2). Flushing took place mainly from November-March and started in 1979. The flushing water originates from rainwater and groundwater (ratio ≈ 1:1) seeping into the polder (Fig. 4.3), and is low in TP and relatively high in NO_3^-, Cl^-, SO_4^{2-}, Ca^{2+} and HCO_3^-. Table 4.1 gives water quality data for both the flushing water and the lake, prior to flushing. The phytoplankton of the flushing water is dominated by green algae and diatoms and chlorophyll *a* during winter is usually

< 10 μg l^{-1}. How much flushing water should be pumped into Veluwemeer? It was assumed that this large and wind-exposed lake may be approximated as a completely mixed flow-through reactor. Chloride data from the lake during the first flushing period, confirmed that the flushing water and the lake water mix thoroughly (PER, 1986). It should be noted that during ice-cover mixing of flushing water and lake water will be less intense, leading to a so-called plug flow pattern (maximum replacement of lake water by flushing water) or short-circuit flow pattern (direct flows via the deep navigation channel to the outlet, and consequently minimum replacement of lake water from the shallow areas by flushing water).

	Flushing water **mg l^{-1}**	**Veluwemeer before flushing** **mg l^{-1}**
TP	0.09 (0.07-0.11)	0.42 (0.24-0.56)
TN	5,3 (3.4-6.6)	5.0 (4.3-5.6)
NO_3^--N	3.3 (1.4-5.5)	0.8 (0.0-1.6)
Cl^-	280 (232-355)	100 (80-110)
Ca^{2+}	140 (117-186)	45 (30-60)
HCO_3^-	230 (212-257)	86 (26-154)
SO_4^{2-}	324 (153-810)	56 (47-86)

Table 4.1 *Concentrations in flushing water and in Veluwemeer before the flushing.*
Flushing water: TP (total-P), TN (Kjeldahl-N+NO_3^--N), NO_3^- and Cl^- are inflow weighted mean values for November-March 1979-80 to 1983-84; range is min/max of monthly means. Ca^{2+} and HCO_3^- are mean values for November-March 1980-81; SO_4^{2-} mean value for 1981, range is min/max.
Veluwemeer: TP, TN, NO_3^- and Cl^- in Veluwemeer are mean values for the winter 1978-79; Ca^{2+}, HCO_3^- and SO_4^{2-} are mean values for the years 1971-1972; range is min/max (data from Municipal Waterworks Amsterdam).

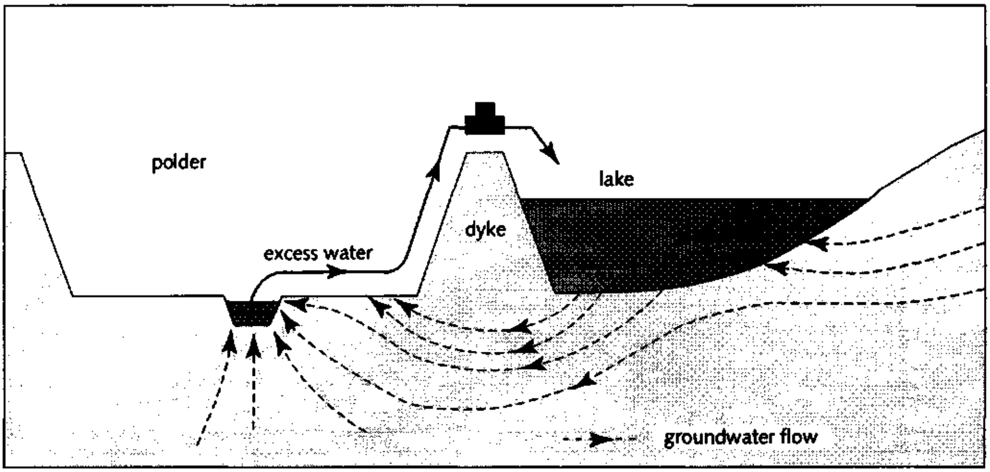

Fig. 4.3 *Hydrology of Veluwemeer.*

The mass balance for a conservative substance in a well-mixed lake is given by:

$$V \cdot \frac{dC}{dt} = Q \cdot C_i - Q \cdot C \qquad (1)$$

where:

V = lake volume (m^3)
C = in-lake concentration of the substance ($g\ m^{-3}$)
C_i = inflow concentration of the substance ($g\ m^{-3}$)
Q = water inflow, outflow ($m^3\ d^{-1}$)

Solving this differential equation gives the time development during flushing:

$$C_t = (C_0 - C_i)\, e^{-\rho t} + C_i \qquad (2)$$

where:

C_t = in-lake concentration at time t ($g\ m^{-3}$)
C_0 = in-lake concentration at time t = 0 ($g\ m^{-3}$)
ρ = Q/V, flushing rate (d^{-1})

Eq. (2) was used to determine the needed quantity of flushing water for the period November-March. For a 95% renewal of the original lake water (volume $42.10^6\ m^{-3}$) in a period of 150 d, the flushing rate should be $0.02\ d^{-1}$ ($Q = 0.84.10^6\ m^3\ d^{-1}$ or $126.10^6\ m^3$ for the whole flushing period). Besides the inflow of polder water, there is a natural water inflow from small streams (unfortunately still high in TP) and seepage (volume ratio streams:seepage ≈ 1:1) in the flushing period of about $15.10^6\ m^3$. Therefore, the objective for pumping is $111.10^6\ m^3$. Table 4.2 gives the actual water inflow.

	Total water inflow $10^6\ m^3$	Water renewal %
1979-80	102	91
1980-81	97	90
1981-82	128	95
1982-83	113	93

Table 4.2 *Total water inflow for Veluwemeer in the period November-March (intensified flushing and natural flushing) and water renewal (calculated by Eq. 2, see text).*

Monitoring

Water samples were collected from the upper 0.5 m at five locations in Veluwemeer-Drontermeer at 1-2 weeks intervals. Except for occasional short summer periods in the deeper navigation channel, the water column of the lake is completely mixed. Chemical analyses were carried out according to Netherlands standard methods (NEN). Chlorophyll *a* was determined using the acetone extraction method until 1985. From that date ethanol was used as the extractant, in accordance with standardization agreements. This produced significantly lower values and therefore all original data before 1985 were corrected by a multiplication factor of 0.67 (Griffioen, pers. comm.). Phytoplankton samples, fixed with iodine-formaline, were quantified in counting chambers. Volumes of the algae were measured at 400x magnification under an Olympus BH microscope, using an OSM micrometer eyepiece. It was found that the volumes of the cells of diatoms and green algae were fairly constant. An average value was calculated for each species and this value was used for estimating the biovolume for that species through the whole sampling period. The width of the cyanobacterial filaments was constant as well, so this was only measured occasionally. The length of the filaments was determined by measuring at least 30 filaments of each species. The standard error of the mean was about 15%. Except for the spring period, a constant filament length was used over the year to calculate total filament volume per liter. During the spring the mean filament length was significantly lower.

Water and nutrient budgets

Water and nutrient budgets on a monthly basis were established for Veluwemeer-Drontermeer. Budgets for chloride were set up as well. Detailed information on methods, including the evaluation of uncertainty, can be found in PER (1986). A budget for water or for a conservative substance (e.g. chloride), for a given space and time period, can be written as:

$$\textit{inflow} - \textit{outflow} = \Delta\ \textit{storage} \qquad (3)$$

where:
inflow = sum of all inflows
outflow = sum of all outflows
Δ storage = difference in storage between beginning and end of budget period

In practice, the budgets will not fully balance. A residual balancing term will appear in which neglected flows and inaccuracies are accumulated:

$$\textit{inflow} - \textit{outflow} = \Delta\ \textit{storage} - \textit{residue} \qquad (4)$$

If the residual term in the water budget significantly differs from zero, considering the errors in the other terms, it must be concluded that the budget is incorrect. In that case certain water flows must have been overlooked. A well-balanced water budget is not necessarily a correct water budget; errors in the inflow, outflow and storage might compensate for each other. A chloride budget provides an extra check for the accuracy of the water budget. In the mass budget for non-conservative substances the residual term shows the effects of mass flows that were not included in the flow measurements, in case of TP the net effect of sedimentation and release from the lake sediments. As all errors in the water budget are transferred to the TP budgets, the water budgets should be balanced and correct. A simple statistical analysis was applied (PER, 1986) to assess the confidence limits of the budget terms. Fig. 4.4 shows the residual terms in the water budgets, including the confidence limits, and it may be concluded that the residual terms (about -10%/+10% of average water inflow) do not differ significantly from zero. In other words, the water budgets provide a sound basis for setting up the TP budgets.

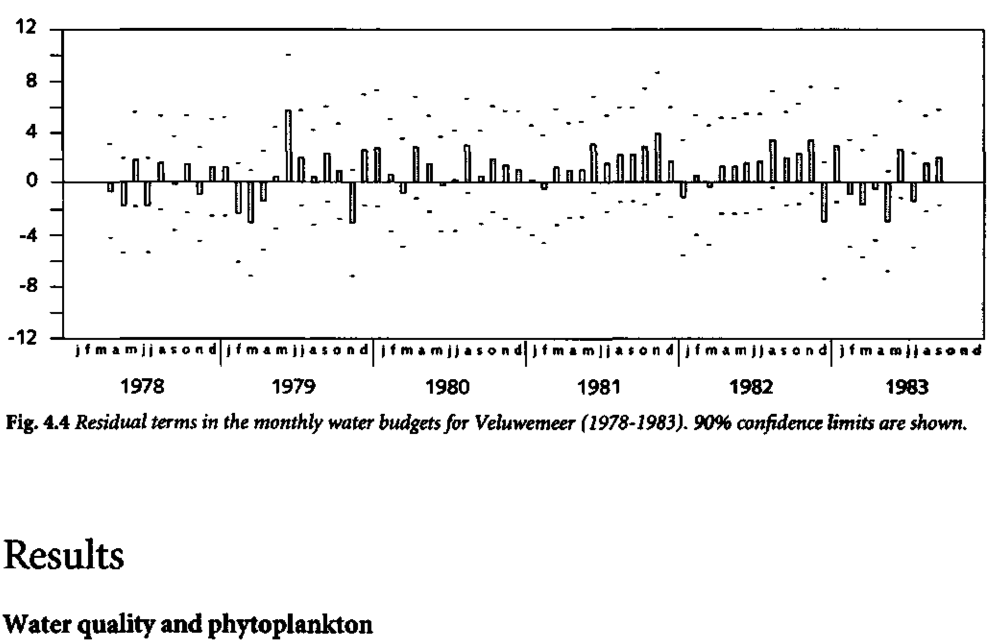

Fig. 4.4 *Residual terms in the monthly water budgets for Veluwemeer (1978-1983). 90% confidence limits are shown.*

Results

Water quality and phytoplankton

Water quality and phytoplankton data are presented for the period 1977-1985 (Figs. 4.5-4.8). As stated above, P loading reduction was achieved at the beginning of 1979 and the intensified winter flushing started in 1979-80. Periods of ice-cover are also shown. There were cold winters with long periods of ice-cover in 1979, 1982 and 1985. Chlorophyll *a* (Fig. 4.5) showed a sharp decrease during the first flushing period, but did not nearly reach the low levels of the flushing water (10 $\mu g\,l^{-1}$). Obviously, during certain periods, primary production could catch up with the washout of algal cells (see below). Mean and maximum chlorophyll *a* levels during summer were considerably reduced after the measures. Although the algal biovolume shows the same trend (Fig. 4.5), it is obvious that the decrease in algal biovolume is less pronounced than the decrease in chlorophyll *a* and ash-free dryweight (Fig. 4.6). A first major change in the phytoplankton species composition was not observed until 1982 (Fig.

4.5), when the dominance of *Oscillatoria agardhii* was broken. In the second half of May 1982, the species disappeared almost completely and in June and July a great variety of green algae appeared. In August there was a second bloom of diatoms and a gradual increase in cyanobacteria. By September 1982, the bloom of cyanobacteria was back again. After the flushing in the cold winter of 1985, *Oscillatoria agardhii* lost ground again and ever since the phytoplankton has been a mix of cyanobacteria, green algae and diatoms (see also chapter 7). Before the measures were taken, transparency varied between 0.20 m in summer and 0.50 m in winter. After the measures, the summer Secchi depth increased to 0.30 m, increasing to 0.40-0.50 m after the species shift in the phytoplankton in 1985 (Fig. 4.6). pH of the lake water changed significantly. Summer pH values dropped by more than one unit (Fig. 4.7).

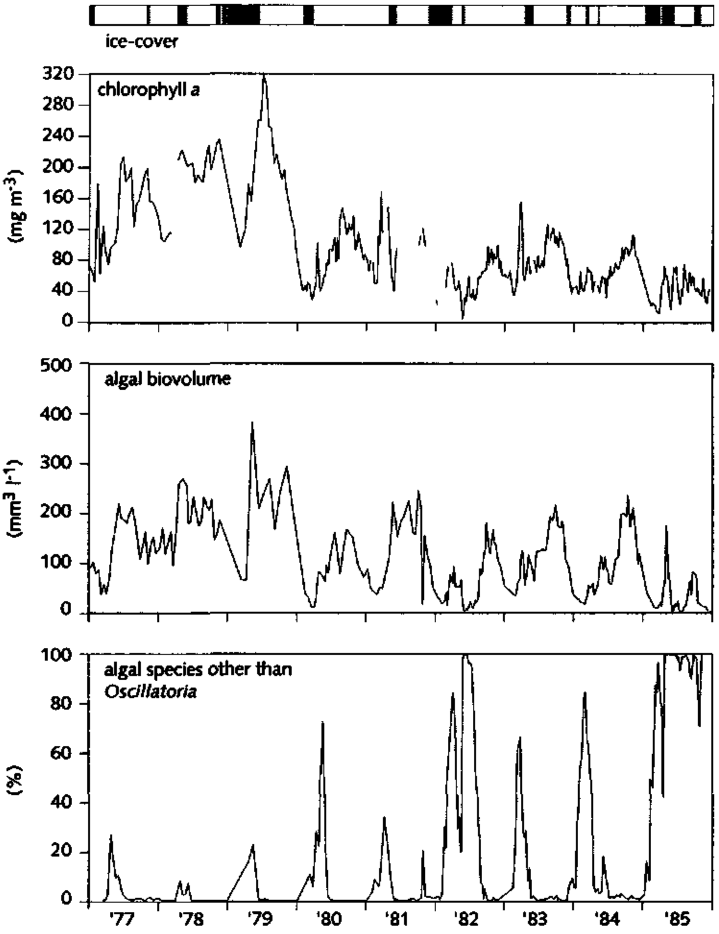

Fig. 4.5 *Chlorophyll a, algal biovolume and relative abundance of algal species other than Oscillatoria agardhii in Veluwemeer (1977-1985). Periods of ice-cover are also shown.*

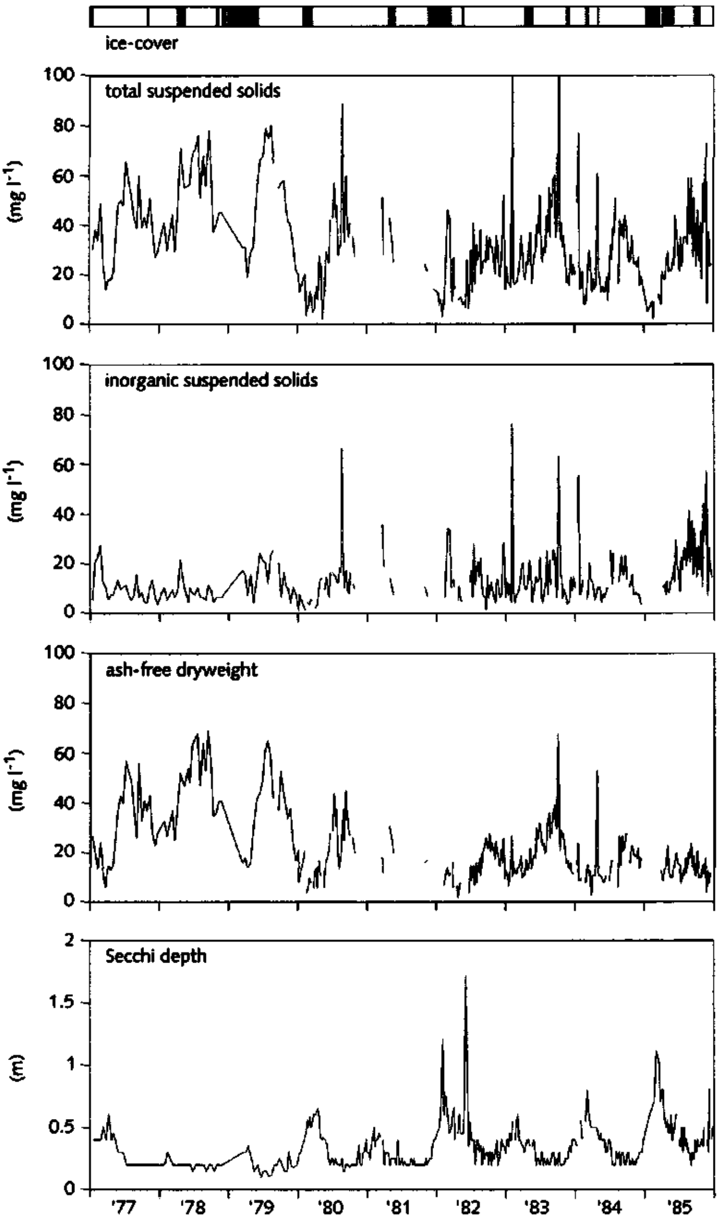

Fig. 4.6 *Total suspended solids, inorganic suspended solids, ash-free dryweight and Secchi depth in Veluwemeer (1977-1985). Periods of ice-cover are also shown.*

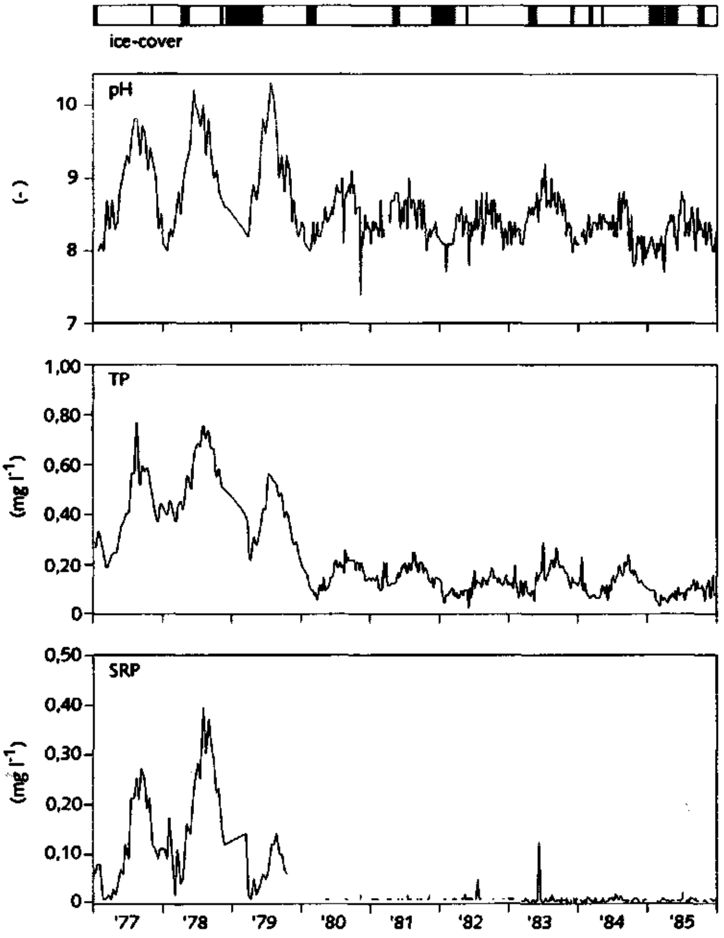

Fig. 4.7 *pH, TP and SRP in Veluwemeer (1977-1985). Periods of ice-cover are also shown.*

Before 1980, TP and SRP (soluble reactive phosphorus) used to show a sharp increase in the summer and decrease in the fall. After the measures, for TP the same pattern is observed, but much less pronounced (Fig 4.7). Mean TP summer values dropped from 0.40-0.60 mg l^{-1} to 0.10-0.20 mg l^{-1}. Before the measures, SRP accumulated in the water during summer up to 0.20-0.30 mg l^{-1}, afterwards it continued to be < 0.02 mg l^{-1}. Although the N loading increased due to the winter flushing, the mean summer concentrations for TN (including Kjeldahl-N, NO_3^- and NO_2^--N) practically halved after 1979 (Fig. 4.8). The winter flushing resulted in a doubling of the NO_3^- concentration in early spring. NO_3^-, however, disappeared very rapidly, probably because of denitrification.

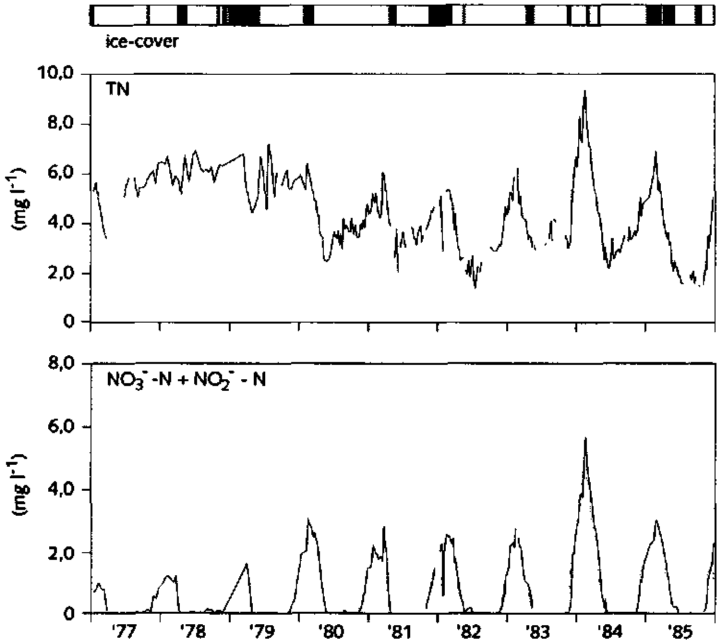

Fig. 4.8 *TN (Kjeldahl-N+NO_3^--N+NO_2^--N) and NO_3^--N+NO_2^--N in Veluwemeer (1977-1985). Periods of ice-cover are also shown.*

Phytoplankton dynamics during flushing

In spite of the intensified flushing, during mild winters (for example 1980-81) chlorophyll *a* and biovolume of *Oscillatoria*, remain fairly high. It was suggested above that primary production could catch up with the washout of algal filaments. For a well-mixed lake the net growth of *Oscillatoria* filaments can be calculated by means of a simple model and the actual data on water outflow and *Oscillatoria* biovolume during the flushing period:

$$\frac{\Delta B}{\Delta t} = (\mu - \rho)\, B \qquad (5)$$

where:

ΔB = increment of biovolume during month ($mm^3\ l^{-1}$)
B = biovolume, monthly mean value ($mm^3\ l^{-1}$)
μ = net growth rate ($month^{-1}$)
ρ = flushing rate ($month^{-1}$)

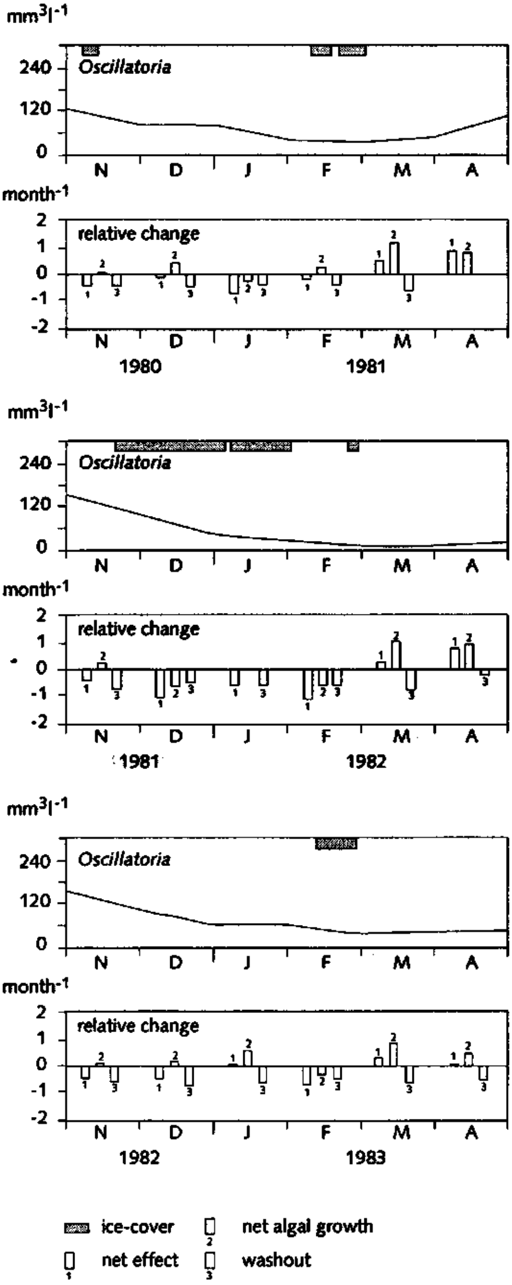

Fig. 4.9 *The effects of washout and net algal growth on the biovolume of Oscillatoria in winters 1980-81, 1981-82 and 1982-83.*

The effects of both washout and net growth of *Oscillatoria* on a monthly basis are shown in Fig. 4.9, for the winters 1980-81, 1981-82 and 1982-83. Particularly in early spring (March-April), the intensified flushing is insufficient to control algal biomass. Simulations with increased flushing rates, assuming net growth rates as calculated for the winter 1980-81, show a significant effect of an additional flushing of 5-10.10^6 m^3 $month^{-1}$ (Fig. 4.10). The increased flushing rates which were applied in the winter periods of 1981-82 and 1982-83, were based upon these results. The strongest decline in algal biovolume, due to mortality (negative net algal growth) and washout, occurred during the cold winter (long ice-cover) of 1981-82 (Fig. 4.9). Note that the assumption of ideal mixing does not apply during ice-cover (see above). Therefore, Eq. (5) cannot actually be used for calculating the contribution of mortality and washout, during periods of ice-cover. In conclusion, it is recommended to concentrate the flushing in the period November-February for winter flushing of *Oscillatoria* lakes, and to assume conservative behavior (net growth = 0) of the algae. Then, for a well-mixed lake, removal of 95% of the *Oscillatoria* can be achieved by flushing with three times the lake volume (ρ = 0.75 $month^{-1}$). Flushing under the ice-cover may be more effective, provided that plug flow conditions can be approximated.

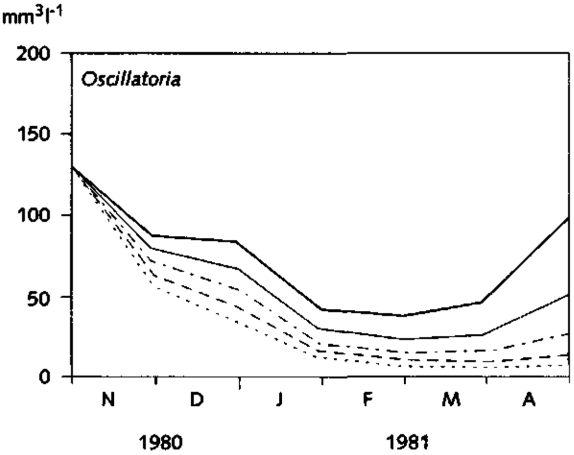

Fig. 4.10 *Model simulations of the effects of extra flushing on the biovolume of Oscillatoria in winter 1980-81. The effects of the nominal flow (bold line) and extra flows of 5, 10, 15 and 20.10^6 m^3 $month^{-1}$ are shown.*

Phosphorus dynamics

Mass budgets for TP were established on a monthly basis. The residual term in the mass balance equation gives the TP retention or net effect of sedimentation and release from the sediments (Fig. 4.11). Over the whole period of 1978-1983, the TP retention is about 50% of the input. Usually, the residual term is positive, which means that sedimentation is the dominant process. In spring and early summer the reverse may occur and release exceeds sedimentation, resulting in a rise in TP. Net release is observed, both in the years before and after the restoration measures. The TP mass budgets do not answer the question whether the actual (gross) P release was reduced by the measures or not. A possible reduced P release may be masked by simultaneously reduced P sedimentation or vice versa. A modeling approach may carry us a step further.

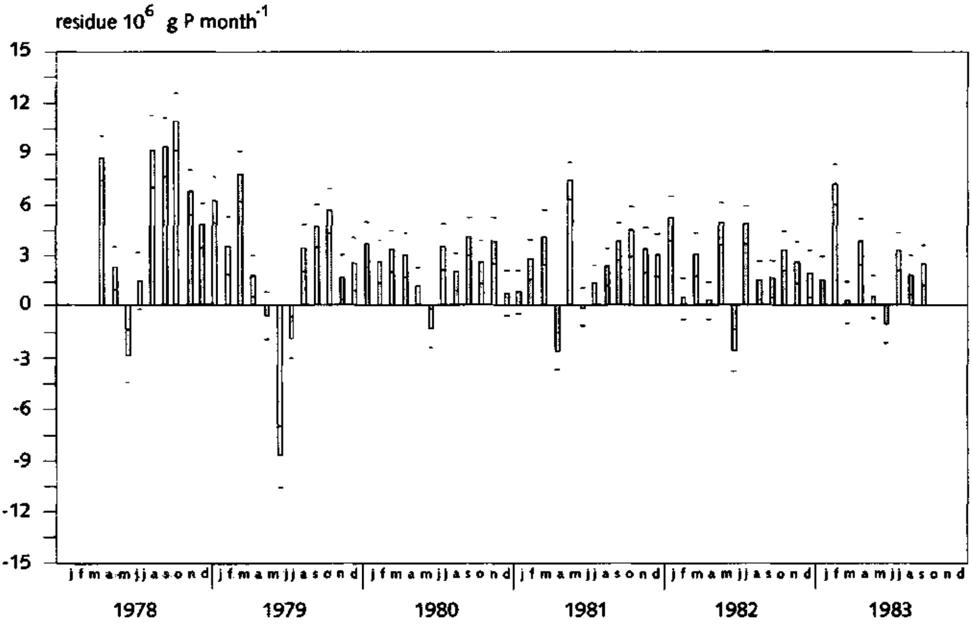

Fig. 4.11 *Residual terms in the monthly TP mass budgets for Veluwemeer (1978-1983). 90% confidence limits are shown.*

For an estimate of the actual sedimentation and release rates, the following mass balance equation was used (with a time step $\Delta t = 3$ months):

$$\frac{\Delta P}{\Delta t} = L_{ext} - (\rho P - \rho_i a P) + L_{int} - \sigma_s a P \qquad (6)$$

where:
P = TP in the lake (mg m^{-3})
L_{ext} = external P loading (mg m^{-3} d^{-1})
ρ = flushing rate (Q/V), based on total water outflow excl. evaporation (d^{-1})
ρ_i = flushing rate (Q_i/V), based on water outflow by infiltration Q_i (d^{-1})
a = fraction of TP in suspended solids
L_{int} = internal P loading (mg m^{-3} d^{-1})
σ_s = sedimentation rate (d^{-1})

A special feature of this model is the explicitly formulated infiltration process. In dry periods, infiltration into the sediments (5 mm d^{-1}) is the main water outflow. Particularly after the restoration measures, P in the lake is mainly present in algae and other suspended solids and these forms of P are not removed by infiltration. So, the outflow of TP from the system will be less than expected on the basis of total water outflow. The underlying assumptions for this model are: sedimentation is proportional to particulate TP in the lake, only dissolved TP is removed by infiltration and the lake is completely mixed and has a constant volume. The model has two unknown factors, *viz.* L_{int} and σ_s. According to Van Straten (1986) an estimate for both factors can be obtained from separate TP budgets for the winter period and the summer period. If internal loading during winter is assumed to be zero, then the sedimentation rate can be derived from the winter budgets. Next the internal loading during summer can be calculated from the summer budgets, assuming that the sedimentation rate remains the same (Van Straten, 1986). Brinkman & Van Raaphorst (1986) developed a P release model and suggested a release rate during winter of 0.5 mg m^{-3} d^{-1}. Boers (1991) found a winter release rate of 0.1 mg m^{-3} d^{-1} for the Loosdrecht lakes. Therefore, a range in σ_s and L_{int} was calculated, under the assumption of (1) L_{int}(winter) = 0 and (2) L_{int} (winter) = 0.5 mg m^{-3} d^{-1} (Table 4.3). From these budget calculations it can be concluded that a pronounced drop in P release from the sediments has occurred in the summer of 1980, compared with both previous summer periods. Obviously, the winter flushing resulted in a better binding of P to the sediments.

Winter	**Sedimentation rate σ_s (d^{-1})**		**Summer**	**Internal loading L_{int} (mg m^{-3} d^{-1})**	
	for L_{int} winter = 0	**for L_{int} winter = 0.5**		**for L_{int} winter = 0**	**for L_{int} winter = 0.5**
				σ_s min σ_s max 0.0072 - 0.0170	σ_s min σ_s max 0.0358 - 0.0684
1978-79	0.0135	0.0358	78	1.0 - 3.8	9.2 - 18.5
1979-80	0.0122	0.0416	79	5.2 - 8.4	14.5 - 25.0
1980-81	0.0072	0.0457	80	0.0 - 1.1	4.0 - 9.0
1981-82	0.0170	0.0684	81	0.0 - 1.7	5.1 - 10.9
1982-83	0.0164	0.0576	82	0.0 - 0.0	1.9 - 5.4
			83	0.1 - 0.6	4.5 - 9.5

Table 4.3 *Sedimentation rate σ_s and internal loading L_{int} for TP in Veluwemeer-Drontermeer.*
σ_s calculated from winter TP budgets (December-February) and Eq. (6), assuming that (1) L_{int} during winter = 0 and (2) L_{int} during winter = 0.5. L_{int} during early summer (May-July) calculated from summer TP budgets and Eq. (6), assuming that σ_s winter = σ_s summer.

Discussion

The hypothesis was that intensive flushing during winter with water low in TP and algae and rich in Ca^{2+} and HCO_3^- could interrupt the self-perpetuating process of the persistent algal blooms of *Oscillatoria agardhii* and bloom-mediated P release by the sediments. Additionally, the clear water in spring, as a result of flushing, would favor other algal species than *Oscillatoria agardhii*, which prefers the dim-light conditions of turbid waters (Mur *et al.*, 1978). The study focused on the period 1977-1978 to 1985. At the beginning of 1979 the external P loading of the lake had been reduced from 2.7 to 1.5 g m^{-2} y^{-1}. The first winter flushing took place from November 1979-March 1980, and in the following summer TP and chlorophyll *a* showed a dramatic decline. SRP that used to accumulate during summer up to 0.20-0.30 mg l^{-1}, was below 0.02 mg l^{-1} ever since. The summer pH decreased from 9.5-10.0 to 8.5-9.0. However, the dominance of *Oscillatoria agardhii* was not yet broken and the summer Secchi depth only increased from 0.20 to 0.30 m. The flushing continued during the next winter periods. Flushing together with cold winters and prolonged periods of ice-cover, was more successful. After ice-out in 1982 and in 1985 the water was relatively clear (Secchi depth ≈ 0.50 m) and this may have triggered the shift in species composition that was observed. The cyanobacterial dominance was temporarily broken in 1982 and from 1985 onwards the phytoplankton composition was a mix of green algae, diatoms and cyanobacteria. The cold winter of 1978-79, one year before the first winter flushing and still with the high external loading, failed to produce such a shift in species. Apparently, load reduction and flushing in combination with a cold winter, ultimately resulted in a major change to the system. Secchi depth in summer, however, was still limited and varied from 0.40 to 0.50 m.

Limiting factors for algal growth

Fig. 4.12 shows TP and TN *vs.* chlorophyll *a* for 1978-1985, in relation to the limitation lines for algal biomass, which were presented in chapter 3. Although Veluwemeer deviates from the P-limitation line for cyanobacteria-dominated lakes, these results suggest a shift from excess P towards more P-limited algal growth. Bioassays confirmed the limiting role of P during spring and early summer (Kerkum, 1983). Wind-induced resuspension in this large and shallow lake, resulting in comparatively high levels of non-algal particulate P, may be responsible for the deviation from the P-limitation line for *Oscillatoria* lakes. Note the decrease in summer TN in spite of an increased external N loading, due to the winter flushing (17 g m^{-2} y^{-1} in 1978 to 35 g m^{-2} y^{-1} in 1980-1983). TN levels seem to follow the algal biomass, which is limited by other factors, such as light or P. Occasionally, in late summer, N may be the limiting factor for algal growth (Kerkum, 1983).

Secchi depth

Considering the dramatic drop in chlorophyll *a*, the increase in transparency is disappointing. This discrepancy can be explained by a reduced chlorophyll *a* content of the filaments of *Oscillatoria agardhii* (Fig. 4.13). Apparently, the turbidity of the water (expressed

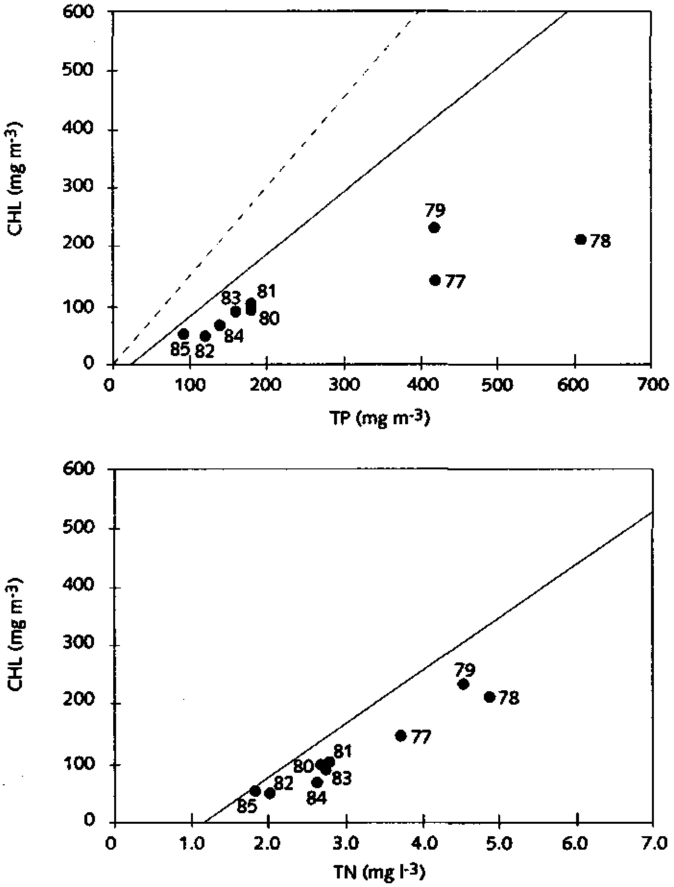

Fig. 4.12 *Chlorophyll a in relation to TP and TN in Veluwemeer. Mean values April-September (1978-1985). The indicated lines approximate the maximum value for chlorophyll a in relation to TP (CHL = -24 + 1.04TP) and TN (CHL = -95.2 + 0.09TN); the broken line is for lakes dominated by filamentous cyanobacteria (CHL = 1.54TP) (see chapter 3).*

as inverse Secchi depth) during the *Oscillatoria* years is related to number and volume of the *Oscillatoria* filaments, rather than to chlorophyll *a*. This result agrees with the light theory (Preisendorfer, 1986; Buiteveld, 1995; see also chapter 3) suggesting that Secchi depth is particularly sensitive to changes in light scattering by particles (such as algal filaments) compared to changes in light absorption by chemical substances (such as chlorophyll *a*). In 1985, after the species shift from cyanobacteria to green algae and diatoms, the summer Secchi depth increased from 0.30 to 0.40-0.50 m. The higher chlorophyll *a* content per unit P of *Oscillatoria*, as compared to other algal species (see chapter 3), is a possible explanation for this increase in water clarity.

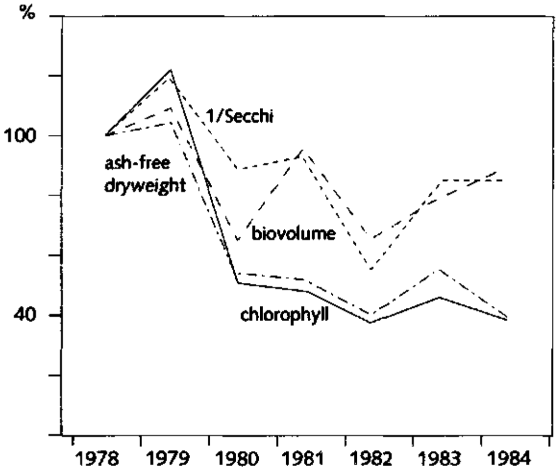

Fig. 4.13 *Inverse Secchi depth, biovolume and chlorophyll a in Veluwemeer (1978-1984). Data expressed in relative numbers, with 1978 at 100%. Mean values for periods dominated by Oscillatoria agardhii (July-September; in 1982 September-November; in 1984 August-October). Inverse Secchi depth values were corrected for background light attenuation by subtracting 1* m^{-1}.

Water-sediment interactions

The effects of flushing and reduced external loading on the P dynamics are of special interest. In 1979, the external loading decreased by 44% and, almost instantaneously, because of this load reduction and the flushing, TP in the lake dropped by 66%. The effects predicted by the empirical models, which are based on a multitude of lakes varying in loading with nutrients and water (see chapter 3), are significantly weaker (Table 4.4). The quick response of Veluwemeer (from 1979 to 1980) is remarkable and indicates a discontinuity in the water-sediment interactions.

	TP before restoration	**TP after restoration**	**Reduction**
	TP (mg m^{-3})	**TP (mg m^{-3})**	**%**
measured	470	160	66
calculated with OECD model	420	200	52
calculated with CUWVO model	250	120	52
calculated with Lijklema model	280	140	50

Table 4.4 *TP in Veluwemeer-Drontermeer before and after restoration, annual mean values.*
OECD model (OECD, 1982): $P = 1.02 \{P_i / (1 + \sqrt{\tau})\}^{0.88}$. *CUWVO model (chapter 3):* $P = P_i (0.201 \log q + 0.322)$. *Lijklema model (Lijklema et al., 1988):* $P = 0.698 \{P_i / (1 + \sqrt{\tau})\}^{0.88}$. *Before restoration: 1977-1978; after restoration: 1980-1983. The hydraulic residence time (*τ *= lake volume/outflow) and the areal hydraulic loading (*q *= outflow/lake area in* $m\ y^{-1}$*) are based upon 1979-1983 data, excluding or including the flushing water. As only dissolved P can be removed by infiltration, the outflow by infiltration has been multiplied by the fraction of dissolved P in TP (0.33 before restoration, 0.1 after restoration). For explanation of the models see chapter 3.*

Calculations with a simple P budget model (Eq. 6) showed a pronounced drop in sediment P release during summer from 1979 to 1980 (Table 4.3). The calculated values for summer P release after restoration, under the assumption of zero internal loading during winter, agree fairly well with observations in continuous flow experiments with Veluwemeer sediments. Brinkman & Van Raaphorst (1986) measured 0.8-2.3 mg m^{-3} d^{-1} (in 1983) and Van der Molen *et al.* (1994) 0.8-1.5 mg m^{-3} d^{-1} (in 1987).

The summer internal loading was calculated from Eq. (6), by using the winter sedimentation rate. It was assumed that the sedimentation rate is constant over the year. However, it could be argued that flushing with water rich in Ca^{2+} and HCO_3^- leads to an enhanced P sedimentation rate during the summers from 1980 onwards, due to possible coprecipitation of SRP with calcite (House & Donaldson, 1986; Danen-Louwerse *et al.*, 1995). During intensive photosynthesis, consumption of CO_2 results in a higher pH and a shift from HCO_3^- to CO_3^-. This may lead to the precipitation of $CaCO_3$ when the ion activity product exceeds the solubility product. Dissolved phosphate can coprecipitate with calcite during crystal growth. Data on the actual calcite formation are lacking, but an indication for the potential formation of calcite crystals can be derived from the degree of saturation of the solution with respect to calcite, generally expressed as the saturation index (SI), where K_{so} is the solubility product for pure calcite ($K_{so} = 10^{-8,35}$):

$$SI = \frac{[Ca^{2+}]\,[HCO_3^-]\,/\,[H^+]\ \times 10^{-10.33}}{K_{so}} \tag{7}$$

Unfortunately, seasonal data on Ca^{2+} and HCO_3^- in Veluwemeer over the years 1979-1980 are not available. Only SI values for 1972, before the flushing and 1982, after the flushing, could be calculated (Table 4.5). Supersaturation and possibly calcite formation during spring (April-May) has increased from 1972 to 1982. The summer values (June-July) show a decrease.

	Before flushing				**After flushing**			
	1972				**1982**			
	April	**May**	**June**	**July**	**April**	**May**	**June**	**July**
Ca^{2+}	1.3	0.9	0.9	0.9	3.0	2.7	2.5	2.3
HCO_3^-	1.3	0.9	0.6	0.7	2.5	2.2	2.0	1.8
H^+	$10^{-8.8}$	$10^{-9.2}$	$10^{-9.5}$	$10^{-9.5}$	$10^{-8.4}$	$10^{-8.5}$	$10^{-8.3}$	$10^{-8.6}$
SI	11.2	13.4	17.9	20.9	19.7	19.7	10.4	17.2

Table 4.5 *Ca^{2+}, HCO_3^- (in mmole l^{-1}) and H^+ (in mole l^{-1}) and the saturation index (SI) for calcite before and after the flushing of Veluwemeer. Data for 1972 are from Municipal Waterworks Amsterdam.*

The incorporation efficiency of P in the calcite crystals shows a significant decrease when SRP drops from 100 to 1 mg m^{-3} (House & Donaldson, 1986; Danen-Louwerse *et al.*, 1995). The calcite crystal growth, however, may be severely inhibited by enhanced SRP (range 0-300 mg m^{-3}; House, 1987). These complex interactions between calcite and P make it extremely difficult to understand the P dynamics in relation to the flushing. Before the flushing, calcite formation and therefore coprecipitation may have been inhibited by high SRP, although high SRP also increases the incorporation efficiency. After the flushing SRP is low, so calcite formation should not be inhibited, but the incorporation efficiency is low as well. A detailed analysis of the lake water data gives some further indications on the P sedimentation in relation to calcite formation. Lijklema (1994) calculated the partition of P over different dissolved and suspended pools, before and after the restoration measures (Fig. 4.14). It is evident that the average inorganic suspended P fraction (including P incorporated in calcite crystals) has been reduced significantly, in favor of the P fraction incorporated in algae. These results indicate that Ca-P coprecipitation rather decreased than increased as a result of the restoration measures. Danen-Louwerse *et al.* (1995) estimated Ca-P coprecipitation in Veluwemeer for 1985-1987, based upon tentative annual Ca budgets for the lake and the relationship between SRP and the incorporation efficiency. The P removal by coprecipitation varied from 5.0-8.5.10^{6} g y^{-1}, which is about 15% of the total P input (or 30% of the P retention).

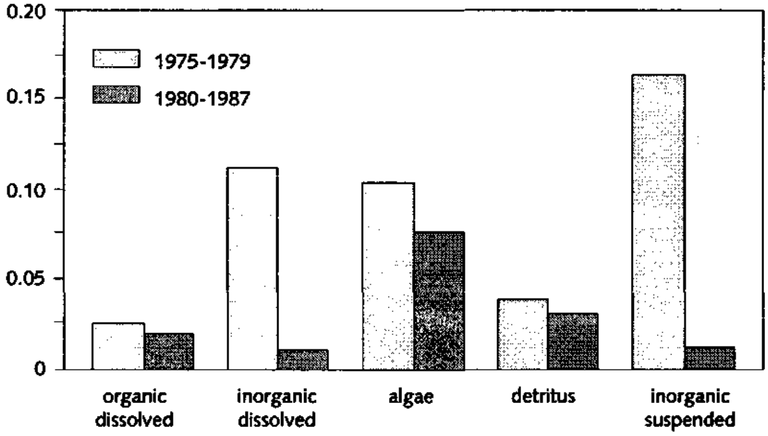

Fig. 4.14 *Partitioning of P in Veluwemeer, before (1977-1979) and after (1980-1987) the restoration measures (from Lijklema, 1994).*

Mechanisms for P release

P release from the sediments obviously decreased substantially (Table 4.3), but which mechanisms can explain the reduction in P release in the first year after the flushing? The hypothesis was that due to the high buffering capacity of the flushing water, the pH of the lake water would remain relatively low, resulting in a reduced release of P from the sediments. The mechanisms controlling the pH of the lake water are especially emphasized here. Indeed, pH values showed a dramatic decline. The question now is whether the lower pH is the effect of buffering by the flushing water (increased levels of HCO_3^-, increased precipitation of $CaCO_3$) or simply the consequence of reduced photosynthesis (reduced CO_2 uptake), in 1980 as compared to 1979. The latter explanation seems unlikely as the increase in algal biomass in the spring of 1980 is not substantially lower than the increase in the spring of 1979 (chlorophyll *a* and algal biovolume, Fig. 4.5; ash-free dryweight, Fig. 4.6). Some tentative pH calculations for the spring periods of 1979 and 1980 may show that the increased precipitation of $CaCO_3$ could have played a major role in the pH buffering (Uunk, 1980). pH can be calculated from changes in alkalinity and total inorganic carbon, according to Stumm & Morgan (1996) (Fig. 4.15). Note that CO_2 uptake does not influence the alkalinity. Changes in inorganic carbon resulting from net algal growth can be estimated with the following simple growth equation (Eq. 8):

$$106\,CO_2 + 108H_2O + 16NH_4^+ \rightleftarrows C_{106}H_{264}O_{110}N_{16} + 105O_2 + 16H^+ \tag{8}$$

where:
$C_{106}H_{264}O_{110}N_{16}$ is organic algal biomass
(expressed as ash-free dryweight, mg l^{-1} or mmol l^{-1})

For a first approximation a closed aqueous system is assumed: no exchange of CO_2 from the air or the sediments and no deposition of $CaCO_3$ and algae. Alkalinity changes due to the production of H^+ (see Eq. 8) and the assimilation of ions such as NO_3^-, NH_4^+ and HPO_4^{2-} may be neglected (Stumm & Morgan, 1996). Alkalinity changes resulting from other processes in the water-sediment system (such as nitrification, denitrification, sulfate reduction etc.) are assumed to be of minor importance for the pH of the lake water (Stumm & Morgan, 1996). Then, from the spring conditions for pH and HCO_3^- (> 90% of total inorganic carbon at pH 8-9) and the CO_2 uptake in 1979 and 1980, the summer pH can be derived (Table 4.6, Fig. 4.15). The calculated pH values are much higher than the measured values, indicating that major buffering processes must have been overlooked. However, the difference between calculated and measured pH is particularly large for 1980, indicating an extra buffering process (i.e. precipitation of $CaCO_3$) in that year. Assuming no $CaCO_3$ precipitation in 1979, the CO_2 compensation (from the air and the sediments) can be derived from the difference in measured and calculated pH (Fig. 4.15) and is estimated at 0.62 mmol l^{-1}. Recalculating the 1980 pH, with an equal CO_2 input of 0.62 mmol l^{-1}, gives a pH of 9.5 (Fig. 4.16) and this value still deviates strongly from the measured pH value of 8.8. Enhanced $CaCO_3$ precipitation during the spring of 1980, putting a ceiling on the obtainable pH values, is the most likely explanation for this deviation. Although $CaCO_3$ precipitation will probably have occurred in 1979 as well, these calculations indicate that in the spring of 1980 the impact of this buffering process was stronger than in the year before. More evidence for the enhanced $CaCO_3$ precipitation comes from field observations (Fig. 4.17) and from fishermen reporting about their fyke-nets clogged with deposits.

		Spring 1979	Spring 1980
increment in ash-free dryweight over 1 April-1 July	mg l^{-1}	35	30
net CO_2 uptake by the algae over 1 April-1 July	mmol l^{-1}	1.05	0.90
total carbonate carbon (= HCO_3^-) 1 April	mmol l^{-1}	1.6	2.7
pH measured 1 April		8.7	8.4
pH calculated 1 July		10.8	10.2
pH measured 1 July		10.0	8.8

Table 4.6 *pH calculations for spring 1979 and spring 1980.*
Ash-free dryweight data are in Fig. 4.6. CO_2 uptake calculated with Eq. (8). pH calculated with Fig. 4.15. HCO_3^- data are from 1972 (Municipal Waterworks Amsterdam) and 1982.

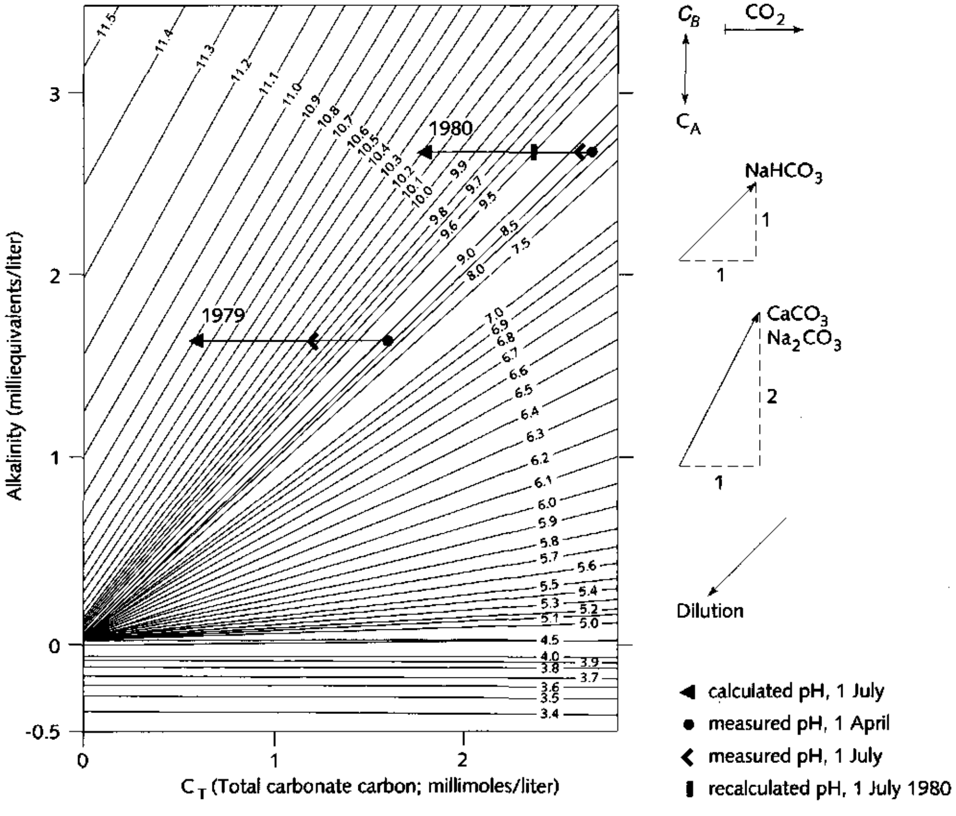

Fig. 4.15 *Alkalinity vs. total carbonate carbon with lines of equal pH (from Stumm and Morgan, 1996). Alkalinity (or acid neutralizing capacity) is defined as HCO_3^- + $2CO_3^-$ + OH^- - H^+ in meq l^{-1}. Total carbonate carbon is H_2CO_3 + HCO_3^- + CO_3^{2-} in mmol l^{-1}. The point moves as a vector in the diagram as a result of the addition (or removal) of acid (C_A) or base (C_B), CO_2, $NaHCO_3$ and the dissolution or precipitation of $CaCO_3$ or Na_2CO_3.*
For the spring of 1979 and 1980, the effect of algal CO_2 fixation on pH is calculated, assuming a closed system (no compensation with CO_2 from the air or the sediments and no precipitation of $CaCO_3$ and algae). The initial pH on 1 April and the calculated and measured pH on 1 July are shown. A recalculated pH for 1980 is also shown, assuming an equal CO_2 compensation in 1979 and 1980 (see text). The data are in Table 4.6.

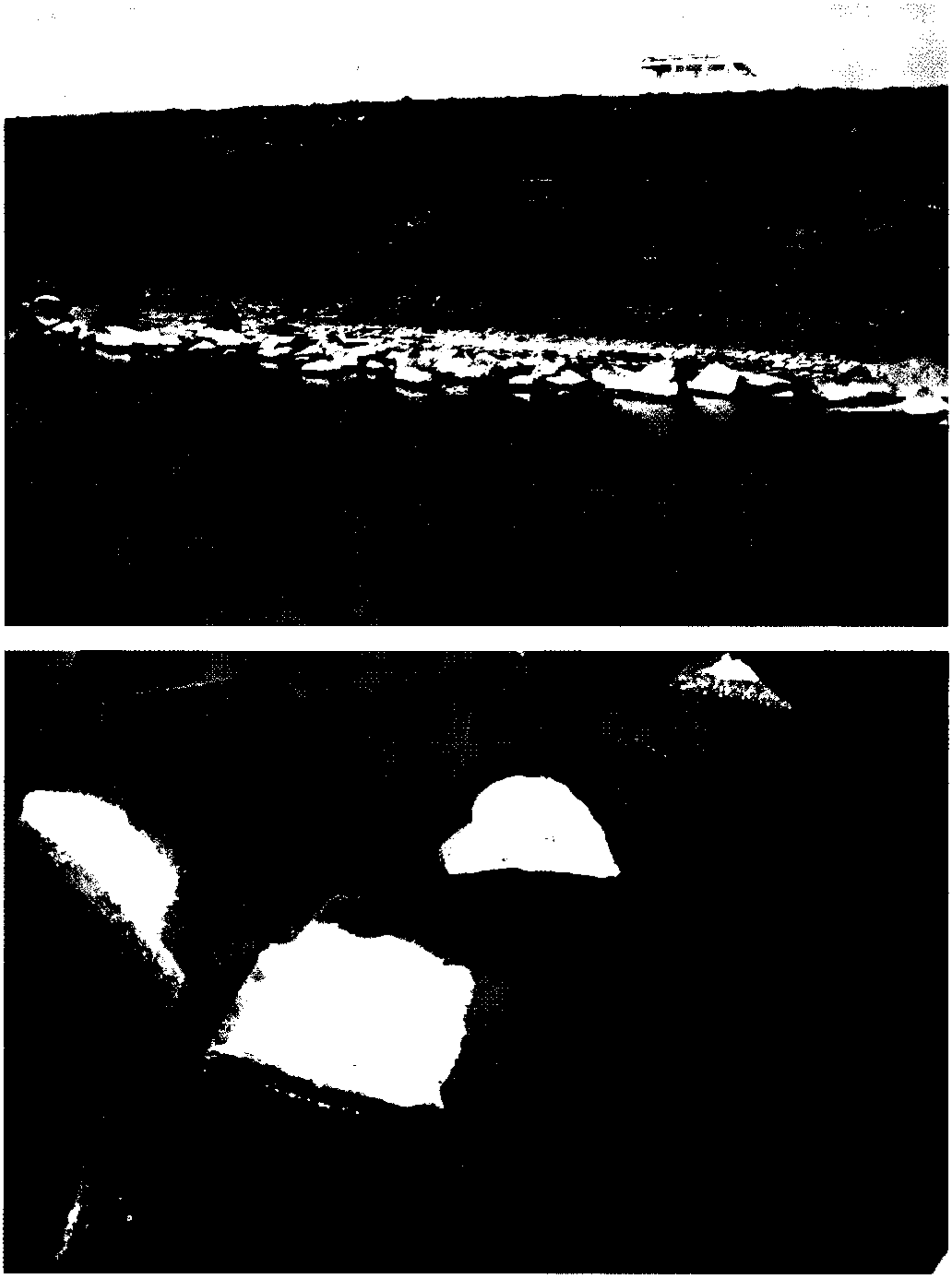

Fig. 4.16 *White deposits on lake shore stones in Veluwemeer (April 1980), indicating the precipitation of calcite (Harry Hosper).*

An alternative explanation for the dramatic reduction in P release from 1979 to 1980, was suggested by Los *et al.* (1988), and later by Jagtman *et al.* (1992) and Van der Molen *et al.* (1994). The authors suggested that the enhanced NO_3^- levels in winter and spring have promoted denitrification in the sediments, leading to better oxygenation of the sediments and hence a better P binding. Smits & Van der Molen (1993) and Delft Hydraulics (1994) applied the sediment-water exchange model SWITCH to Veluwemeer and calculated a triple increase in the denitrification flux in spring 1980, as compared to spring 1979. However, as NO_3^- in the lake water dropped to extremely low levels by April-May 1980, the effects on the redox conditions and particularly the P binding during the summer may be questioned.

Finally
Will the P release increase again if the intensified winter flushing would be stopped? The alkalinity and Ca^{2+} content of the lake water will go down, following the rate of flushing by the natural (lower alkalinity) inflow. Within 1-2 years the original *pre-flushing* conditions will be back, with a relatively low pH buffering capacity. The current favorable lake conditions (low TP, low chlorophyll *a* and extended vegetated areas, see chapter 7), suggest a more or less stable clear water state. Hence, it seems unlikely that stopping the winter flushing would be followed by the same 'explosive' P release from the sediments, as experienced in the 1970s. However, it remains uncertain whether or not the present lake will be resistant to occasional increases in external nutrient loading (for example resulting from mild and wet winters). A high external loading may produce phytoplankton blooms, triggering a strong P release from the sediments. Winter lake flushing contributes to the sustainability of low TP levels, and should therefore be continued.

Whole-lake studies have some evident limitations as well as potentials. On the one side lake behavior can be described in relation to altered external conditions, but only circumstantial evidence can be produced for the causal relationships. For studying specific mechanisms, experiments under controlled conditions are necessary. On the other hand, whole-lake studies are a vital method for studying the integrated and often unexpected ecosystem effects, leading to promising ideas and hypotheses for research and lake management. However, for proper evaluation and interpretation comprehensive (and expensive) monitoring programs are also of great importance.

Acknowledgments

The lake manager, Rijkswaterstaat-Directorate IJsselmeergebied, is kindly acknowledged for his cooperation in this whole-lake experiment. Jan Eulen, Leo van Ballegooijen and Jan van der Hout assisted in the data analysis. Valuable contributions to the discussion came from Paul Boers, Bert Lijklema, Diederik van der Molen and Jan Uunk.

Biomanipulation in shallow lakes: concepts, case studies and perspectives

Introduction

Lake restoration in the Netherlands has been focused on the reduction of external P loading. However, the shallow lake ecosystems are resistant to restoration due to both the internal P loading from the sediments (see chapter 4) and the persistent structure of the present biotic communities in the lakes. Additional measures may be necessary to initiate and accelerate the recovery process. Algae have made the water turbid, submerged plants have disappeared, and the fish stock is now dominated by large numbers of planktivorous and benthivorous fish, such as roach (*Rutilus rutilus*) and bream (*Abramis brama*). The natural predatory fish in these waters, pike (*Esox lucius*), is absent because there is no vegetation for spawning or for hiding. Water turbidity is stabilized by the present fish stock, (1) by wiping out the large and most effective grazers on phytoplankton and (2) by stirring up the sediments. In these lakes devoid of macrophytes, wind and waves have free play, thus contributing to the stability of the turbid water state. Fish stock management could be a promising tool in lake restoration. The interaction of fish and zooplankton grazing on algae, was emphasized in the 1960s by Hrbáček *et al.* (1961), Brooks & Dodson (1965) and Brooks (1969). Later, other researchers discussed the relevance of top-down control of algal blooms, through fish stock management (Hurlbert *et al.*, 1972; Shapiro *et al.*, 1975; Shapiro, 1978, 1980; Andersson *et al.*, 1978; Fott *et al.*, 1980; Moss, 1983, 1987; Lampert, 1983; Benndorf *et al.*, 1981, 1984; Carpenter *et al.*, 1985; McQueen *et al.*, 1986; Edmondson, 1988, 1991); or through stimulation of filter-feeding benthic organisms (Reeders & Bij de Vaate, 1990; Reeders *et al.*, 1993). Shapiro *et al.* (1975) introduced the term 'biomanipulation' for the biological component of lake restoration. Later he defined this as making use of biological interactions within lakes in order to vary algal abundance and type. Examples of procedures are: elimination of benthivorous fish, manipulations of algal populations by lowering pH, artificial vertical circulation, stimulating algal viruses, increasing abundance of larger zooplankters by reducing the planktivorous fish or, by providing refuges for zooplankters (Shapiro, 1978). In this chapter discussion of

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biomanipulation is restricted to the management of fish stocks. In the Netherlands an ecosystem-based approach, including biomanipulation, was stimulated by CUWVO (1983). The CUWVO report brought about a great deal of theoretical and experimental research and the state-of-the-art has been presented by Hosper *et al.* (1987), Van Donk & Gulati (1989) and Gulati *et al.* (1990). Most of the biomanipulation research in the USA and Europe, had been focused on relatively deep lakes (> 5 m) and on stocking with predatory fish, rather than removal of fish (Benndorf, 1988; Gulati *et al.*, 1990; Carpenter & Kitchell, 1993; De Bernardi & Giussani, 1995). In the Netherlands, biomanipulation is based on the hypothesis of 'alternative stable states', suggesting that at moderate nutrient levels in shallow lakes two alternative stable states may exist: a turbid water state and a clear water state (May, 1977; Timms & Moss, 1984; Scheffer, 1990). A major disturbance of the turbid water system by a substantial reduction of the fish stock, both planktivores and benthivores, would trigger a shift from the algae-dominated turbid water state, into the macrophyte-dominated clear water state. This chapter considers key processes in the functioning of shallow lake ecosystems, the phenomenon of alternative stable states and the perspectives of biomanipulation, particularly fish stock reduction. Results of long-term case studies are discussed with special reference to the factors determining the success of biomanipulation.

Key processes in shallow lake ecosystems

The lakes referred to here have a mean depth of 1 to 4 m and are polymictic, which means that they are vertically mixed throughout the year. Typical features are the intense water-sediment interaction and the potentially large impact of aquatic vegetation. Turbidity of the lake water is caused by both phytoplankton and resuspended (in-)organic sediments. Phytoplankton abundance is the net result of production and loss processes. Production is controlled by external and internal nutrient loading and the availability of sunlight. Loss factors are grazing by zooplankton and other filter feeders, mortality and net sedimentation of algae (see chapter 1). Fig. 5.1 shows a simplified food chain from phytoplankton and benthos up to predatory fish, fish-eating birds and fishing. Manipulations at the top of the food chain, such as reduction of planktivores or stimulation of predatory fish, may cascade down and result in reduced phytoplankton abundance. Wind-induced waves and the feeding activities of benthivorous fish lead to resuspension of the finer sediment particles. Submerged macrophytes can play a key role in stabilizing the clear water state, e.g. by providing refuge to the zooplankton against fish predation and by protecting the sediments against wave action and benthivorous fish feeding. The following aspects of lake ecosystem functioning, which are relevant to the application of biomanipulation, will be discussed: (1) zooplankton dynamics and the 'spring clear water phase', (2) the role of top predators in structuring the food chain, (3) the role of submerged macrophytes and (4) the resuspension of sediments by benthivorous fish.

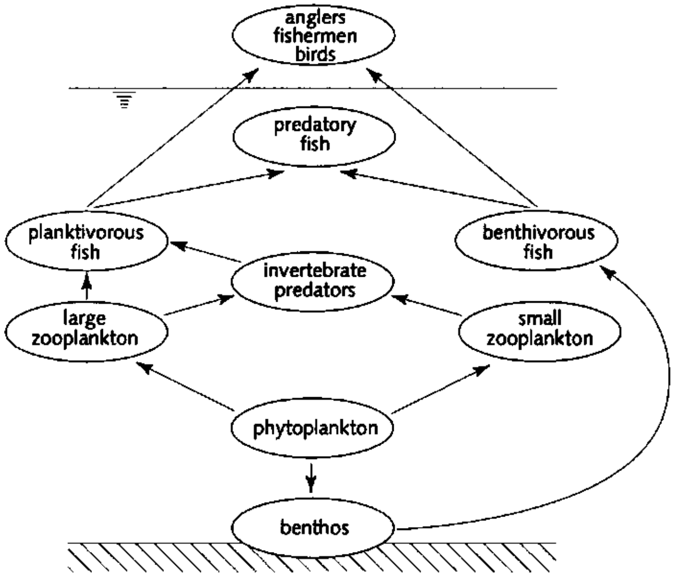


Fig. 5.1 *Simplified food chain of a shallow lake ecosystem.*

Zooplankton dynamics and the 'spring clear water phase'

Planktonic algae are grazed by all kinds of animals represented by the zooplankton. The filtering capacities of *Daphnia* populations, however, are the only ones likely to develop the scale of consumption exploitable in practical biomanipulation (Reynolds, 1994). The larger zooplankton species, in the temperate zones species such as *Daphnia galeata*, *D. pulex* and *D. magna*, are especially effective as grazers (Gulati, 1989). In eutrophic lakes, grazing by zooplankton increases rapidly in the spring and this may give rise to a clear water phase with extremely low phytoplankton levels (Gulati, 1983; Lampert *et al.*, 1986; Sommer *et al.*, 1986). Such a clear water phase may last for a period up to a month in May-June (Sommer *et al.*, 1986) and evidently, for shallow lakes, clear water in that period of the year will be crucial to the development of submerged vegetation. A collapse in the grazer community is usually observed in summer and subsequently algal biomass increases again (Sommer *et al.*, 1986). In many of the hypertrophic lakes in the Netherlands, however, a distinct clear water phase does not occur anymore. Some lakes fail to show any increase in numbers of large-bodied *Daphnia* whatsoever (Loosdrecht lakes), other lakes may show an increase in large-bodied *Daphnia*, but the enhanced grazing is not sufficient for a major improvement of transparency (Tjeukemeer) (Lammens *et al.*, 1992a). Which factors control the success of *Daphnia*? The quality and quantity of food resources on the one side, and planktivorous fish and invertebrate planktivores on the other, are generally considered to be important in controlling the dynamics of *Daphnia* populations. (Threlkeld, 1987). Grazing effectiveness may be severely reduced by the type of algae. Larger algae, such as colonial or filamentous cyanobacteria (*Oscillatoria, Lyngbya* and *Aphanizomenon*) have a mechanically-depressive effect on the filtering rate (Bloem & Vijverberg, 1984; Reynolds, 1994). At low filament concentrations, growth and reproduction of *Daphnia* are not affected. At higher concentrations, however, growth and reproduction may be halted. The critical filament concentration depends on both the morphology and physiological state of the filaments and the *Daphnia* body size (Gliwicz, 1990).

All juvenile fish and many adult fish feed on zooplankton. The most common planktivorous fish species in algae-dominated Dutch lakes are bream (< 20 cm) and roach (Lammens *et al.*, 1992b). Generally in temperate lakes, planktivory will show a conspicuous seasonal cycle: relatively low predation in the spring by the overwintering fish population; high predation in the summer, after the eggs of the fish hatch in June-July and low predation in the autumn after a part of the fish stock has died from food limitation. As the food demand and the production of the YOY (young-of-the-year) fish is significantly higher than of the older fish, a more than proportional increase in planktivory may be expected during the summer (Cryer *et al.*, 1986; Barthelmes, 1988). What is the effect of the planktivorous fish on the zooplankton community? Brooks & Dodson (1965) studied the zooplankton in Crystal Lake (USA) before and after the introduction of the planktivorous 'glut herring' (*Alosa aestivalis*). Ten years after *Alosa* had become abundant in the lake the zooplankton was resampled. The modal size of the zooplankton in the presence of *Alosa* was 0.285 mm, whereas the modal size in the absence of *Alosa* was 0.785 mm. This seems clear evidence that predation by *Alosa* falls more heavily upon the larger zooplankters, eliminating those organisms more than about 1 mm in length. In their classical paper, the authors presented the 'size efficiency hypothesis', suggesting that (1) larger zooplankters compete more efficiently and can also take larger particles than smaller zooplankters, (2) that when fish predation is low the small zooplankters will be competitively eliminated by large forms and (3) conversely, that when fish predation is high the most efficient grazers will be eliminated by the fish. Although there is abundant evidence that planktivorous fish can alter species composition and size structure of zooplankton communities, the evidence is less clear that these predators actually regulate the seasonal dynamics, and the spring peak of *Daphnia* in particular. As accurate data on fish biomass or numbers are hard to obtain, seasonal time series of both *Daphnia* and fish stocks are very scarce. Mills & Forney (1987) presented detailed data for Oneida Lake (USA) and showed strong inverse correlations between the numbers of the YOY yellow perch (*Perca flavescens*) and *Daphnia* during the summer, indicating the role of predation in that period of the year. The best demonstration of the role of fish in the timing and magnitude of the spring peak of *Daphnia* is a massive natural fish kill. The case study of Lake Mendota (Vanni *et al.*, 1990; Kitchell, 1992) offers an excellent example. In this lake approximately 85% of the dominant planktivore cisco (*Coregonus artedii*) population perished because of unusual high summer temperatures and consequent depletion of hypolimnetic oxygen in late summer of 1987. After fish mortality, the larger *Daphnia pulicaria* replaced the smaller *Daphnia galeata mendotae*, resulting in greater grazing pressure on phytoplankton and a much longer spring clear water phase. Similar effects of catastrophic (winter) fish kills and subsequent pronounced clear water phases, are described by Schindler & Comita (1972), De Bernardi & Giussani (1978) and Haertel & Jongsma (1982).

Invertebrate planktivores occupy a special position in the pelagic food web. Like other zooplankton, they are vulnerable to predation by fish, yet they can prey heavily on certain zooplankton (Kerfoot, 1977; Lane, 1978; Murtaugh, 1981; Hanazato & Yasuno, 1989; Hanazato, 1990; Mackay *et al.*, 1990; Luecke *et al.*, 1992). Many invertebrates feed on *Daphnia*, such as the crustaceans *Neomysis spp.*, *Leptodora kindtii* and *Bythotrephes longimanus*, the cyclopoid copepod *Cyclops vicinus*, the larvae of the phantom midge *Chaoborus* and water mites. The impact of invertebrate predation on the *Daphnia* dynamics, however, seems to be limited. Threlkeld (1987) concluded that, although correlations suggest that invertebrate predators may control *Daphnia*, experimental manipulations of invertebrate predators have not resulted in significant changes in timing or magnitude of seasonal peaks. For shallow Dutch lakes, it is unlikely that invertebrate predators are able to suppress the spring peak of *Daphnia*. *Neomysis integer* is found in Wolderwijd, but the population during spring mainly consists of non-carnivorous juveniles (see chapter 6). For Tjeukemeer, Boersma (1994) concluded that the high mortality of small daphnids cannot be explained by invertebrate predators. The only invertebrate predator found in the Loosdrecht lakes is *Leptodora kindtii*, but this species mainly occurs in summer and is known to feed on the smaller zooplankton (Gulati *et al.*, 1992). However, after fish removal from an isolated part of the Loosdrecht lakes (Breukeleveense plas), *Leptodora kindtii* was observed in the end of May in relatively high numbers (Van Donk *et al.*, 1990a, see below). In some lakes in the Netherlands, the new invader *Bythotrephes longimanus* may influence the summer zooplankton (Ketelaars & Van Breemen, 1993).

In conclusion, the fact that 'spring clearing' in many shallow lakes in the Netherlands fails to appear, may be explained by high stocks of bream (< 20 cm) and roach and high densities of filamentous cyanobacteria (see chapter 3). Resuspension of sediments caused by high stocks of benthivorous fish (see below) or wind, may be an additional factor preventing the spring clearing of the water.

The role of top predators

Predatory fish

Important predatory fish include pike, pike-perch (*Stizostedion lucioperca*) and perch (*Perca fluviatilis*). Pike may have played an important regulatory role in structuring the food chain in shallow lakes and ponds in the Netherlands before they became hypertrophic (Grimm, 1989, 1994; Grimm & Backx, 1990). The survival of young pike appears to be strongly related to the availability of refuges, which are usually provided by aquatic vegetation. Pike need hiding places to reduce the risk of intraspecific predation and to provide cover for their own hunting. Pike are able to swallow prey of a size up to two thirds of their own length and make no distinction among fish species, making cannibalism quite common. Moreover, pike larvae attach themselves to plants for their first few days. In waters with abundant emergent and submerged vegetation the survival of young pike is relatively high and their large numbers might regulate the abundance of young bream and roach. Hosper *et al.* (1987) suggested a

Fishing

From the 1960s onwards, in more and more lakes the commercial fishing became legally restricted to the catch of eel (*Anguila anguila*) and in those lakes fishing can now be considered irrelevant with respect to food chain interactions. In a number of lakes though, among others IJsselmeer and De Wieden, there still is commercial fishing for species such as pike-perch and perch. In 1991, the annual catch of pike-perch (> 42 cm) in De Wieden amounted to 1-2 kg ha^{-1}, compared to a catch of pike-perch (3-40 cm) by the cormorants of 2 kg ha^{-1} (Van Dam *et al.*, 1995). The possible substantial effects of commercial fishing on fish communities can be illustrated by the Friesland lake area (14,000 ha), where an intensive gill net fishing on pike-perch came to an end in 1977. Lammens *et al.* (1990) monitored the fish community in Tjeukemeer (2,100 ha), one of the Friesland lakes, from 1971 to 1988. Both large pike-perch (> 50 cm) and bream (> 32 cm) showed a marked increase in numbers after 1977, but roach (> 15 cm), perch (> 15 cm) as well as the smaller pike-perch (< 50 cm) substantially decreased. The anglers were not happy with this situation and in the winters of 1989-1994, intensive seine and gill net fishing was carried out in order to improve the stock of the smaller and more catchable pike-perch (Lammens & Klein Breteler, 1995). The larger bream were also removed in order to reduce competition for benthic food organisms, with the commercially interesting eel. The annual catch varied from 5-7 kg ha^{-1} pike-perch and 30-50 kg ha^{-1} bream. As a result, the stock of large pike-perch showed a drastic decline, whereas the total bream stock remained fairly constant. The biomass of smaller pike-perch, as well as the biomass of the larger roach and perch (> 15 cm), doubled. Small fish (bream, roach, perch and smelt < 15 cm) halved in biomass. These changes in the fish community suggest a reduction in the planktivore predation pressure on zooplankton, with possible effects on phytoplankton biomass. Indeed, recent observations in the Friesland lakes indicate a downward trend in chlorophyll *a* (Waterschap Friesland, 1995; see also chapter 7), but unfortunately zooplankton data are not available.

In conclusion, pike seems the best candidate for controlling the recruitment of bream and roach. However, because of pike's dependency on vegetated littoral zones, an effective top-down control will be restricted to relatively small lakes and ponds (< 10-20 ha). The pike predation in larger lakes will be insufficient. Intensive winter fishing in large lakes, over periods of several years, may substantially influence the stock of planktivores and thus zooplankton grazing. Large colonies of cormorants may be helpful in clearing lakes.

The role of submerged macrophytes

Though the role of pike in controlling the YOY fish, especially in larger lakes, may be questioned, more agreement exists on the relevance of vegetation for clear water lakes (Moss, 1990; Jeppesen *et al.*, 1990b; Meijer *et al.*, 1990). Submerged macrophytes may reduce turbidity in many different ways, not just by providing habitat for the pike. Meijer *et al.* (1990) and Scheffer *et al.* (1993) suggested a model for the interactions in shallow lakes leading to turbidity, demonstrating the significance of macrophytes (Fig. 5.3). The positive effect of vegetation on water clarity is the result of a number of mechanisms including:

- aquatic plants provide a refuge against planktivorous fish for phytoplankton-grazing zooplankton (Timms & Moss, 1984; Schriver *et al.*, 1995; Stansfield *et al.*, 1995);
- structural complexity (provided by plants) promotes the piscivorous fish species perch (Persson, 1994) and pike (Grimm, 1994) and deters the planktivorous-benthivorous bream (Lammens, 1986) resulting in more top-down control of planktivores and less fish-induced resuspension;
- vegetation reduces the availability of nutrients for phytoplankton, by uptake from the water and by promoting denitrification in the sediment (Van Donk *et al.*, 1990b, 1993; Gumbricht, 1993);
- plants may release allelopathic substances which are toxic to algae (Wium-Andersen *et al.*, 1987; Jasser, 1995);
- wind-induced resuspension of sediments is reduced by vegetation (Jackson & Starrett, 1959; James & Barko, 1990).

Although the relative importance of these submechanisms is often hard to assess and may vary between lakes, analysis of extensive data sets supports the view that there is an overall positive 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 (Fig. 5.4). Large lakes may develop subsystems of shallow clear water areas (macrophyte-dominated) and deeper turbid water areas (algae-dominated) (Scheffer *et al.*, 1994).

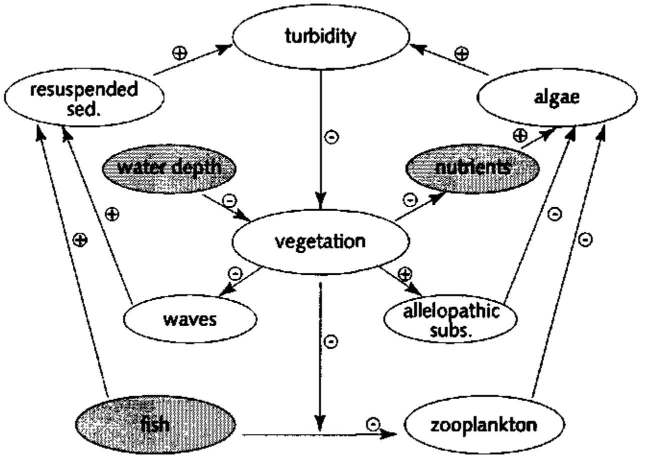


Fig. 5.3 *Interactions in shallow, eutrophic lakes with a key role for the submerged vegetation.*
The qualitative effect of each route in the diagram can be determined by multiplying the signs along the way. In this way it can be seen that both the vegetated and the turbid state are self-reinforcing. The shaded boxes are possible steering variables for lake management and the effects of measures can be determined in a similar way (from Scheffer et al.*, 1993b).*

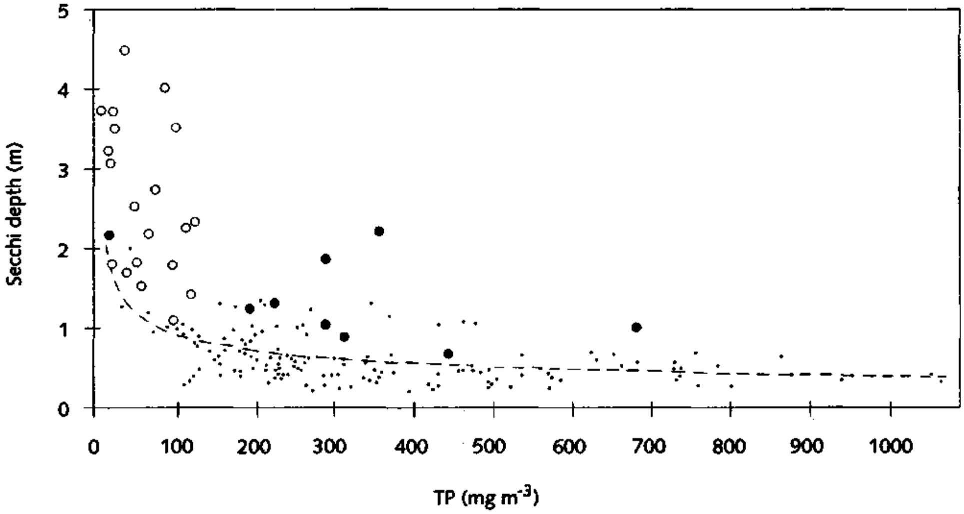


Fig. 5.4 *Summer mean Secchi depth in relation to lake water TP for shallow Danish lakes.*
○ *lakes with a high cover of submerged macrophytes and a surface area > 3 ha;* ● *lakes with a high cover of submerged macrophytes and a surface area < 3 ha; and* • *lakes with only minor or unknown cover of submerged macrophytes (from Jeppesen et al., 1990b).*

Resuspension of sediments by fish

In shallow Dutch lakes, large bream and common carp (*Cyprinus carpio*) represent the benthivorous fishes. In particular, bream appears to be exceptionally successful in the turbid waters that have sediments rich in benthic organisms and hardly any vegetation to hinder feeding. The reduced risk of predation and the fact that bream can efficiently use zooplankton as well as benthos as a food source (Lammens, 1986), are additional factors for the success of bream. Almost all the hypertropic, shallow lakes in the Netherlands are infested with bream, with stocks of around 100 kg ha^{-1} in large lakes such as the Loosdrecht lakes (Van Donk *et al.*, 1990a) and Wolderwijd (Meijer *et al.*, 1994b, chapter 6) to over 500 kg ha^{-1} in smaller lakes and ponds (Meijer *et al.*, 1990; Driessen *et al.*, 1993). Large numbers of common carp may occur locally, mainly originating from stocking. The larger bream (> 20 cm) grub up the sediments intensively in search of food (mainly midge larvae), each bream processing tens of liters of mud daily, often to a depth of several centimeters into the sediment (Lammens, 1986). This feeding behavior promotes nutrient release and turbidity of the overlying water (Meijer *et al.*, 1990; Havens, 1993; Breukelaar *et al.*, 1994) and hampers plant growth through direct mechanical disturbance of the plant roots (Crivelli, 1983; Ten Winkel, 1987). Breukelaar *et al.*, (1994) studied the effects of benthivorous bream and carp in sixteen experimental ponds (0.1 ha, mean depth 1 m, sandy clay/clay sediment), stocked with bream (> 25 cm) or carp (> 40 cm) at densities varying from 0 to 500 kg ha^{-1}. The fish biomasses stocked correspond to densities found in shallow Dutch lakes (see above). It was concluded that starting from a bream or carp biomass of 100 kg ha^{-1} significant effects on suspended solids, TP and TN may be expected. In the bream ponds, suspended solids roughly doubled, rising from 50-100 to 200 kg ha^{-1}. The response is leveling off with further increases in bream biomass from 200 to 500 kg ha^{-1}. The resuspension effect of bream appeared to be twice as great as that of carp. These results clearly indicate the relevance of fish-induced resuspension for small and shallow lakes with a fine sediment. A spring clear water phase (see above), supposed to trigger the submerged vegetation, may be completely masked by the effects of resuspension. Note that in deeper lakes and in lakes with coarser sediment the effects will be proportionally weaker. Due to the lower bream stocks in large lakes, fish-induced resuspension in these large lakes is apparently less important. However, low numbers of benthivorous bream could possibly loosen the top layer of the sediment, making the sediment more susceptible to wind-induced resuspension in the large lakes.

Alternative stable states

From the conceptual models presented above (Figs. 5.2 and 5.3), it can be inferred that simply due to the presence or absence of aquatic vegetation, both the clear water state and the turbid water state are self-reinforcing. Different buffering mechanisms result in a stable clear water state or a stable turbid water state. Apparently, lake ecosystems show resistance to change with increasing as well as decreasing nutrient loading. Resistance is defined here after Pimm (1991): 'Resistance measures the consequences when a variable is permanently changed. How much do other variables change as a consequence? If the consequent changes are small, the system is relatively resistant'. Resistance of the ecosystem during eutrophication, as well as during the reverse process of oligotrophication, gives rise to the typical phenomenon of hysteresis (Fig. 5.5). Note that at the same nutrient loading the lake 'under eutrophication' and 'under oligotrophication', may show a largely different algal biomass.

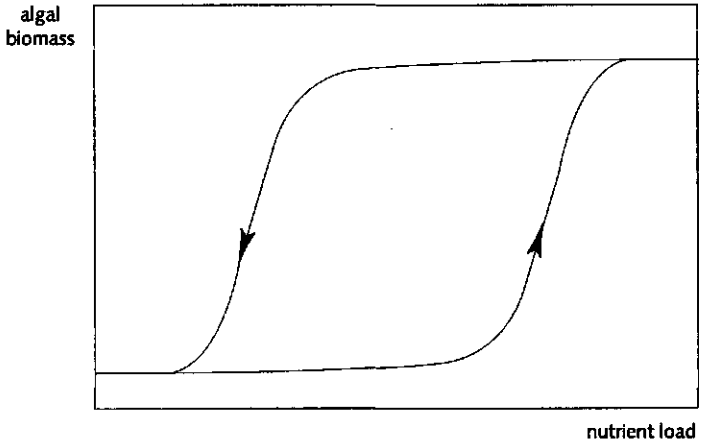


Fig. 5.5 *Eutrophication and oligotrophication in relation to algal biomass, showing a typical hysteresis curve.*

Theory

Theory indicates that natural multi-species assemblies of plants and animals are likely to possess several different equilibrium points (May, 1977). If there is a unique stable state the system will tend to this state (like a marble seeking the bottom of the cup) from all initial conditions, and following any disturbance. If there are many alternative stable states, the state into which the system settles depends on initial conditions. The system may return to this state following small perturbations, but large disturbances are likely to carry it to some new region of the dynamical landscape. If there is a unique stable state historical events are unimportant; if there are many alternative stable states historical events can be of overriding significance. The dynamic behavior of ecosystems having two or more stable states is such, that a continuous variation in a control variable can produce discontinuous effects (May, 1977). It will be obvious that questions of this kind are very important in the understanding and management of ecosystems. Scheffer (1990) explored the significance of multiple stable states for shallow, freshwater systems and demonstrated by the use of simple mathematical models that several ecological relationships may give rise to the existence of alternative equilibria over a certain range of nutrient levels. His mathematical analysis supports the idea that shallow lakes may possess two alternative stable states: a clear vegetated one with low fish stocks and a turbid unvegetated state with high densities of planktivorous and benthivorous fish. The landscape of alternative stable states is visualized in Fig. 5.6 by means of the 'marble in a cup' analogy. At low nutrient levels the system has only one stable equilibrium, a clear water state. Increase of the nutrient level gradually changes the shape of the stability

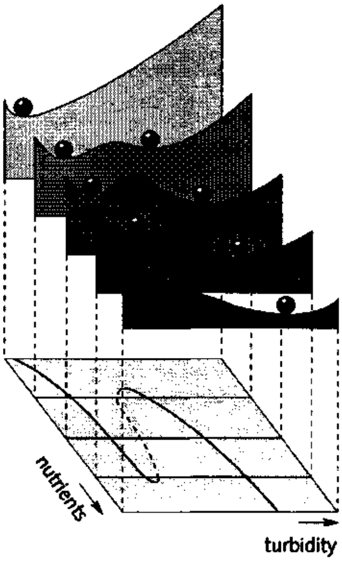


Fig. 5.6 *'Marble in a cup' representation of stability at five different nutrient levels. The minima correspond to stable equilibria, maxima to unstable breakpoints (see text for explanation) (from Scheffer, 1990).*

landscape, and gives rise to an alternative turbid equilibrium. However, if no major disturbances occur, the system will stay in its current state, responding only slightly to eutrophication. If the nutrient level is raised further, the stability of the clear state decreases, and slight perturbations are enough to cause a shift to the turbid equilibrium. At still higher nutrient levels the clear equilibrium disappears, causing an irreversible shift to a turbid state. Efforts to restore the system by decreasing the nutrient level will change the stability landscape again, but even at nutrient levels at which the system was formerly clear, there will hardly be any response to the measures. An alternative equilibrium may be present, but the stable state is sustained. Only a severe reduction of nutrient level will result in a shift to the clear state.

Evidence from the field

Lakes shifting between the alternative stable states of clear and turbid, are well-known in fishery science (Klapper, 1992). Without any noticable change in nutrient conditions, vegetated clear water lakes with pike and tench (*Tinca tinca*) can change from one year to another to a lasting state of non-vegetated turbid water lakes with pike-perch (Klapper, 1992). Shifts from turbid to clear and back to turbid were observed in the 2 m deep Lake Sewekower (Germany) and Klapper (1969) explained these changes by the weather conditions at the start of the growing season. The cold winter of 1962-63, followed by an extremely cold spring, resulted in a low algal biomass and clear water at the start of the growing season. Submerged macrophytes took advantage of the favorable light conditions, colonized the whole lake and stabilized the clear water state. Three years later in the warm spring of 1966, the opposite occurred and the lake shifted back to a stable turbid water state with a transparency of 0.5 m. As noted before, catastrophic fish kills during cold winters may produce similar effects of switching lakes (Schindler & Comita, 1972; De Bernardi & Giussani, 1978; Haertel & Jongsma, 1982). Timms & Moss (1984) studied two linked, shallow freshwater basins with similar hydro-morphological conditions and nutrient loading: Hudson's Bay and Hoveton Great Broad in the Norfolk Broads (UK). Hudson's Bay supported a large stand of water lilies and the adjacent open water was clear; large-bodied Cladocera dominated the zooplankton. By contrast Hoveton Great Broad showed algal blooms and the water was turbid; zooplankton populations were of rotifers and small-bodied Cladocera. The authors concluded that both lakes seem to correspond to two alternative community states. They suggested nutrient competition between algae and macrophytes, the secretion of algae-inhibiting metabolites by macrophytes and especially the refuge function of macrophytes to zooplankton, as the relevant buffering mechanisms for the clear water state. The two moderately eutrophic lakes Tåkern and Krankesjön (Sweden), have during the past few decades shifted 'spontaneously' several times between a clear water state with abundant submerged vegetation and a turbid water state with high phytoplankton densities (Blindow *et al.*, 1993). For both lakes it was most likely that water level fluctuations, affecting submerged macrophytes, caused these shifts, either through changes in light availability or through catastrophic events such as drying out or mechanical damage by ice movement (Blindow *et al.*, 1993). Macrophyte control by herbicides in the 1960s caused a shift to the turbid water state in the small Dutch lake IJzeren Man (Driessen *et al.*, 1993).

Nutrient thresholds for a sustainable clear water state

Scheffer's model (Fig. 5.6) suggests the existence of alternative stable states at moderate nutrient levels. At low nutrient levels only the clear state will be stable, at high nutrient levels the turbid state will be stable and at intermediate levels clear water and turbid water may exist as alternative stable states. The question now, is how to quantify the appropriate nutrient levels for the different states. The results from the multi-lake studies (chapter 3) can help to find the TP limits for the stable clear water state. Stable clear water with Secchi depth > 1 m, can be expected (apart from high non-algal turbidity) at TP < 43 mg m^{-3} for *Oscillatoria* lakes or TP < 66 mg m^{-3} for mixed phytoplankton lakes (Table 3.4 in chapter 3). If non-algal turbidity is high, lower TP levels will be required. Indicating the upper and lower TP limits for the existence of alternative stable states is more difficult. Algae-dominated turbid water (CHL > 100 mg m^{-3}) is associated with TP > 100 mg m^{-3} (Fig. 3.5 in chapter 3). However, these high TP levels do not necessarily exclude the existence of an alternative clear water state. Danish multi-lake studies clearly showed the existence of vegetated clear water lakes at high TP levels (Fig. 5.4). This is particularly true for small lakes (< 3 ha), indicating the importance of a high shoreline:area ratio for the clearing effects of submerged vegetation. For larger lakes (> 3 ha), both clear waters and turbid waters are found at TP levels of 50-100 mg m^{-3} (Fig. 5.4). In the Netherlands, several biomanipulation case studies in small high TP lakes also showed a more or less stable clear water state (see next sections). Along with Jeppesen *et al.* (1990b, 1991, in press), it is tentatively concluded that alternative stable states may be expected at TP = 50-100 mg m^{-3}. In very small lakes a sustainable clear water state is possible at higher TP levels, due to the stronger clearing effects of submerged vegetation.

Biomanipulation in shallow lakes

The idea of alternative stable states implies that at moderate nutrient levels one drastic intervention could tip the balance towards a new stable equilibrium of clear water (Fig. 5.6). Essentially, biomanipulation measures include the substantial reduction of planktivorous and benthivorous fish. By reduction of the overwintering planktivorous fish stock (cf. the natural winter fish kills), a *Daphnia*-mediated, spring clear water phase is forced. Benthivore reduction, particularly in productive clay-bottom lakes, further supports the clearing of the lake. Clear water during spring provides chances for submerged vegetation and a sustainable clear water state. In addition to fish stock reduction, stocking of pike fingerlings may help to reduce the YOY fish during summer. For assessing the perspectives of biomanipulation for lake restoration three questions are relevant: (1) Is substantial fish stock reduction technically feasible? (2) Will the water clear up after the fish removal? and (3) Will the new clear water state be stable? (Fig. 5.7).

The technical feasibility of substantial fish reduction is a prerequisite for the success of biomanipulation. Additionally, immigration of fish from adjacent lakes should be prevented, e.g. by the construction of fish barriers. Here, we will pass over this technical subject and

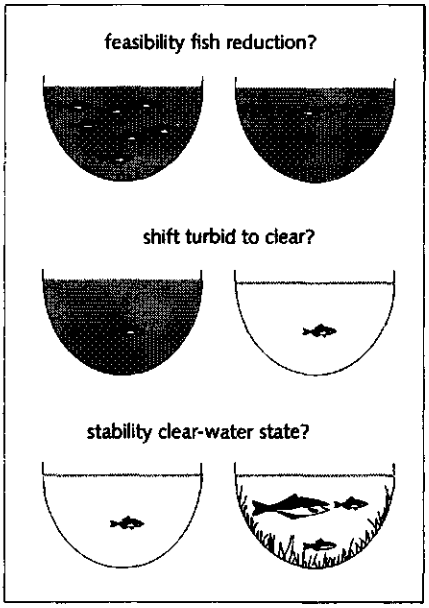


Fig. 5.7 *Three questions relevant for assessing the chances for biomanipulation.*

focus attention on the questions of clearing-up after the fishing, the reestablishment of submerged vegetation and the stability of the clear water state.

Results of case studies

A number of whole-lake case studies has been evaluated for testing the applicability of biomanipulation for shallow lakes in the Netherlands (Table 5.1). Note that the lakes studied mostly differ in surface area, TP and original fish stock. The small lakes in particular had a high fish stock and were rich in TP.

Table 5.2 summarizes the Secchi depth effects in relation to total fish stock reduction, the peaking of *Daphnia*, the reduction of benthivorous fish and possible wind resuspension effects. The possible effects of inedible algae and invertebrate predators (*Neomysis*, *Leptodora*) on the response of *Daphnia* are also shown.

Case study	year	area ha	mean depth m	TP mg m^{-3}	Fish stock kg ha^{-1}		Fish reduction %	Fish immigration
					before	after		
Zwemlust (ZL)	1987	1.5	1.5	1000	800	10	98	no
Bleiswijkse Zoom (BZ)	1987	3.1	1.1	250	760	120	84	no
Noorddiep (ND)	1988	4.5	1.5	200	690	145	79	no
Breukeleveense plas (BP)	1989	180	1.5	100	150	60	60	yes
Klein Vogelenzang (KV)	1989	20	1.5	300	260	200	30	yes
IJzeren Man (IJM)	1990	11	1.8	250	710	120	83	no
Sondelerleijen (SL)	1992	25	1.5	300	500	75	85	no
Wolderwijd (WW)	1991	2555	1.6	120	210	45	79	no
Duinigermeer (DM)	1992	28	1.0	100	150	40	73	no

Table 5.1 *Biomanipulation case studies.*

References:

ZL: Van Donk et al. (1989, 1990b, 1993); Van Donk & Gulati (1995);
BZ: Meijer et al. (1990, 1994a, 1995);
ND: Walker (1994); Meijer et al. (1994a, 1995); Van Berkum et al. (1996);
BP: Van Donk et al. (1990a);
KV: Van der Vlugt et al. (1992);
IJM: Driessen et al. (1993);
SL: Clewits (1994);
WW: Meijer et al. (1994b), see chapter 6;
DM: Van Berkum et al. (1995); Witteveen & Bos (1995).

Explanation:

ZL: after complete fish removal, stocked with 10 kg ha^{-1} rudd (Scardinius erythrophthalmus);
BP: after 60% fish reduction, fish immigrated from adjacent waters;
KV: 60 kg ha^{-1} removed in April 1989, 40 kg ha^{-1} in December 1989. Fish immigrated from adjacent waters;
IJM: after complete fish removal, stocked with 120 kg ha^{-1} roach, rudd and other species;
SL: major fish removal took place in early 1992; also fish removals in early 1991 and 1993;
All lakes, except Noorddiep, were stocked with pike fingerlings.

Table 5.2 shows that all lakes (except for SL), where the winter fish stock was substantially reduced (> 75% and no immigration), cleared up during the following spring. The clearing can be explained by *Daphnia* grazing (ZL, WW, DM) or by a combination of *Daphnia* grazing and reduced benthivorous feeding (BZ, ND, IJM). Despite effective total fish removal and benthivore reduction, SL failed to show a clear water phase. This lack of response could be explained by the predation of *Neomysis integer* on *Daphnia* and wind-induced resuspension (Table 5.2). BP and KV did not clear up either and apart from the ineffective fishing, inedible algae, invertebrate predators (BP) and wind-induced resuspension (BP) could explain the lack of response in these lakes. KV did not clear up in the spring, but according to Van der Vlugt *et al.* (1992), KV showed a *Daphnia* peak and clear water phase in the fall, after the collapse of the cyanobacteria bloom. Apparently, food quality prevented the peaking of

	ZL	BZ	ND	BP	KV	SL	IJM	WW	DM
clearing up	■	■	■	□	□	□	■	■	■
total fish reduction	■	■	■	□	□	■	■	■	■
Daphnia ↑	■	■	■	□	□	□	■	■	■
Inedible algae	■	■	■	□	□	■	■	■	■
Inv. predators	■	■	■	□	■	□	?	■	?
benthivore reduction	□	■	■	□	□	■	■	□	□
wind resuspension	■	■	■	□	■	□	■	□	□

Table 5.2 *Will the lake clear up after the fish reduction?*
Secchi depth effects in the following spring (May-June), in relation to total fish reduction, peaking of Daphnia, the reduction of benthivores and possible wind resuspension effects. The possible effects of inedible algae and invertebrate predators (Neomysis, Leptodora) on the response of Daphnia are also shown. Criteria are from Hosper et al. (1992) and Hosper & Meijer (1993) or explained in the text. Susceptibility to wind resuspension based on wind fetch and mean depth, according to Hosper & Meijer (1993). Data from references in Table 5.1 and Meijer (unpublished results). For names of lakes, see Table 5.1.

Legend:	■ positive result/conditions	□ negative result/conditions
clearing up:	■ significant increase Secchi depth (> bottom)	□ no or minor increase
fish reduction:	■ > 75% and no immigration of fish	□ < 75% or immigration of fish
Daphnia ↑:	■ peak of large-bodied *Daphnia* (> 100 l-1)	□ no peak
inedible algae:	■ < 50,000 ml^{-1} filamentous cyanobacteria	□ > 50,000 ml^{-1}
inv. predators:	■ < 100 m^{-2} *Neomysis*, < 5 l^{-1} *Leptodora*	□ > 100 m^{-2} *Neomysis*, > 5 l^{-1} *Leptodora*
benth. reduction:	■ > 50% and reduction > 150 kg ha^{-1}	□ < 50% or < 150 kg ha^{-1}
wind resusp.:	■ low	□ moderate or high

Daphnia populations in the spring. Unfortunately, the fishing was ineffective in both *Oscillatoria* lakes (BP and KV). Therefore, the current case studies give no clue as to the question whether or not an effective fish reduction can result in the removal of an *Oscillatoria* bloom, through the grazing by *Daphnia.* As several alternative explanations are available for the failing biomanipulation in BP and KV (with a relatively low fish reduction), the case studies do not allow firm conclusions to be drawn about the necessary amount of fish to be removed for successful clearing of the lakes.

The next question refers to the stability of the clear water state during the following summer and the summers of subsequent years. Attention is focused on the long-term results for Secchi depth and submerged vegetation, during July-August (Fig. 5.8). That period (the summer) is the most critical for lake clarity because at that time the young born fish prey upon the zooplankton and the benthivores are most active.

All cleared lakes (except for WW), remained clear throughout the summer and showed a significant increase in submerged macrophytes in the first growing season after the fish removal (Fig. 5.8). Within one or two years, 30% to 80% of the lake area was covered with a dense vegetation. BZ and IJM returned to the turbid water state after seven and five years, respectively. Both small lakes ND and ZL still have clear water during summer, respectively seven and eight years after the fish reduction.

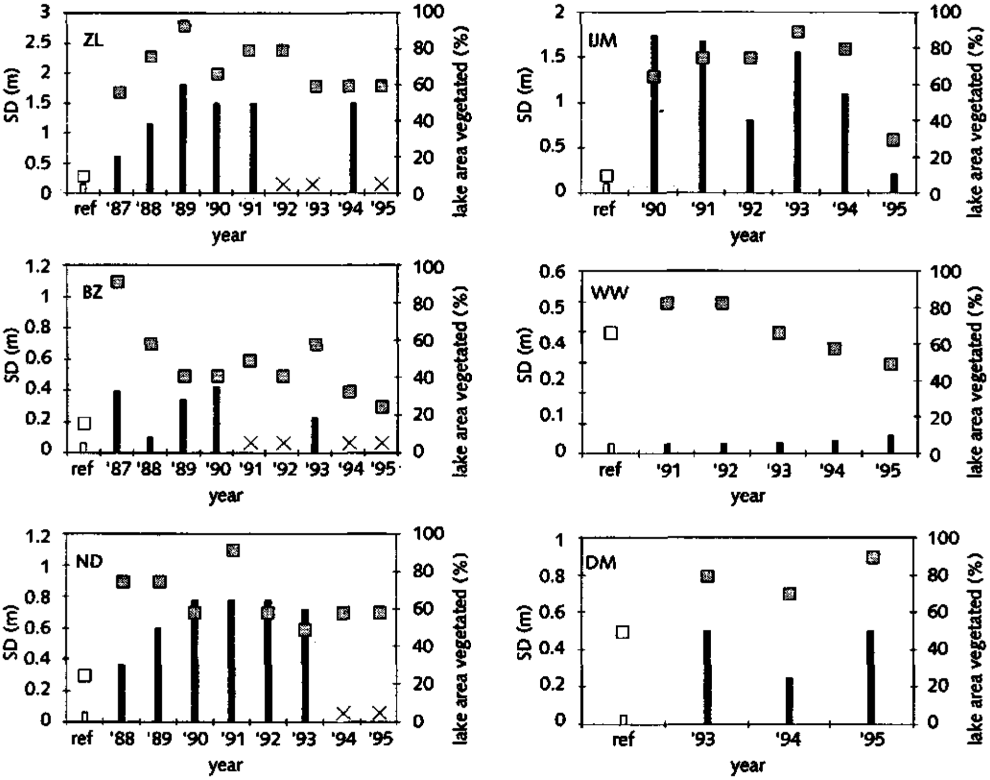


Fig. 5.8 *Will the clear lake be stable?*

Submerged vegetation and Secchi depth during summer (July-August) in the years following fish reduction. Vegetation in % of lake surface with dense macrophyte beds (covering 50-100% of the lake bottom). Bars: lake area vegetated; □ : Secchi depth; Ref: reference or control lake (no fish reduction) in year 1, or experimental lake in year 0. Vegetated lake area was derived from vegetation maps and qualitative information on coverage (pers. comm. with lake managers). Data from references in Table 5.1 and Meijer (unpublished results). Names of lakes in Table 5.1.

Discussion

The fish stock in the algae-dominated lakes tends to impose a homeostasis on the system, resisting recovery of the lake. Biomanipulation, including a substantial fish stock reduction, could trigger a shift from a stable turbid water state to an alternative stable clear water state. Case studies were evaluated, for testing the applicability and perspectives of biomanipulation.

Case studies

In an analogous way to natural winter fish kills, biomanipulation aims at drastic reduction of the planktivorous and benthivorous fish stock. The purpose is to trigger a shift to a stable clear water state, with a single winter fishing. Nine case studies were evaluated with respect to the question of (1) clearing up right after the fishing and (2) stability of the clear water state. Six out of nine lakes cleared after reduction of the fish stock (Table 5.2). These six lakes largely vary in surface area, TP and original fish stock, indicating that these factors are not critical to the mechanisms responsible for the clearing process. All cleared lakes have in common that the total fish stock has been reduced by more than about 75%. Conversely, > 75% fish removal is no guarantee for clearing, as was shown for SL. *Daphnia* population peaking and the resultant grazing is the major process in clearing the lakes. In some small lakes the removal of large quantities of benthivores contributed significantly to the clearing. In the shallow Dutch lakes, invertebrate predators play a minor role in the *Daphnia* dynamics during spring (Gulati *et al.*, 1992; Boersma, 1994). However, the case study SL indicated that after fish reduction, *Neomysis* may have been responsible for the absence of a *Daphnia* peak. In BP, *Leptodora* could have been important, but in this lake alternative explanations (inedible algae, ineffective fish reduction) are also available. All cleared lakes, except for WW, showed a rapid response in submerged vegetation. In the large WW, the spring clear water period only lasted for six weeks (see chapter 6) and the vegetated area remained practically unchanged. However, as is shown in chapter 6, the clear water period in May-June 1991 triggered the gradual colonization by dense beds of Characeae, replacing the thinner beds of *Potamogeton pectinatus*, and the water overlying the *Chara* beds is clear. BZ and IJM returned to the turbid water state after seven and five years, respectively. For BZ, the repeated inlet of water from an adjacent lake, rich in TP and cyanobacteria, probably caused the collapse of the submerged macrophytes (Meijer *et al.*, 1994a). In IJM, an explosive development of filamentous green algae (*Spirogyra sp.*) was observed in 1992 (Driessen *et al.*, 1993) and such an epiphytic bloom may also have induced the shift back to turbid water in 1995. Both small lakes ND and ZL are still clear during summer, respectively seven and eight years after the fish reduction. In ND the planktivores and benthivores seem to be controlled by a well-developed stock of piscivores (Walker, 1994; Meijer *et al.*, 1995). Macrophyte beds in varying density and patches of open water provide an optimal habitat for pike as well as perch in this lake (Walker, 1994). In ZL, TP (and SRP) is extremely high and the fish stock developed to 300-400 kg ha^{-1} (mainly planktivorous/herbivorous rudd, Meijer *et al.*, 1995), but apart from occasional algal blooms and related strong declines in submerged vegetation (Van Donk & Gulati, 1995), the lake is still clear during most of the year. Submerged macrophytes act as a sink for nutrients in the water column (by uptake of N and P, and by promoting denitrification), and despite of a high N loading of about 10 g N m^{-2} y^{-1}, the summer phytoplankton is N-limited (Van Donk *et al.*, 1993). Additionally, allelopathic effects from *Ceratophyllum demersum*, may have reduced the phytoplankton biomass (Van Donk & Gulati, 1995). The dynamic behavior of ZL (shifts from clear to turbid and vice versa) points at increasing instability, probably leading to a shift back to the turbid water state.

In conclusion, the case studies showed that substantial fish stock reduction offers a good chance for clearing of the lakes. The influence of filamentous cyanobacteria and invertebrate predators on the peaking of *Daphnia* populations remains uncertain. Rapid colonization of submerged macrophytes, stabilizing the clear water state can be expected in relatively small lakes (< 30 ha). In spite of high nutrient levels, biomanipulated small lakes may remain clear and covered with macrophytes for many years. However, high nutrient levels, ultimately, lead to destabilization and a reverse shift to the turbid water state. Top-down control by predatory fish, pike and perch, can only be expected in optimal habitats: small lakes, with a high degree of 'patchiness'.

De Melo *et al.* (1992) evaluated a large number of biomanipulation experiments with respect to the hypothesis of top-down control of algal biomass. The authors concluded that in many cases the increased water clarity could not be related to increased zooplankton grazing. Alternative explanations include direct nutrient additions by fish, direct nutrient additions by the small-bodied zooplankton associated with increased planktivore biomasses, dead fish effects and bioturbation by fish (De Melo *et al.*, 1992). Our analysis indicated that in some cases (BZ, ND, IJM), the removal of benthivores contributed significantly to clearing of the lakes, but that in all cleared lakes *Daphnia* grazers showed a pronounced peak after the fishing. Alterations in nutrient fluxes resulting from the fishing are irrelevant to the Dutch case studies; all the lakes studied are rich in nutrients, particularly during the period of spring clearing. Reynolds' checklist for successful biomanipulation seems too conservative, in stating that the water body must be small (< 4 ha) and steps should be taken to promote macrophyte growth (Reynolds, 1994). The Dutch results showed that after clearing, also in larger lakes (DM, 28 ha), macrophytes rapidly recolonized the lake bed. Very large lakes (WW, 2,555 ha) need several consecutive spring clear water years for successful reestablishment of the vegetation.

Perspectives

Biomanipulation, i.e. a single winter fishing aimed at a reduction of > 75% of planktivores and benthivores, is a powerful tool for the restoration of small lakes (< 20-30 ha) of moderate productivity (TP = 50-100 mg m^{-3}, or higher TP levels for very small lakes). Lakes with a high stock of benthivores (> 200 kg ha^{-1}) can particularly benefit from the fish reduction. Blooms of filamentous cyanobacteria and invertebrate predators may prevent the clearing of the lake by *Daphnia* grazers. In large lakes and particularly in networks of interconnected lakes the fish stock is more difficult to control. Additionally, in large lake areas the reestablishment of submerged vegetation takes more time. Winter fishing on a regular basis, rather than a single fishing operation, may then be promising. However, case studies are needed for further evaluation of the efficacy of repeated fishing for promoting *Daphnia.* For large lakes, wind-induced resuspension of lake sediments may block the way to a spring clear water phase or prevent submerged macrophytes from colonizing the lake bed. Biomanipulation case studies in windswept lakes could reveal the actual relevance of resuspension in this type of lakes.

As noted above, an alternative stable clear water state may be expected in the TP range of 50-100 mg m^{-3} (or higher TP levels for very small lakes). As more and more lakes in the Netherlands are approaching these nutrient levels (see chapter 7), the chances for biomanipulation are improving. Finally, it should be stressed that the prudent lake manager charged with the responsibility of reducing algal biomass might be best advised to focus first on nutrient abatement and then on biomanipulation (De Melo *et al.*, 1992; Reynolds, 1994; De Bernardi & Giussani, 1995).

Acknowledgments

The lake managers of the case studies are kindly acknowledged for their fruitful cooperation. Valuable contributions came from Marie-Louise Meijer, Eddy Lammens, Paddy Walker and Michelle de la Haye.

Whole-lake study of Wolderwijd: biomanipulation for promoting the clear water state

Introduction

Most shallow lakes in the Netherlands are characterized by turbid water and a lack of macrophytes, primarily as a result of eutrophication. The lake restoration strategy has been focused on reduction of the external P loading. However, so far this strategy has not resulted in the desired clear water state (Van Liere & Gulati, 1992; De Deckere *et al.*, 1996). Recovery is hampered by the internal P 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 for restoration of shallow lakes is mainly based upon the concept of 'alternative stable states' (see chapter 5). 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 (< 30 ha) in the Netherlands (see chapter 5), Denmark (Jeppesen *et al.*, 1990a) and the UK (Phillips & Moss, 1994; Moss *et al.*, 1996). 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 and providing refuge for zooplankton (Moss, 1990; Jeppesen *et al.*, 1990b; Scheffer *et al.*, 1993; Meijer *et al.*, 1994a; Schriver *et al.*, 1995). Following the successful pilot studies in small lakes, biomanipulation was suggested to restore the large lake Wolderwijd. It is clear that the results from small lakes cannot be extrapolated to large lakes, without careful consideration of scale effects.

This chapter was adapted from:

Meijer, M-L. and S.H. Hosper (in press). Hydrobiologia.

In the Breukeleveense plas (180 ha), fish reduction failed to result in clear water and several alternative explanations have been postulated: insufficient removal of fish, abundance of filamentous cyanobacteria, predation of *Leptodora kindtii* on *Daphnia*, and the strong impact of wind-induced resuspension of the peaty lake sediments (Van Donk *et al.*, 1990a, 1994). Filamentous cyanobacteria, such as *Oscillatoria agardhii*, are a less favorable food source for zooplankton (Gliwicz, 1990). In comparison to the Breukeleveense plas, Wolderwijd offers a better chance 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* after removal of the fish stock (unpublished 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 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. Transparency, nutrients and the biotic components of the lake ecosystem were monitored. The three years after the main intervention (1991-1993) were compared with two preceding years (1989-1990). A photographic report of the biomanipulation project is given in the appendix to this chapter.

Study site

Wolderwijd is a large and shallow lake in the central part of the Netherlands with an area of 2,555 ha (Fig. 6.1). Water depth varies from 0.5 m to 2.5 m (locally 5.0 m), the mean depth is 1.60 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 discharge into the lake. Sluices in the south of the lake provide the outflow into Nijkerkernauw. A sluice in the north connects Wolderwijd with Veluwemeer. Since 1970 the lake has been characterized by blooms of *Oscillatoria agardhii* (Berger & Bij de Vaate, 1983) and a poorly developed submerged vegetation of *Potamogeton pectinatus* and *P. perfoliatus*. The external P loading is 0.5-1.0 g P m^{-2} y^{-1} and varies with the inflow from streams. From 1981-1984 and from 1989 onwards, the lake has been periodically flushed with excess polder water (Fig. 6.2), that is low in TP (< 100 mg m^{-3}) and high in Ca^{2+} and HCO_3^-. In the adjacent Veluwemeer the flushing with polder water had started already in 1979 and had been very successful (see chapter 4; Hosper, 1984; Hosper & Meijer, 1986; Jagtman *et al.*, 1992). In this lake, internal P loading strongly decreased, probably due to the pH buffering effect of the formation of $CaCO_3$. The number of cyanobacteria in Veluwemeer significantly reduced by the flushing, particularly during cold winters with long periods of ice-cover. Although the flushing of Wolderwijd was less intense, TP and chlorophyll *a* more than halved (Fig. 6.4) and the phytoplankton became more diverse. Summer Secchi depth, however, increased from 0.20 to 0.30 m only (Figs. 6.3 and 6.4).

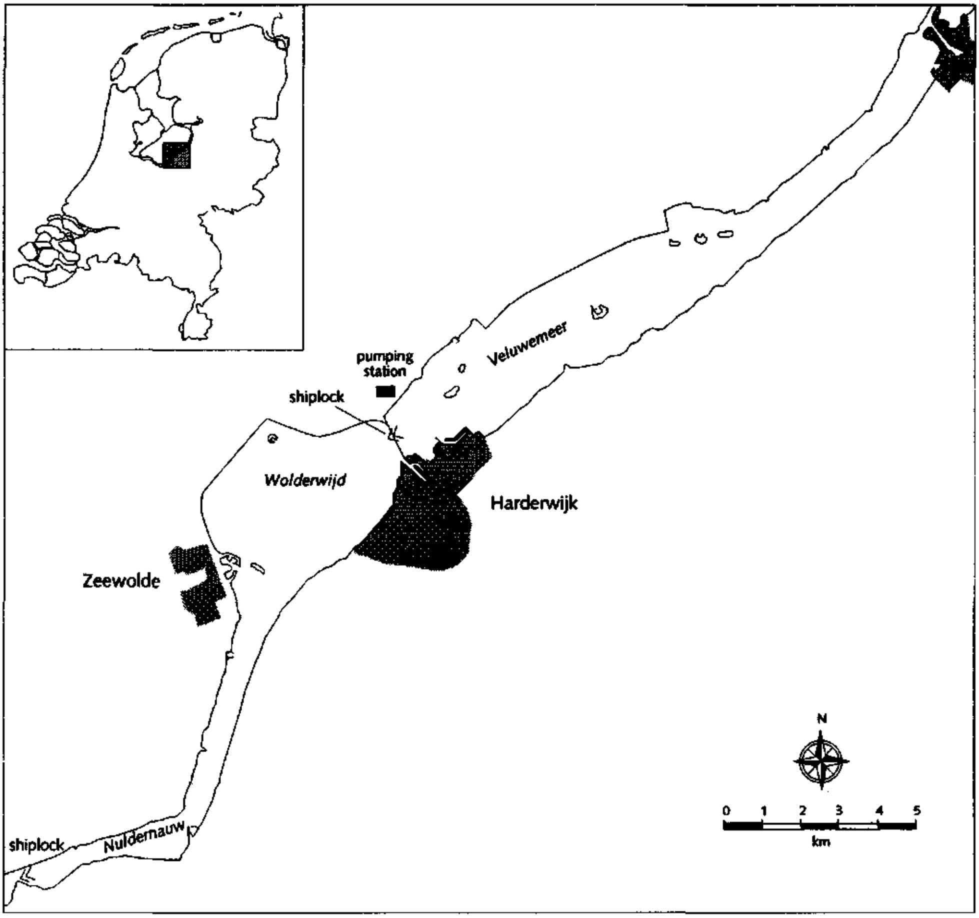


Fig. 6.1 *Lake Wolderwijd in the Netherlands.*

Materials and methods

Biomanipulation

The objective of the fish stock removal had been 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) indicated that above 20 kg ha^{-1} of planktivorous fish, the abundance of zooplankton is strongly depressed and (2) results from biomanipulation experiments in small lakes (Meijer *et al.*, 1990), showed that effects on turbidity can be expected above 50-100 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 fishing was carried out between

November 1990 and June 1991, using large seine-nets (180 m, 770 m and 1200 m in length), trawls and fyke-nets. 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 and roach were restocked elsewhere. The rest was transported to a fish processing plant. The original objectives were realized. For details on 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 harbors 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.

Lake flushing

To reduce the number of filamentous cyanobacteria, thus enhancing the chances for *Daphnia*, flushing of the lake with polder water was intensified from 1989 onwards (Fig. 6.2). As a result of the flushing, the hydraulic residence time of Wolderwijd (calculated on the basis of inflow), was 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).

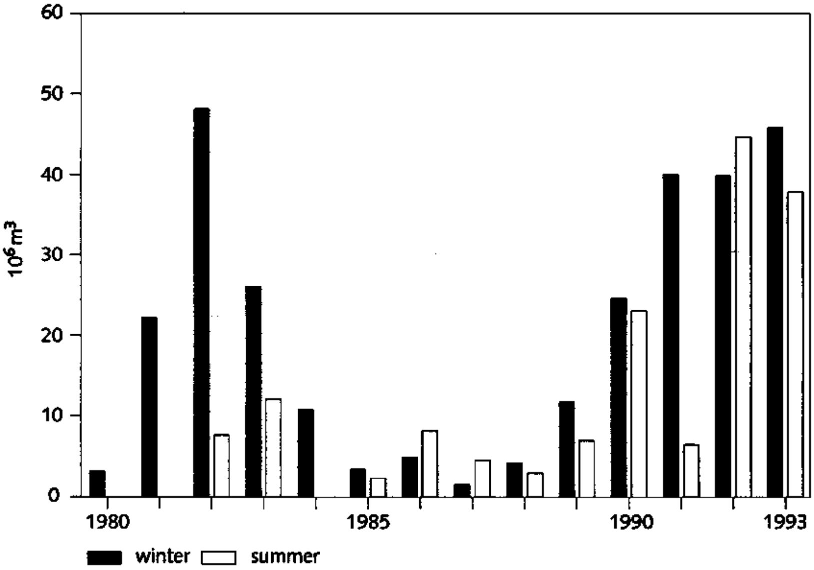


Fig. 6.2 *Flushing of Wolderwijd (volume 41.10^6 m^3). Total flushing in winter (October-March) and summer (April-September) from 1975 to 1993.*

Sampling and analysis

Every two weeks, three parts of the lake were sampled (deep, shallow and center of the lake). In each part 10-15 samples were taken along a 500 m transect with a transparent 1.5 m perspex tube (Ø 5 cm). Statistical analysis showed no significant differences between the parts (Van Nes *et al.*, 1992). Differences were only found above the *Chara* vegetation (after 1991, see below). Therefore, only data from the center of the lake are presented here. The 10-15 samples were mixed to a composite sample of 25-30 l for analysis of nutrients, chlorophyll *a* and phytoplankton. N, P, 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 individual^{-1}) of *Daphnia* were determined. The composition of phytoplankton was determined by taking a 1.0 l sample that was then fixed with Lugol solution. At least 200 individuals were determined. The vegetation coverage was classified in three density groups (0-15%, 16-50% and 51-100% coverage of the lake bottom) by extrapolating from points on a 50 x 100 m grid in the lake. The density of the mysid shrimp, *Neomysis integer*, was monitored monthly by sampling 10 parts of the lake (differing in 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, unpublished results).

Results

Transparency, nutrients and phytoplankton

In 1989 and 1990, before the fish were removed, 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 (Fig. 6.3). This clear water phase lasted for six weeks. The high transparency coincided with extremely low concentrations of chlorophyll *a* (3 μg l^{-1}, Fig. 6.3) and inorganic suspended solids (4 mg l^{-1}, not shown). The next year, in May 1992, the transparency reached a peak value of 0.9 m, but this clear water phase only lasted for two weeks. However, in the part of the lake covered with Characeae (see below), the water remained clear until August. In 1993, a Secchi depth of 0.9 m was observed in the open water for one week only, but again the water remained clear above the Characeae 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 than in all other years (Fig. 6.4). In May-June, at the start of the growing season for vegetation, a distinct clear water phase occurred, with Secchi depth values about twice as high as in all previous years (Fig. 6.5). Comparative data are also shown for the adjacent lake Veluwemeer, as it is very similar to Wolderwijd, but had no fish reduction (Fig. 6.5). In 1991, TP and TN were relatively low (Fig. 6.4). Cyanobacteria, predominantly *Oscillatoria agardhii* (10,000-70,000 ind ml^{-1}), dominated the phytoplankton in 1989 and 1990. The dominance of cyanobacteria was broken early 1991, but returned in the summer of 1993 (Fig. 6.6).

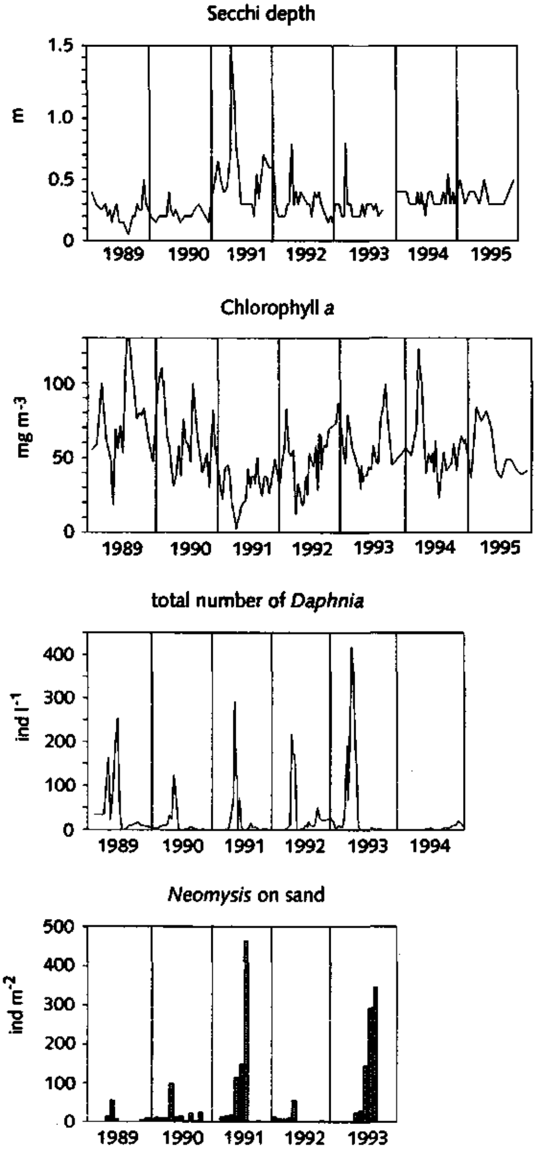


Fig. 6.3 *Secchi depth, chlorophyll a, Daphnia and Neomysis in Wolderwijd (1989-1993), before and after the fish stock reduction (November 1990 to June 1991).*

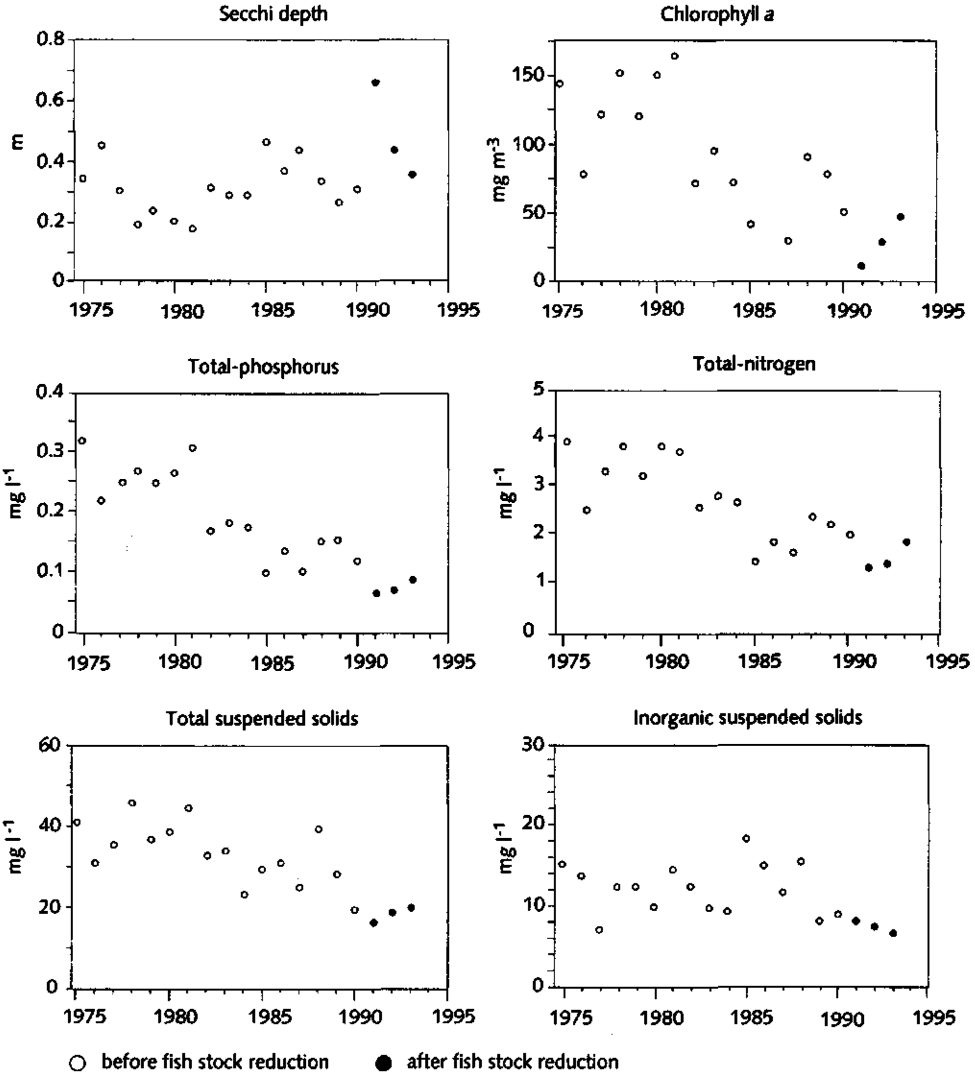


Fig. 6.4 *Secchi depth, chlorophyll a, TP, TN, total suspended solids and inorganic suspended solids in the open water of Wolderwijd. Mean values (April-September) for 1975-1993, before and after the fish stock reduction (November 1990 to June 1991).*

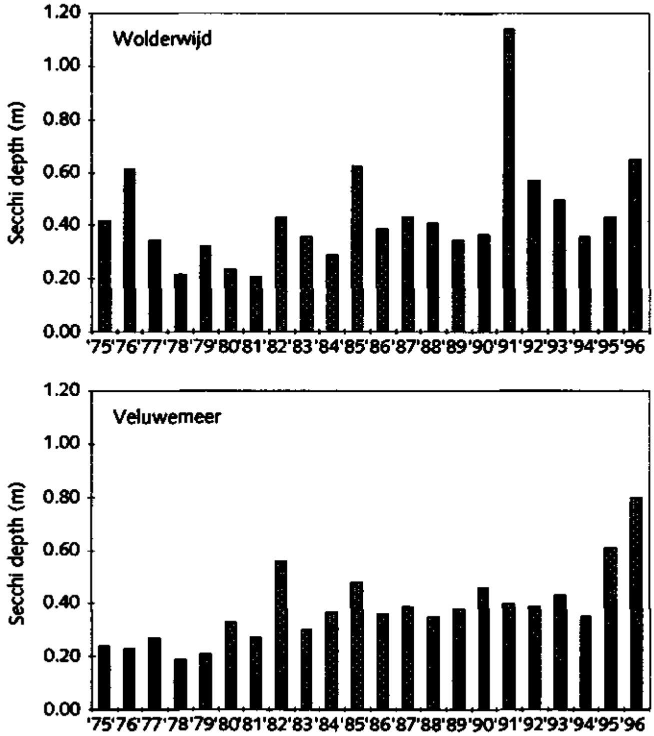


Fig. 6.5 *Spring Secchi depth in Wolderwijd and Veluwemeer. Mean values (May-June) for 1975-1995.*

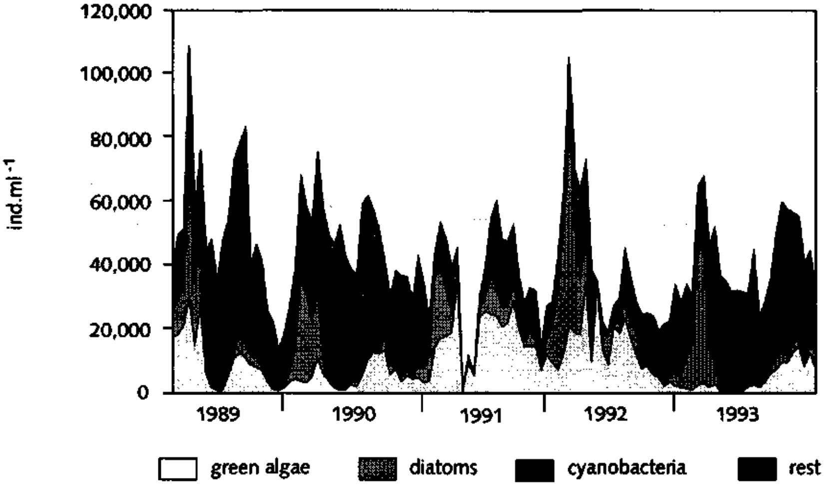


Fig. 6.6 *Phytoplankton species composition in Wolderwijd (1989-1993), before and after the fish stock reduction (November 1990 to June 1991).*

Daphnia and *Neomysis*

Daphnia developed a high density in spring every year (Fig. 6.3). The population was mainly composed of *Daphnia galeata*, both before and after the fish reduction. In 1991 and 1992 the highest densities coincided with the clear water phase. *Daphnia* slightly recovered in summer only in 1992, while in all the other years *Daphnia* was almost absent from July onwards. Each summer the average length of *Daphnia* decreased (Fig. 6.7), probably as a result of selective fish predation by YOY fish. During the clear water phase in 1991, neither 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 mysid shrimp *Neomysis* integer reached high densities in July 1991 and 1993 (over 400 m^{-2} on sand) (Fig. 6.3). In other years *Neomysis* was present, but the densities were low (< 100 m^{-2}).

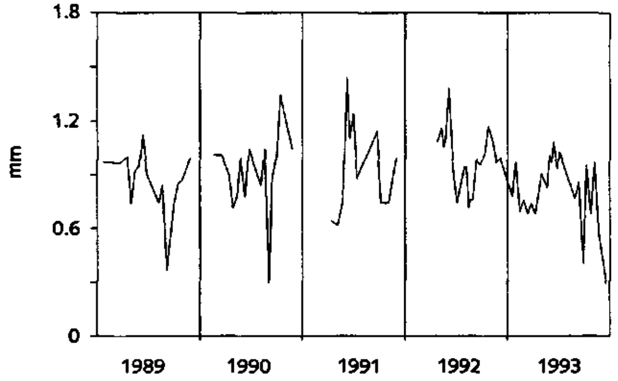


Fig. 6.7 *Length of Daphnia in Wolderwijd (1989-1993), before and after the fish stock reduction (November 1990 to June 1991).*

Macrophytes

During 1989-1993, the total vegetated area of the lake remained the same, about 1,000 ha (Fig. 6.8), 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 was replaced by Characeae (Figs. 6.8 and 6.9). The *Chara* vegetation consisted mainly of *Chara contraria* and *C. vulgaris*. 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. No significant difference was found in TN and TP, but DIN and SRP were higher inside the vegetation area ($p < 0.05$, Wilcoxon signed rank test) (Table 6.1).

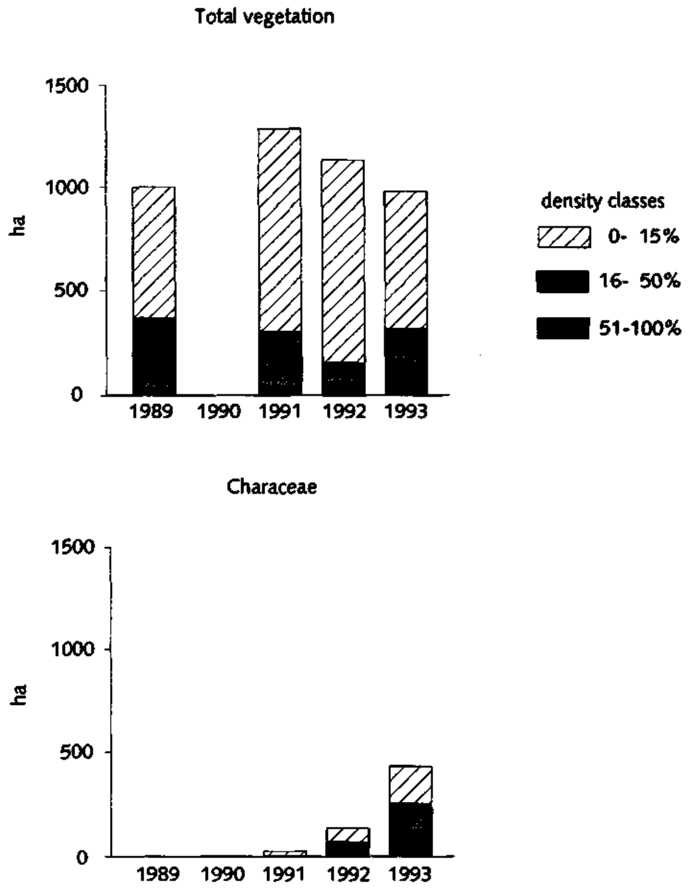
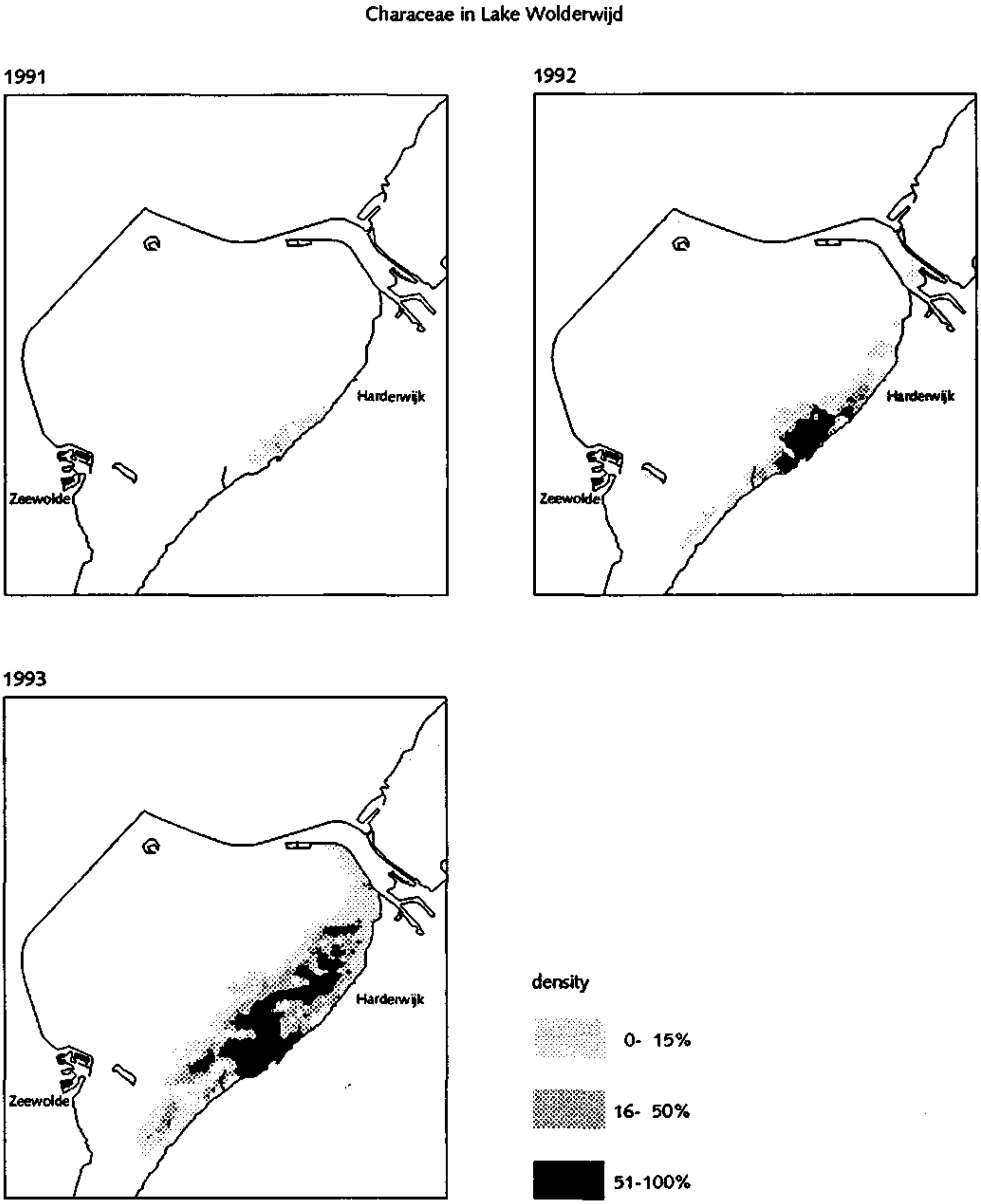


Fig. 6.8 *Submerged macrophytes in Wolderwijd (1989-1993), before and after the fish stock reduction (November 1990 to June 1991). Vegetated area (ha) and density classes (% of bottom covered by vegetation) for total vegetation and for Characeae are shown.*

		inside vegetation		**outside vegetation**	
Secchi depth	(m)	0.6	(0.13)	0.3	(0)
chlorophyll *a*	(mg m^{-3})	12	(5)	38	(5)
TP	(mg m^{-3})	60	(20)	100	(30)
TN	(mg m^{-3})	1370	(250)	1800	(50)
SRP	(mg m^{-3})	3	(0)	< 1	(0)
DIN	(mg m^{-3})	450	(15)	60	(13)
ISS	(mg l^{-1})	2.7	(1.3)	7	(1.2)

Table 6.1 *Water quality inside and outside the Chara vegetation in Wolderwijd (June-July 1993). Standard deviation within brackets (n = 4 or 5). DIN = dissolved inorganic nitrogen:* NO_3^-+NO_2^-+NH_4^+*-N. ISS = inorganic suspended solids.*



Characeae in Lake Wolderwijd

Fig. 6.9 *Characeae distribution in Wolderwijd (1991-1993). In 1989: no Characeae were present. In 1990: 1 ha.*

Fish

The initial fish stock of 205 kg ha^{-1} was reduced to 45 kg ha^{-1} (Fig. 6.10). 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 young fish (YOY), of which 30 kg ha^{-1} consisted of ruffe (*Gymnocephalus cernua*). The dominant fish species 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 YOY recruited, dominated by perch (*Perca fluviatilis*) (58%). 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, results from electro-fishing indicated a pike biomass of less than 3 kg ha^{-1}.

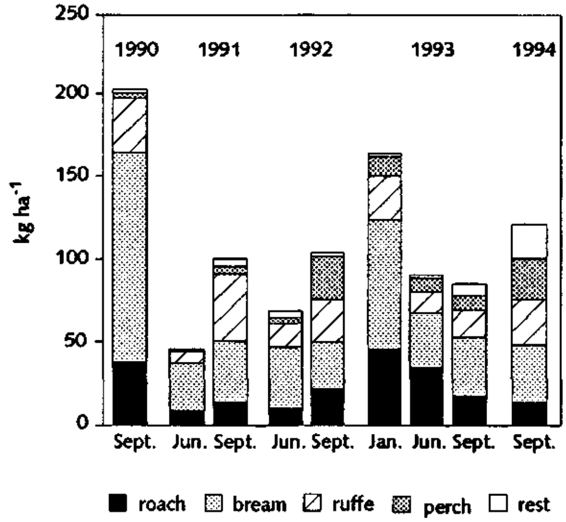


Fig. 6.10 *Fish stock in Wolderwijd (1990-1994). Fish stock reduction was carried out from November 1991 to June 1991. Additional fishing took place from January to May 1992 and February to August 1993.*

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 (< 30 ha) (see chapter 5; Van Donk *et al.*, 1990b; Jeppesen *et al.*, 1990a; Meijer *et al.*, 1994a; Van Berkum *et al.*, 1995; Phillips & Moss, 1994; Moss *et al.*, 1996). Apart from the technical feasibility of the fish removal, in larger lakes, factors such as wind-induced resuspension of sediments and the more difficult recolonization by macrophytes, may reduce the chances for successful biomanipulation (Hosper & Meijer, 1993; Reynolds, 1994). The results from 1991 showed that it was technically feasible to remove the bulk of the fish stock and to realize the objectives for planktivorous and benthivorous fish. In 1992 and 1993, the objective for the fish reduction was not achieved because the fish reduction had started too late in the season. For optimal fish reduction the fishing should start in November at the latest (Perrow *et al.*, in press), in order to spread the fishing over a longer period with more intervals without fishing. 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 (1,650 ha; Hanson & Butler, 1994), Finjasjön (950 ha; Annadotter, 1994) and Sätofta Bay of Ringsjön (400 ha; Hamrin, 1993). The clear water phase in Wolderwijd lasted for about six weeks, indicating that in this lake the impact of wind-induced resuspension on turbidity is not as dominant as in other large lakes in the Netherlands, such as the Breukeleveense plas, where biomanipulation was not successful (Van Donk *et al.*, 1990a, 1994). From the results of biomanipulation in smaller lakes, it was expected that the reduction of benthivorous fish would lead to a reduction of the resuspension of sediments (Meijer *et al.*, 1990; Breukelaar *et al.*, 1994; Van Berkum *et al.*, 1995). However, the original biomass of benthivorous fish in Wolderwijd (90 kg ha^{-1}) was low compared to the biomass in the small lakes (300-450 kg ha^{-1}) (Meijer *et al.*, 1994a). 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 on 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 biomanipulation case studies the reduction of the fish stock usually leads to an increase in large-bodied *Daphnia* in the next spring (Van Donk *et al.*, 1990b; Faafeng & Brabrand, 1990; Hanson & Butler, 1994; Meijer *et al.*, 1994a). However, in Wolderwijd after the fish reduction, neither a change in *Daphnia* species, nor a significant difference in length or density in the *Daphnia* population was found in 1991, compared with both the previous years. Yet, in spring 1991 the lake cleared and the clear water phase coincided with a *Daphnia* peak. Two possible explanations for the minor difference in *Daphnia* length and density before and after the fish reduction are: (1) food limitation of *Daphnia* in 1991 and (2) a non-representative sampling of *Daphnia*. Food limitation is indicated by the extremely low chlorophyll *a* levels and the low fecundity of the *Daphnia* (Taylor, 1985), during the clear water phase (< 2 eggs $adult^{-1}$). During that period the grazing was also two to eight times the primary production (Meijer *et al.*, 1994b). The other option is that large *Daphnia* may have been underestimated during sampling, because of concentration of the *Daphnia* near the bottom during the clear water period, as has been shown in enclosure experiments in Denmark (Schriver *et al.*, 1995). Although the cold winter and the flushing certainly will have contributed to providing favorable conditions for spring clearing, the fish reduction appeared to be necessary for realizing a spring clear water phase. In previous years with a long ice-cover (1979, 1982, 1985 and 1987) or flushing (1981-1983), but without fish reduction, no major increase in Secchi depth was observed in May-June (Fig. 6.5). The adjacent Veluwemeer, also low in TP, chlorophyll *a* and numbers of *Oscillatoria* in spring 1991 (Table 6.2), but without fish reduction, failed to show a clear water phase (Fig. 6.5).

	Wolderwijd	Veluwemeer
TP (mg m^{-3})	49	47
chlorophyll *a* (mg m^{-3})	36	52
Oscillatoria (fil ml^{-1})	1500	5700

Table 6.2 *TP, chlorophyll a and Oscillatoria in Wolderwijd and Veluwemeer in early spring 1991. Mean values for March-April.*

Each year *Daphnia* was absent from July onwards and the algal biomass increased. Predation by YOY fish and invertebrates, such as *Neomysis*, is the most likely explanation for the summer decline of *Daphnia*. Meijer *et al.* (1994b) stressed the importance of *Neomysis* for predation on *Daphnia* in 1991. Recent results, however, indicated 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 by YOY and *Neomysis*, decreases from 26% to 14% of the *Daphnia* biomass per day (6% by YOY, 8% by *Neomysis*), which is in the range of daily production of *Daphnia* (Meijer *et al.*, 1994b).

Role of piscivorous fish

The increase of the fish biomass in summer was mainly caused by the production of YOY of perch and ruffe. The biomass of YOY of bream and roach was relatively low. The proportion of piscivorous fish was also very low. A survey of 300 Danish lakes indicated that TP levels of 70-100 mg m^{-3} gave a stable situation with a high percentage (30%) of piscivorous fish (Jeppesen *et al.*, 1990b). However, in Wolderwijd with TP of 70-90 mg m^{-3}, the share 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 (1991, 1994), perch can only become important in clear, vegetated systems (chorophyll $a < 5\text{-}10$ mg m^{-3}). In most of the Danish lakes with a high percentage of piscivorous fish the coverage of macrophytes was also high. In Wolderwijd, the limited abundance of submerged and emergent vegetation probably restricts the development of pike and perch. Therefore, in the short term wé do not expect these predators to be able to control the planktivorous fish. Besides, field evidence demonstrating the role of pike as a regulator of the food web, is scarce. Even in biomanipulation experiments in small lakes with higher biomasses of pike, the pike was not very successful in controlling the production of planktivorous and benthivorous fish (see chapter 5; Meijer *et al.*, 1994a, 1995). Despite of this lack of control by pike, the water in the smaller lakes remained clear during summer, because of the abundant macrophyte growth (Van Donk *et al.*, 1990b; Van Berkum *et al.*, 1995; Meijer *et al.*, 1994a). 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, 1994).

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 respond 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. The availability of oospores probably limited the colonization by *Chara* in 1991. Experiments in 1993 showed a marked response after the introduction of oospores or plants (Stam, unpublished results). 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 is 10-100 fold lower than inside the meadows (Stam, unpublished results). It is likely that the probability of a dense canopy of *Chara* is highest on sites with a high oospore density. 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 increase with a higher availability of light. As soon as a reasonable area of *Chara* is present, *Chara* itself creates a high transparency (Blindow, 1991; Blindow *et al.*, 1993).

Macrophytes and high transparency

In Wolderwijd, high transparency is restricted to the area above the *Chara* vegetation.
In smaller lakes the presence of dense macrophyte beds over at least 50% of the surface area was sufficient to keep the water clear, also outside the vegetated areas (Meijer *et al.*, 1994a). 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 examination of hypotheses (Scheffer & Beets, 1994). The following are possible mechanisms: macrophytes reduce resuspension of bottom material and increase net sedimentation rates of suspended matter (James & Barko, 1990; Petticrew & Kalff, 1992); macrophytes can act as refuge for zooplankton (Timms & Moss, 1984; Schriver *et al.*, 1995); and macrophytes can reduce algal growth by nutrient competition (Ozimek *et al.*, 1990) or by allelopathy in particular by Characeae (Hootsmans & Blindow, 1993). In smaller lakes (with less wind resuspension) the water stayed clear in the presence of macrophytes including *Potamogeton pectinatus* (Bleiswijkse Zoom), *Elodea nuttalli* and *Ceratophyllum demersum* (Zwemlust), Characeae (Duinigermeer), *Ceratophyllum demersum* and *Nuphar lutea* (Noorddiep). In Zwemlust, competition for N between macrophytes and algae, seems the most likely explanation for the low algal biomass in the presence of macrophytes (Van Donk *et al.*, 1993; Van Donk & Gulati, 1995). Also in the Bleiswijkse Zoom and Noorddiep a

decrease in TN is found at the time that the macrophytes become abundant (Meijer *et al.*, 1994a). 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 Krankesjön (Sweden, 3,200 ha) a decrease in the water level resulted in an abundance of Characeae, followed by an increase in transparency (Blindow *et al.*, 1993). Increased sedimentation and reduced availability of P may have contributed to the high transparency there (Blindow *et al.*, 1993). In Wolderwijd, there is no evidence for a lower availability of P and N within the vegetation (Table 6.1). In Lake Christina (USA, 1,600 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. As in Wolderwijd, the vegetated areas in this Minnesota lake show a higher transparency than the areas without vegetation. An increased net sedimentation was suggested as one of the reasons for the clear water above the macrophytes (Hanson & Butler, 1990, 1994). 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 the difference in transparency may be explained by increased net sedimentation within the *Chara* meadows and reduced mixing of the turbid water from the windswept parts of the lake with water in the vegetated areas

Conclusions

This case study showed that drastic fish stock reduction may lead to clear water in large and shallow lakes. However, in Wolderwijd this was limited in space and time. 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. Creating favorable conditions for a dense *Chara* vegetation will be the most promising way for achieving a shift from the turbid water state to the clear water state. The water remains clear above the *Chara* plants, probably due to increased net sedimentation and reduced mixing between water from the vegetated areas and the non-vegetated areas. To stimulate *Chara* growth, spring clear water periods are necessary. For that reason, it is recommended that the lake manager should continue the fish stock reductions. The fish removal should be substantial in order to get a spring clear water phase. Removal of eggs of cyprinids after the spawning, may lower the production of planktivores. Finally, 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 large areas locally with clear water above the Characeae.

Acknowledgments

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Appendix

Photographic report of the Wolderwijd biomanipulation project.

Plate 1.
Biomanipulation has not applied on such a large scale before: Wolderwijd-Nuldernauw, 2,555 ha (Harry Hosper).

Plate 2.
Enclosure experiments in Wolderwijd demonstrated the effects of fish stock reduction on transparency. Submerged macrophytes covered the bottom soon after clearing of the water (Roel Doef).

Plate 3.
In 1990-91 the fish stock in Wolderwijd was reduced by 75%. Large seine-nets (photo), fykes and trawls were used for the fishing (Bert Boekhoven).

Plate 4.
Celebration on the last day of the fishing (28 May 1991) aboard of the ME 1 of fisherman Gerard Manshanden (Harry Hosper).

Plate 5.
In 1991, a spring clear water phase occurred in the lake, for a period of about six weeks. This photo was taken on 1 June (Harry Hosper).

Plate 6.
Secchi depth increased from 0.50 m to a peak value of 1.70 m, the largest transparency ever observed, since the start of the monitoring in 1972 (Willem Kolvoort).

Plate 7.
Dense Chara meadows increased from 28 ha in 1991 to 438 ha in 1993. The water overlying the vegetated area is crystal clear, outside this area the lake is still turbid. This photo was taken in July 1993 (Roel Doef).

Plate 8.
Chara contraria and Chara vulgaris are the main species in the densely vegetated areas (Willem Kolvoort).

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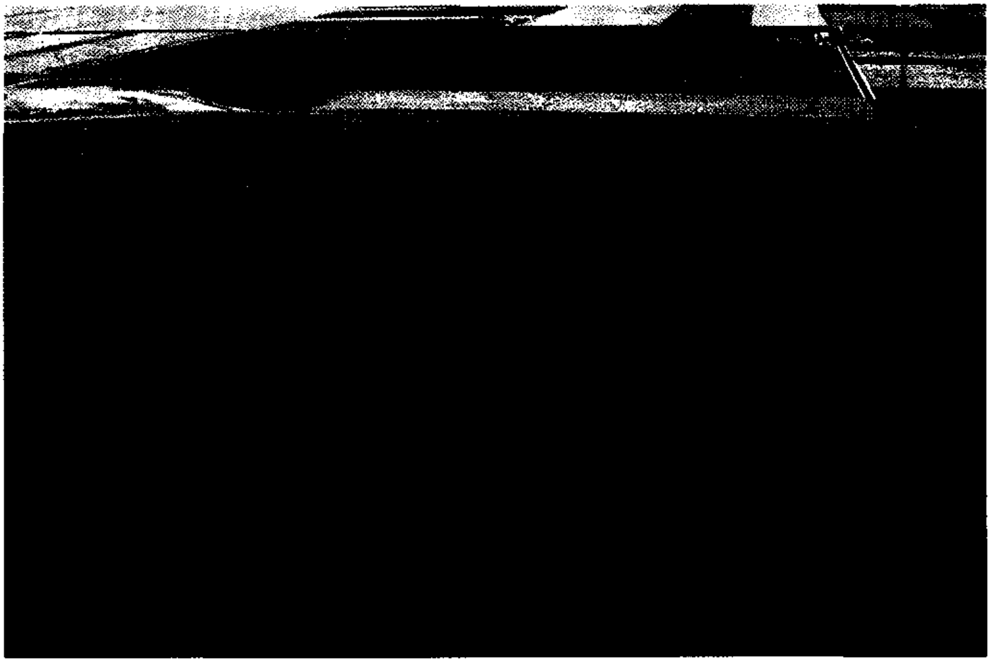

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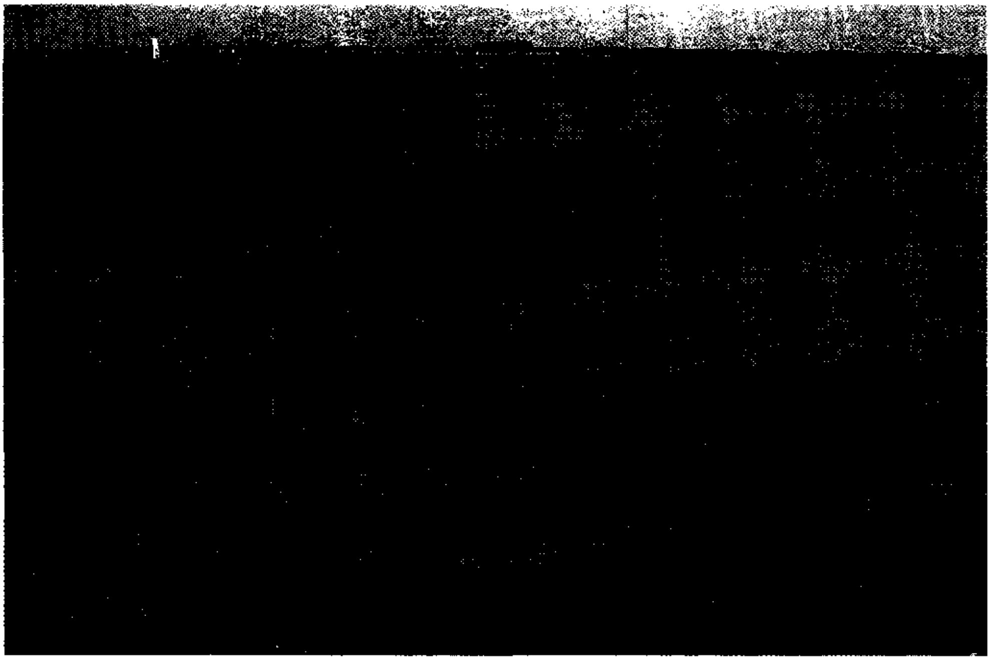

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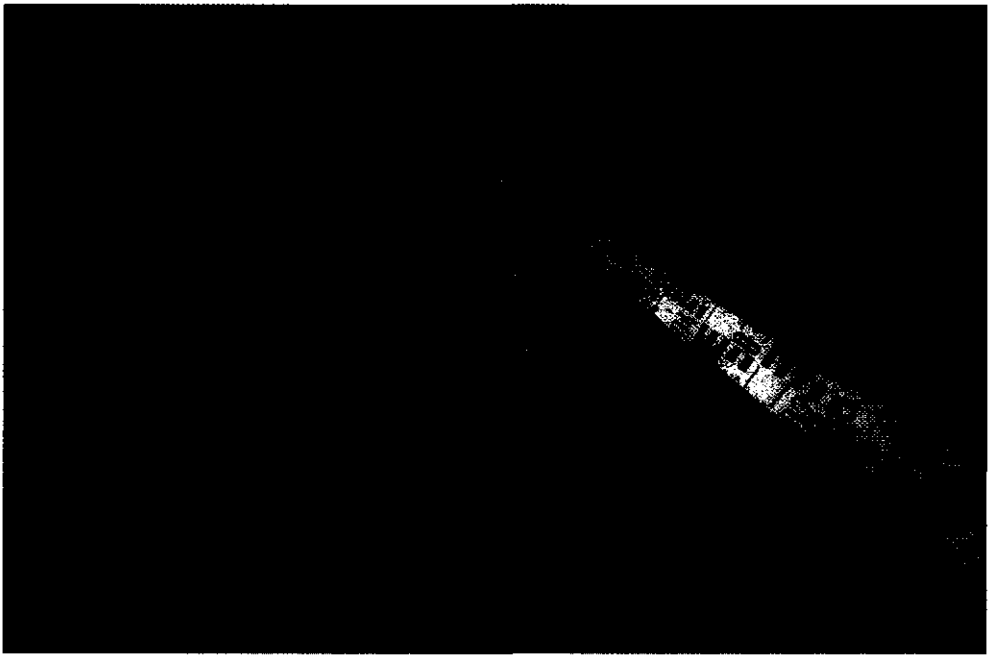

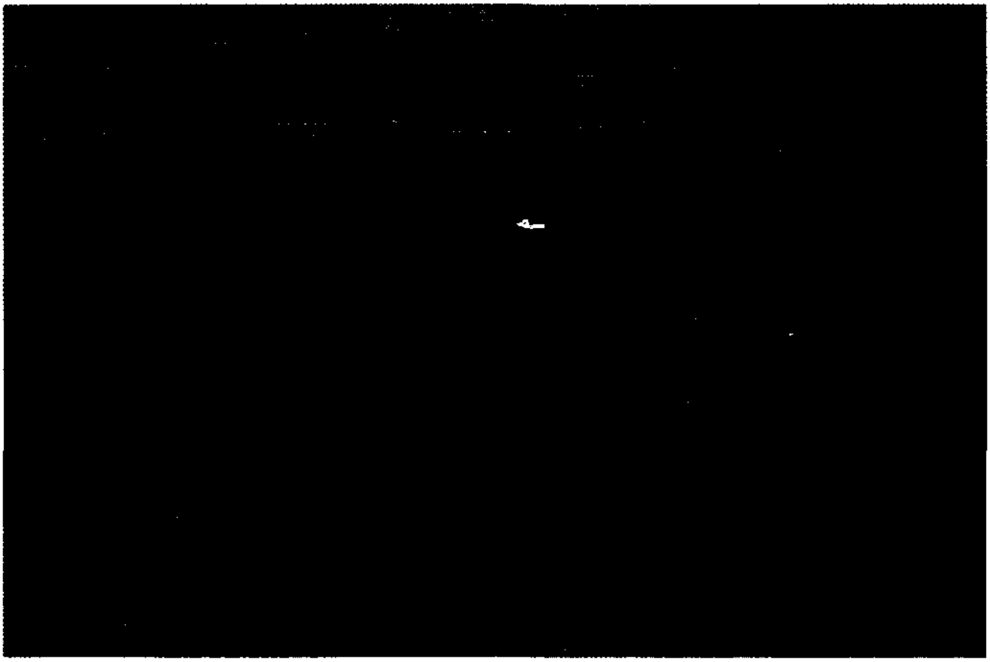

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Guiding lake restoration and management

Eutrophication and oligotrophication

Eutrophication, i.e. the enrichment with plant nutrients (N, P), is the primary cause of algal blooms and concomitant changes in the lake ecosystem, such as the loss of submerged macrophytes and predatory fish. Lake restoration focuses on the control of P loading, rather than of N loading. This P-oriented approach was taken for practical reasons: (1) according to the limiting nutrient concept, the reduction of only one nutrient is sufficient to control algal biomass; (2) N loading originates to a relatively large extent from non-point sources and therefore is more difficult to control, and (3) some species of cyanobacteria (e.g. *Aphanizomenon, Anabaena*) are able to assimilate dissolved, atmospheric N_2. Furthermore, it can be concluded from case studies that a reduction of P loading, with an unchanged high N loading, has been effective in reducing algal biomass (chapter 4). Unfortunately, case studies of the opposite (a reduction of N loading and high P loading), could not be found.

The relationships between nutrient loading and shallow lake response are complex and tend to be different for the process of eutrophication and the reverse process of oligotrophication. Well-documented, long-term case studies of eutrophication and oligotrophication in shallow lakes are scarce. The description of both processes, given below, is based on 'circumstantial evidence' from case studies in the Netherlands (Hofstra & Van Liere, 1992; Van Vierssen *et al.*, 1994; Noordhuis, 1996; chapters 2-6) and conceptual modeling (Moss, 1990; Jeppesen *et al.*, 1990b, 1991; Scheffer *et al.*, 1993; Van Vierssen *et al.*, 1994; chapter 5). The bottom line is that both clear water lakes and turbid water lakes are resistant to changes in nutrient loading and show the phenomenon of hysteresis. Only at certain critical nutrient levels (thresholds), does the system show dramatic changes in algal biomass (Fig. 7.1).

Starting from a macrophyte-dominated clear water state, the process of enrichment can be described as a series of stages and events:

(1) Increase in external nutrient loading, but constant low concentrations in the water.
Loss processes, related to the abundance of macrophytes (reduced resuspension, uptake by plants, denitrification) and the adsorption capacity of the sediments, compensate for the increased loading (not shown in Fig. 7.1). It is assumed here that P, rather than N, limited algal production in the original, macrophyte-dominated lakes. However, biomanipulation case studies have shown that dense macrophyte beds, which recolonized the lake bed after improvement in the water clarity, tend to reduce TN levels (Van Donk *et al.*, 1993; Meijer *et al.*, 1994a). These results suggest that N could have been important as limiting nutrient for algal production, as well.

(2) Increase in TP levels in the water, but constant low algal biomass.

The loss processes can no longer cope with the increased loading and TP levels increase. In certain peat lakes, internal P loading from the sediments may have increased, due to the inlet of external water, which is rich in macro-ions such as bicarbonate, sulfate and chloride (Smolders & Roelofs, 1995; Beltman & Van der Krift, 1997). However, the 'clearing effects' of submerged macrophytes (refuge to algae-grazing *Daphnia* against fish predation, allelopathic effects etc.) still keep the algal biomass at low levels.

(3) Non-linear shift to the algae-dominated turbid water state.

Increasing nutrient levels make the system more susceptible to a collapse of the clear water state. Macrophytes become overgrown with periphyton (Van Vierssen *et al.*, 1994; Van Donk & Gulati, 1995) and blooms of (inedible) phytoplankton species will occur more often (Van Donk & Gulati, 1995), decreasing the chances for submerged vegetation. As most shallow lakes are rather uniform in depth, light conditions are fairly similar throughout the lake. Consequently, with deteriorating light conditions, the macrophytes may suddenly disappear from large areas. Additionally, increased nutrient levels may coincide with increased levels of pollution, including chemicals toxic to *Daphnia* and macrophytes. In the 1970s, the heavily polluted Rhine river water (feeding many lakes) was acutely toxic to *Daphnia magna* (Slooff *et al.*, 1985). Other perturbations, such as the intentional destruction of submerged vegetation, heavy benthivore stocking or exceptional weather conditions, may also trigger the shift to the turbid water state (see next section). The TP thresholds are difficult to specify. It is tentatively concluded from a large amount of field data in Denmark on TP, Secchi depth and vegetation (Jeppesen *et al.*, 1990b), that the clear water state may be stable up to TP = 100 mg m^{-3} (chapter 5). In small lakes (< 3 ha), however, a sustainable clear water state is possible at higher TP levels, due to the relatively strong impact of submerged vegetation in small water bodies.

(4) Increase in algal biomass, roughly following the P-limitation line.

The slope of the line may differ from lake to lake, due to variation in the CHL/TP ratios for different phytoplankton species and in the availability of TP for algal biomass.

(5) Algal biomass is leveling off.

The upper limit is determined by the availability of light, which depends on mixing depth (lake depth) and non-algal turbidity (chapter 3). In shallow lakes in the Netherlands, the final phytoplankton community consists of either filamentous and well-mixed cyanobacteria (e.g. *Oscillatoria agardhii*) in the shallower lakes (z = 1-2 m) or a mix of green algae and diatoms, with occasional blooms of colonial and scum-forming cyanobacteria (e.g. *Microcystis aeruginosa*) in the deeper lakes (z = 2-4 m) (Berger, 1987; Schreurs, 1992; Ibelings, 1992; Mur & Schreurs, 1995). TP may continue to rise, due to bloom-mediated P release from the sediments (chapter 4).

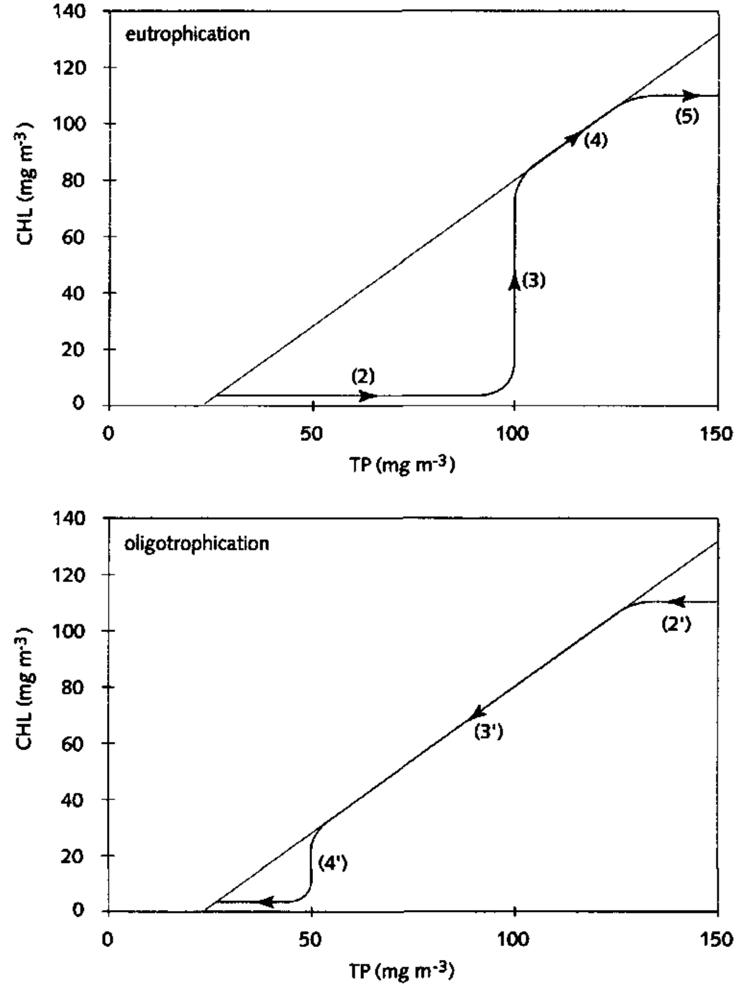


Fig. 7.1 *Effects of eutrophication (upper panel) and oligotrophication (lower panel) on summer algal biomass for a hypothetical shallow lake, showing the phenomenon of hysteresis. The line indicates maximum chlorophyll a in relation to TP (chapter 3). See text for explanation.*

The reverse process of oligotrophication runs a different course in the lower TP ranges. Starting from an algae-dominated turbid water state:

(1') Decrease in external P loading, but only a minor reduction in summer TP.
Summer TP levels may be controlled to a large extent by the strong internal P loading from the sediments (not shown in Fig. 7.1).

(2') Decrease in TP levels, but constant high summer algal biomass.
P is in excess and algal biomass is limited by other factors, e.g. light or N.

(3') Decrease in algal biomass, roughly following the P-limitation line.
The phytoplankton becomes P-limited and algal biomass goes down. The threshold TP level where the phytoplankton shifts from light limitation to P limitation depends on lake depth and non-algal turbidity (chapter 3). As stated above, the slope of the P-limitation line may vary with phytoplankton species and other factors. Secchi depth shows a gradual increase or may jump to higher values, with a shift in phytoplankton species (e.g from *Oscillatoria* to green algae).

(4') Shift to the macrophyte-dominated clear water state.
If TP reaches such a low level that the transparency of the water allows the reestablishment of macrophytes, the lake (or the shallower parts of the lake) shifts to the clear water state. This lower TP threshold depends on phytoplankton species composition and lake depth. *Oscillatoria*-dominated lakes may produce more algal biomass per unit P than lakes with a mixed phytoplankton community and consequently the TP threshold will be lower for these lakes. It will be clear that macrophyte reestablishment in deeper lakes requires a lower algal biomass (and lower TP) in the water column. Apart from the impact of non-algal turbidity, clear water (SD > 1 m) in shallow lakes can be expected at TP < 50 mg m^{-3} or even lower levels for *Oscillatoria*-dominated lakes (chapter 3). Strong wind-induced resuspension of sediments may prevent the lake from clearing up.

Note that in a certain TP range, both turbid water and clear water may be possible as alternative stable states. Ideally, lake restoration efforts should be aimed at TP < 50 mg m^{-3}. However, in the TP range of about 50-100 mg m^{-3} (or higher TP levels for very small lakes), additional in-lake measures or special natural events may trigger the shift from the algae-dominated turbid water state to the macrophyte-dominated clear water state (see next section).

Stable states, buffers and switches

In shallow lakes, phytoplankton blooms, and particularly blooms of *Oscillatoria agardhii*, may be self-reinforcing and therefore resistant to the reduction of external P loading. Additionally, resuspension of sediments by wind and benthivorous fish may contribute to the stability of the turbid water state. Conversely, in shallow lakes of moderate productivity, the submerged vegetation plays a key role in stabilizing the clear water state. Special natural events or actions ('switches') may trigger a shift from the one state to the other (Table 7.1).

Stable state:	**Turbid water**	**buffering mechanisms**	**forward switches to 'clear water'**
Factors contributing to stability	*Oscillatoria* bloom	resistant to low TP, low light and low temperature (1)	prolonged snow-covered ice (7) washout by winter flushing (8)
		reduced edibility for *Daphnia* grazers (2)	
	phytoplankton bloom	bloom results in high pH, high sediment oxygen demand and thus high internal P loading, more blooms (3)	control P release by sediment removal, sediment treatment or 'hard water' flushing (9)
		bloom results in turbid waters, low piscivores, high planktivores, low grazing, more blooms (4)	lower water level in spring to promote submerged vegetation (10) natural winter fish kills (11) reduce planktivores and promote piscivores (12)
	non-algal turbidity	wind-induced resuspension of sediments in plant-free lakes (5)	reduce wind exposure of sediments (13) or complete drawdown and drying of sediments (14)
		fish-induced resuspension of sediments by benthivores, unhindered by plants	reduce benthivores (15)
Stable state:	**Clear water**	**buffering mechanisms**	**reverse switches to 'turbid water'**
Factors contributing to stability	benthic diatoms	reduce susceptibility of lake sediments to wind-induced resuspension (16)	benthivore stocking (26) storm events (27)
		compete with phytoplankton for N, P (17)	
		promote N loss by denitrification (18)	
	submerged vegetation	competes with phytoplankton for N, P (19)	mechanical destruction of vegetation (28)
		promotes N loss by denitrification (20)	chemicals toxic to vegetation (29) macrophyte grazing by birds (30)
		reduces susceptibility of lake sediments to wind-induced resuspension (21)	increase water level during spring (31)
		excretes substances allelopathic to phytoplankton (22)	benthivore stocking (32) grass carp stocking (33)
		promotes grazing of phytoplankton by providing refuge to *Daphnia* (23)	chemicals toxic to *Daphnia* (34) storm events (35)
		promotes phytoplankton grazing by providing refuge to pike and subsequent top-down control of planktivores (24)	
		reduces fish-induced resuspension by hindering bottom feeding (25)	

Table 7.1 *Stable states, buffering mechanisms maintaining the stable states and switches to trigger a shift from a stable turbid water state to a stable clear water state (forward switch) or vice versa (reverse switch).*

Table 7 (continued) *References: (1) (3) (8) (9): chapter 4; (2) (4) (6) (12) (15) (25): chapter 5; (5) (21): Jackson & Starret, 1959; James & Barko, 1990; Van den Berg et al., 1996; (7): Greenbank, 1945; Raat, 1980; (10) (31): Holcomb et al., 1975; Blindow et al., 1993; Sanger, 1994; (11): Schindler & Comita, 1972; De Bernardi & Giussani, 1978; Raat, 1980; (13): Lürling et al., 1995; (14): Cooke et al., 1993; (16): Delgado et al., 1991; (17) (18): Van Luijn, 1997; Van Luijn et al., 1995; (19): Van Donk et al., 1993); (20): Gumbricht, 1993; Van Donk et al., 1993; (22): Wium-Andersen, 1987; Jasser, 1995; (23): Timms & Moss, 1984; Schriver et al., 1995; Stansfield et al., 1995; (24): Grimm, 1994; (26) (32): Ten Winkel, 1987; Crivelli, 1983; (27) (35): McKinnon & Mitchell, 1994; (28): - ; (29): Driessen et al., 1993; (30): Van Donk, 1997; (33): Small et al., 1985; (34): Hurlbert, 1975; Shapiro, 1980; Scholten et al., 1994.*

The stepwise restoration process of Veluwemeer

How the concept of 'stable states, buffers and switches' can be used in lake restoration will be shown with the case study on Veluwemeer. Veluwemeer suffered from a massive bloom of cyanobacteria (*Oscillatoria agardhii*), persisting year-round. Early in 1979, the P loading of the lake has been reduced and from 1979-80 onwards, the lake has been flushed during winter with water low in TP and rich in Ca^{2+} and HCO_3^-. The winter flushing aimed at breaking the dominance of *Oscillatoria* and reducing the P release from the sediments. It was hypothesized that the *Oscillatoria* bloom supported a self-perpetuating process of algal activity, high pH, P release and even more algal activity (chapter 4). As a result of the measures, TP and chlorophyll *a* showed a dramatic decline and algal growth during summer became P-limited (Fig. 7.2). Note the extremely low levels in 1996, probably due to the cold (long ice-cover) and dry (low external loading) preceding winter and spring (Figs. 7.9 and 7.10).

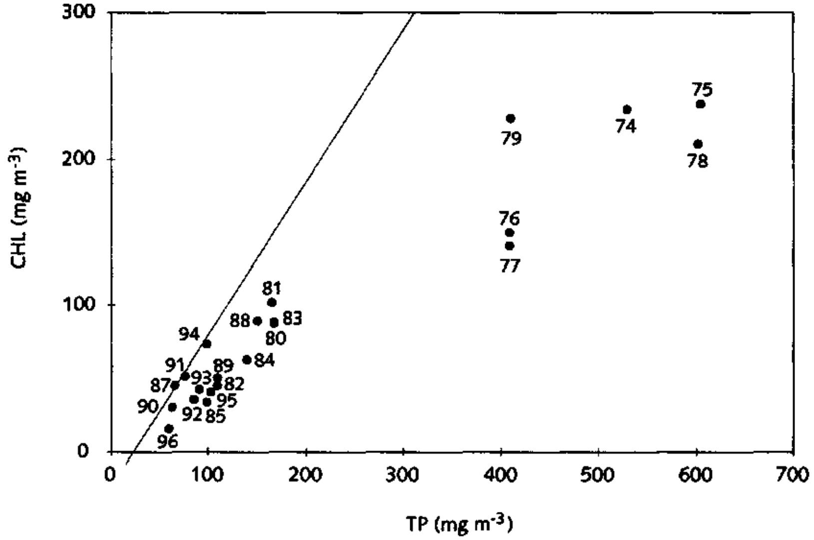


Fig. 7.2 *Chlorophyll a in relation to TP for Veluwemeer, mean values April-September, 1974-1996. The indicated line approximates the maximum value for chlorophyll a in relation to TP (CHL = - 24 + 1.04 TP, chapter 3).*

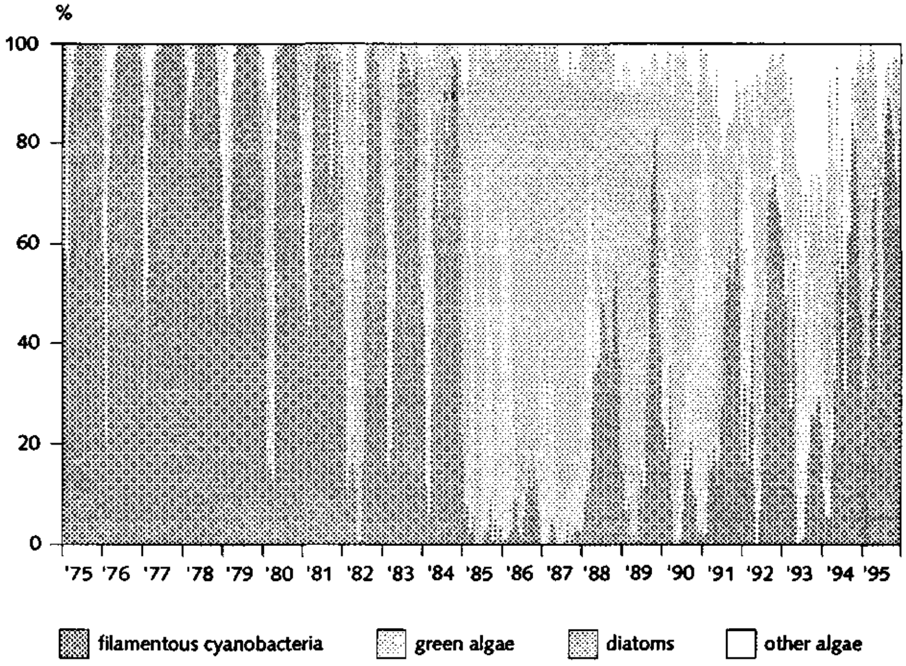


Fig. 7.3 *Phytoplankton species composition in Veluwemeer, 1975-1995.*

For the first years, the intensity of winter flushing was insufficient to break the dominance of *Oscillatoria.* However, the cold winter of 1984-85 (Fig. 7.9) combined with the flushing, ultimately, resulted in a more diverse phytoplankton community (Fig. 7.3) with a varying portion of *Oscillatoria. Oscillatoria* disappeared from the phytoplankton (not shown) after the cold winter of 1995-96. Transparency during spring, in the beginning of the growing season, is particularly important to the growth of submerged macrophytes and therefore to the recovery process of the lake. A distinct 'spring clear water phase' usually occurs in lakes of moderate productivity, induced by zooplankton grazers (chapter 5). Although transparency during spring in Veluwemeer showed an upward trend, Secchi depth in May-June was limited to 0.40-0.60 m only, with a peak of 0.80 m in 1996. Secchi depth during summer (April-September) increased from about 0.20 m to 0.30 m in the first years, and later after the species shift in phytoplankton to 0.40-0.50 m, increasing to 0.70 m in 1996 (Fig. 7.4).

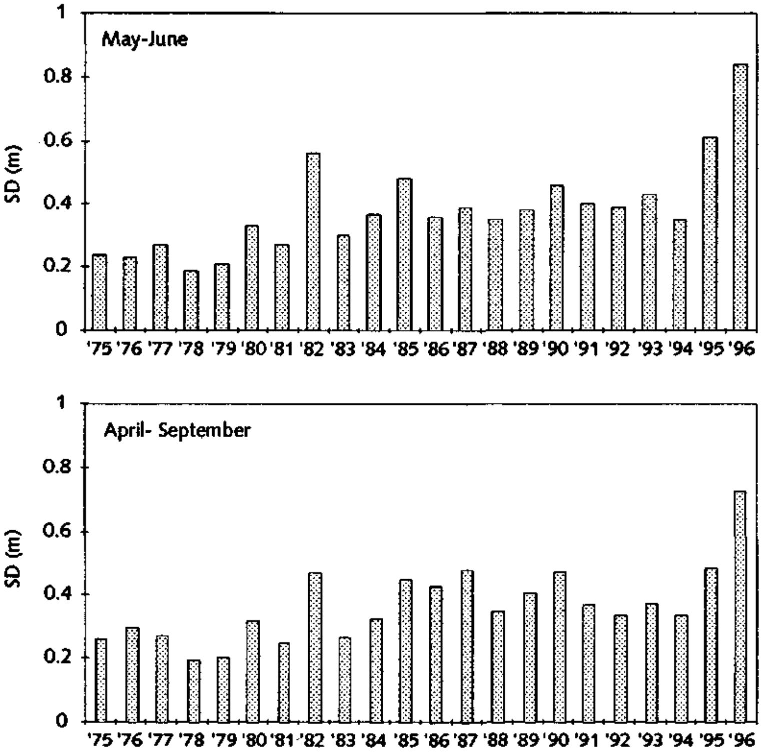


Fig. 7.4 *Secchi depth in Veluwemeer (open water, unvegetated), mean values May-June (upper panel) and April-September (lower panel), 1975-1996.*

From 1985 onwards, after the collapse of the *Oscillatoria* bloom, the sparse vegetation of *Potamogeton pectinatus* in the shallow parts (< 1 m) of the lake gradually became replaced by dense beds of Characeae (Coops *et al.*, 1997), covering about 25% of the lake in 1996 (Fig. 7.5). Surprisingly, the water overlying the *Chara* meadows is clear during summer, whereas the open water outside the vegetated area remains turbid (Fig. 7.6). Obviously, the two alternative stable states of macrophyte-dominated clear water and algae-dominated turbid water can coexist within one lake (Scheffer *et al.*, 1994; Van den Berg *et al.*, in press). A similar development of clear vegetated areas and turbid open waters took place in the adjacent Wolderwijd, following fish stock reduction in 1991 (chapter 6). The final step in the restoration of Veluwemeer (and Wolderwijd) aims at increasing the clarity of the open water areas. The question now is whether this will happen spontaneously, resulting from a continuing expansion of the vegetation, or that additional measures (such as drastic fish stock reduction) are necessary for creating a more pronounced spring clear water phase. The favorable conditions in the summer of 1996 (Figs. 7.2, 7.4 and 7.5), following the extremely cold and dry winter (Figs. 7.9 and 7.10), suggest that the lake is close to a macrophyte-dominated clear water state. After the growing season of 1996, transparency further increased and on 22 October the highest Secchi depth on record of 3.2 m was measured (Griffioen, pers. comm.). It makes sense to await further developments, before deciding upon additional actions, such as fish stock reduction. So far, it remains uncertain whether or not the present clear water lake will be resistant to occasional increases in external nutrient loading (e.g. resulting from a wet and mild winter). An increase in external loading may result in more algal biomass, which may trigger the positive feedback mechanism of P release from the sediments and even more algal biomass (chapter 5). It can be hypothesized, however, that due to the relatively low external P loading since 1979, the binding of P to the sediments will have improved.

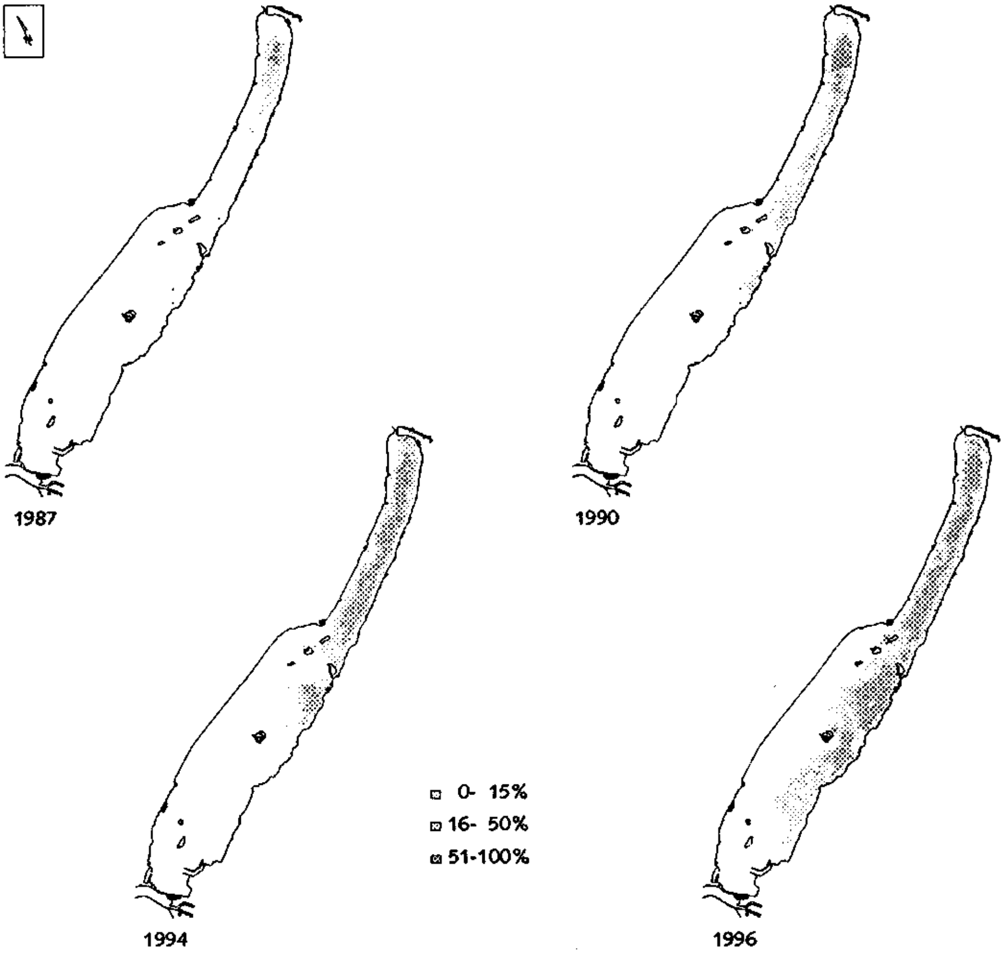


Fig. 7.5 *Characeae in Veluwemeer in 1987, 1990, 1994 and 1996. Density classes (% of bottom covered with vegetation) 0-15%, 16-50% and 51-100% (data from Doef et al., 1991, 1994; De Witte et al., 1995; RDIJ unpublished data).*

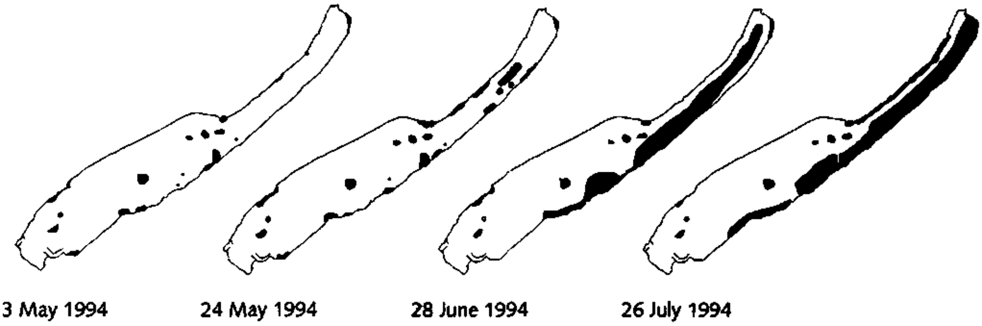


Fig. 7.6 *Clear water areas in Veluwemeer in 1994. Shaded areas indicate bottom visibility from airplane observations (data from Zant et al., 1995). May: unvegetated; June and July: densely vegetated.*

In conclusion, several stages can be distinguished in the restoration process of Veluwemeer (Fig. 7.7). On top of the control of external loading, a series of 'switches' are hypothesized to lead to the ultimate goal of the macrophyte-dominated clear water state:

(1) 'Hard water' flushing
Control of internal P loading by manipulating the carbonate system, through winter flushing with water rich in Ca^{2+} and HCO_3^-. The winter flushing started in 1979-80 and as a result summer Secchi depth increased from 0.20 to 0.30 m.

(2) Washout of Oscillatoria by winter flushing during a cold winter
Breaking the dominance of the *Oscillatoria* bloom by winter flushing in combination with the cold winter 1984-85 (long periods with snow-covered ice). Summer Secchi depth in the open water increased from 0.30 to 0.40-0.50 m, and in the following years large shallow areas (20-30% of the lake) became covered with a dense *Chara* vegetation with clear overlying water.

(3) Reduction of the fish stock
Promoting the macrophyte-dominated clear water state by creating a pronounced spring clear water phase, through drastic reduction of the planktivorous and benthivorous fish stock. Natural winter fish kills may also trigger the clear water state (Schindler & Comita, 1972; De Bernardi & Giussani, 1978; Haertel & Jongsma, 1982). However, for large lakes in the Netherlands such dramatic winter kills are very unlikely (Raat, 1980). As noted above, the favorable conditions in Veluwemeer (and in Wolderwijd) in the summer and fall of 1996, raise the question whether or not biomanipulation is still necessary.

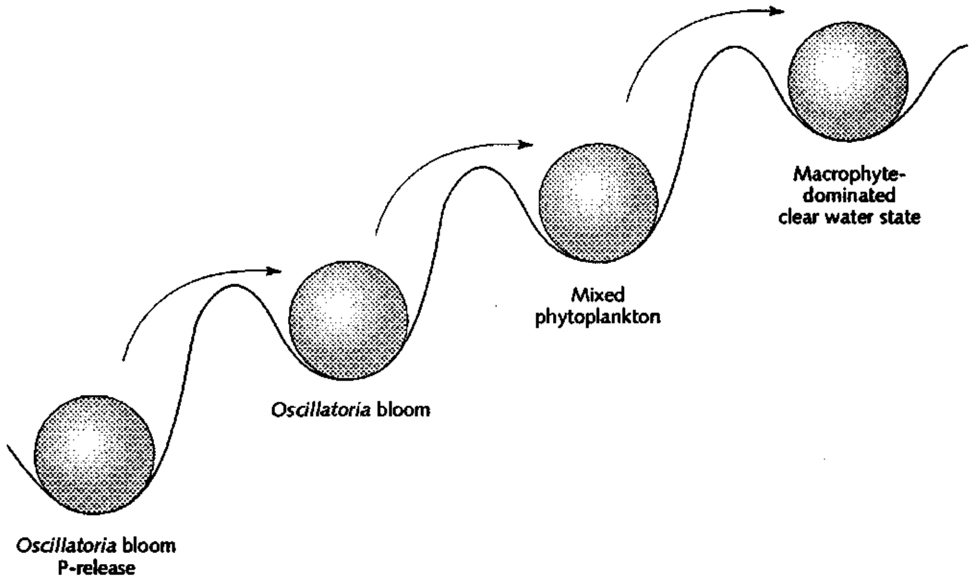


Fig. 7.7 *The stepwise restoration process of Veluwemeer, in addition to the reduction of external P loading. Step (1): 'hard water' flushing to control P release from the sediments; step (2): winter flushing to remove the Oscillatoria bloom and step (3): fish stock reduction to trigger a shift to the macrophyte-dominated clear water state.*

Perspectives for lake restoration in the Netherlands

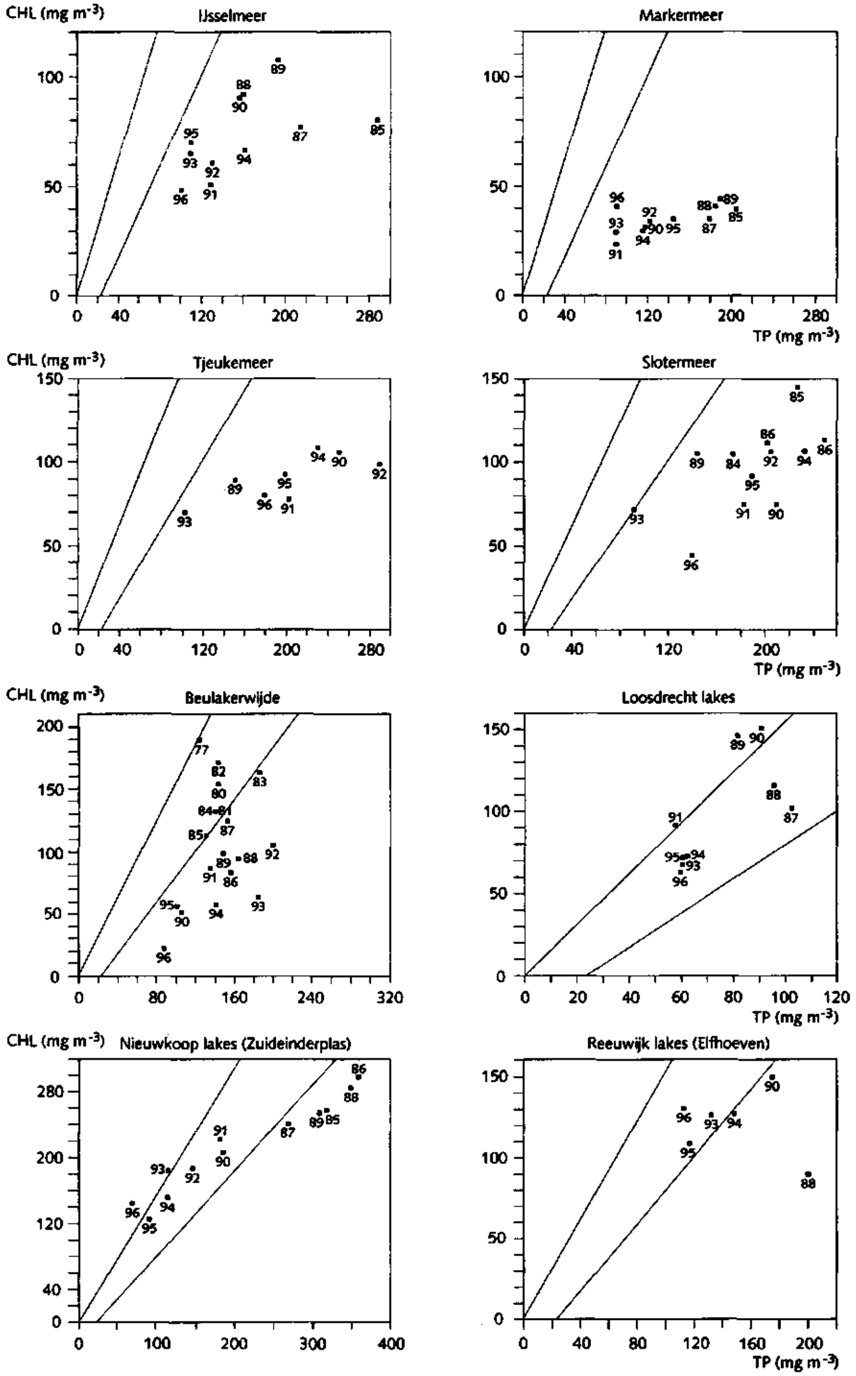
As noted above, filamentous cyanobacteria (*Oscillatoria, Lyngbya*) blooming almost year-round, dominate the phytoplankton of numerous, shallow (z = 1-2 m) lakes, making the water extremely turbid. Deeper lakes (z = 2-4 m) are usually less turbid and show a mixed phytoplankton community with peaks of colonial scum-forming cyanobacteria (*Microcystis, Aphanizomenon*). Lake restoration primarily aims at clearing the water and controlling the scum-forming blooms of cyanobacteria (Anonymous, 1995; Van der Veer *et al.*, 1993, 1995). Here, attention is focused on the restoration of shallow lakes dominated by *Oscillatoria, Lyngbya* etc. (*Oscillatoria*-type algae). First of all, the primary cause of algal blooms, the increased external nutrient loading from point and non-point sources, should be eliminated. Furthermore, negative trends such as pollution with toxic chemicals (causing reduced zooplankton grazing) and the ongoing loss of lake-marginal wetlands and littoral vegetation (loss of pike habitat, loss of nutrient retention capacity) should be reversed.

Trends in TP, chlorophyll and phytoplankton species

TP levels in many surface waters in the Netherlands are going down, as a result of (inter-) national action programs. The TP flow in the Rhine river has been reduced by more than 50% (Fig. 1.5). TP concentrations in the large (and relatively deep, z = 5 m) Rhine-fed lakes IJsselmeer and Markermeer (Fig. 7.8) have closely followed this trend. Obviously, for these lakes there is no delay in response due to the P release from the sediments. In IJsselmeer algal biomass tends to go down as well. In the adjacent Markermeer algal biomass usually is much lower and mainly light-limited, due to wind-induced sediment resuspension (Van Duin, 1992). Massive scum-forming blooms (e.g. *Microcystis aeruginosa*) still occur, particularly in IJsselmeer, during late summer (Ibelings, 1992).

The Friesland lakes, e.g. Tjeukemeer and Slotermeer (Fig. 7.8), showed strongly varying summer TP levels, which correlate with net rainfall during the first half of the year (Fig. 7.10). Low TP concentrations are observed in (extremely) dry years such as 1989, 1993 and 1996. The Friesland lakes receive water from the IJsselmeer (mainly in summer) and from the surrounding agricultural areas (mainly in winter). Apparently, P dynamics are largely controlled by on the one side P-rich drainage water pumped in from the agricultural areas during wet periods, and on the other hand the inlet of water from IJsselmeer, relatively low in TP, during dry periods. Summer chlorophyll *a* levels in the Friesland lakes were relatively low, particularly in Slotermeer, after the cold and dry winter and spring of 1996. *Oscillatoria* was virtually absent in the phytoplankton of Slotermeer, but was still the dominant species in Tjeukemeer, in the summer of 1996 (Maasdam, pers. comm.). Interesting developments showed up in De Wieden lake area, e.g. Beulakerwijde (Fig. 7.8). Chlorophyll *a* has strongly decreased, although TP levels remained relatively stable. Also in this lake area, TP and chlorophyll *a* were extremely low in summer 1996 and *Oscillatoria* practically disappeared after the cold winter (Moonen, pers. comm.). It has been suggested above (chapter 5), that in De Wieden fish-eating cormorants could have played a significant role in the recent changes in the phytoplankton community. The Loosdrecht lakes showed a decline in TP and chlorophyll *a* (Fig. 7.8). However, the algal biomass is still relatively high, and the phytoplankton remains to be dominated by *Oscillatoria*-type algae (Everards, pers. comm.). The turbid water state of the Reeuwijk and Nieuwkoop lakes appears to be extremely stable. In both lakes the favorable 1996 weather conditions did not result in any response, neither in TP and chlorophyll *a* (Fig. 7.8), nor in the dominance of *Oscillatoria*-type algae (Frinking, pers. comm.). It was shown for Veluwemeer, in the previous section, that the cold winter of 1984-85 had contributed to the collapse of the *Oscillatoria* bloom in this lake. The earlier cold winter of 1978-79, however, failed in producing such a response in phytoplankton species (Fig. 7.3) or transparency (Fig. 7.4). Obviously, additional factors (e.g. lake flushing, reduced algal biomass) are necessary for the species shift. Winter 1995-96 triggered a major change in Veluwemeer, resulting in extremely clear water in the fall.

Fig. 7.8 *Chlorophyll a in relation to TP for several lakes in the Netherlands, mean values April-September. The indicated lines approximate the maximum value for chlorophyll a in relation to TP for Oscillatoria-dominated lakes (CHL = 1.54 TP) and for other lakes (CHL = - 24 + 1.04 TP) (chapter 3). Data from the lake management authorities.*


CHL (mg m-3)
IJsselmeer
0
50
100
0
40
120
200
280
89
88
90
95
93
92
91
96
94
87
85
Markermeer
0
50
100
0
40
120
200
280
TP (mg m-3)
96
93
91
92
90
94
95
88
89
87
85
CHL (mg m-3)
Tjeukemeer
0
50
100
150
0
40
120
200
280
93
89
96
95
91
94
90
92
Slotermeer
0
50
100
150
0
40
120
200
TP (mg m-3)
85
86
89
84
92
94
86
95
93
91
90
96
CHL (mg m-3)
Beulakerwijde
0
50
100
150
200
0
80
160
240
320
77
82
80
83
84
81
85
87
89
88
92
91
86
95
90
94
93
96
Loosdrecht lakes
0
50
100
150
0
20
40
60
80
100
120
TP (mg m-3)
89
90
88
87
91
95
94
93
96
CHL (mg m-3)
Nieuwkoop lakes (Zuideinderplas)
0
40
120
200
280
0
100
200
300
400
86
88
87
89
85
91
90
93
92
96
94
95
Reeuwijk lakes (Elfhoeven)
0
50
100
150
0
40
80
120
160
200
TP (mg m-3)
90
96
93
94
95
88

From the limited data set presented above, it is concluded that: (1) TP and chlorophyll *a* may vary strongly with weather conditions (Tjeukemeer, Slotermeer); (2) a cold and dry winter and spring, such as in 1996, may cause a collapse of the *Oscillatoria* bloom (Beulakerwijde), or even trigger a shift from turbid to clear (Veluwemeer); but (3) certain *Oscillatoria* lakes (Nieuwkoop, Reeuwijk, Loosdrecht) are more stable than others (Slotermeer, De Wieden).

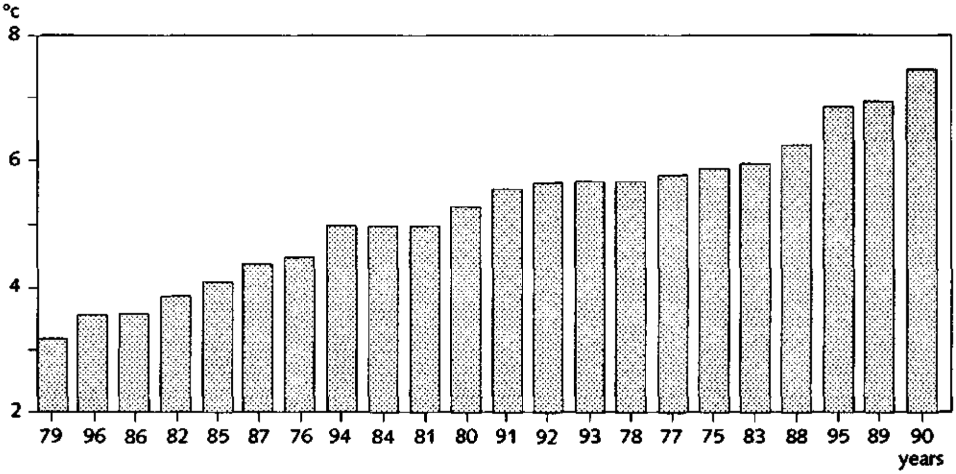


Fig. 7.9 *Average air temperature in the Netherlands (at De Bilt) for October-March, 1975-1996. Data from KNMI.*

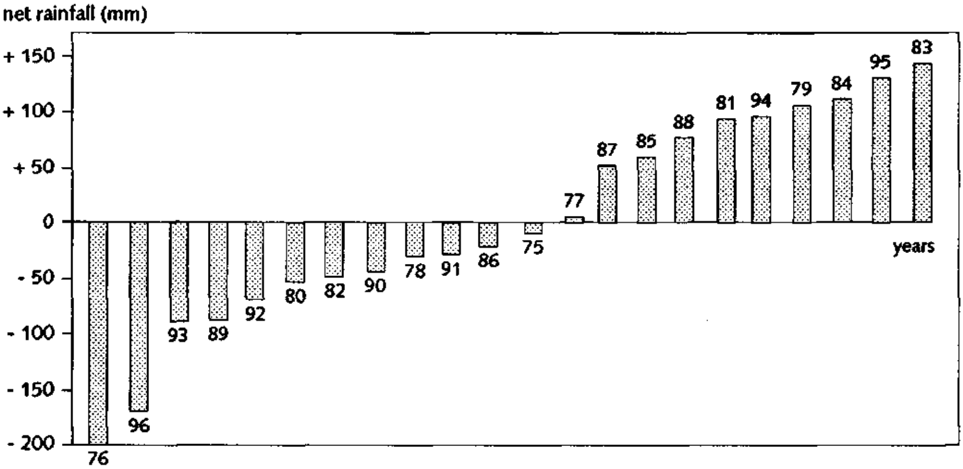


Fig. 7.10 *Net rainfall (rainfall - evapotranspiration) in the Netherlands for January-June, 1975-1996. Data from KNMI.*

Additional in-lake measures

As the turbid water state tends to be resistant to lowering nutrient levels, additional in-lake measures may be necessary (Table 7.1). Certain blockages have to be removed to get the recovery process started: (1) the *Oscillatoria* bloom; (2) the algal bloom-mediated P release from the sediments and (3) the abundance of planktivorous and benthivorous fish, preventing *Daphnia* and submerged macrophytes from developing.

How can the Oscillatoria blooms be removed?

Oscillatoria blooms are particularly resistant to lake restoration efforts, due to the low edibility for *Daphnia* and the low P requirements. For many lakes it will be difficult to achieve TP < 20-50 mg m^{-3}, which is needed for a collapse of the bloom (chapter 3). Therefore, additional switches are needed. A severe winter may contribute to the combat against *Oscillatoria*, as was shown in the previous section. Washout by winter flushing may be a powerful management tool, provided that flushing water is available in sufficient quantity and quality (low in TP, low in algae). It was concluded that conservative behavior (net growth = 0) may be assumed for *Oscillatoria* blooms, during November-February (chapter 4). Thus, blooms can be effectively (> 95%) removed from well-mixed lakes by flushing in this four month period by at least three times the lake volume (flushing rate $\rho > 0.75$ $month^{-1}$) (chapter 4). The large lake IJsselmeer-Markermeer, which is relatively low in TP and algae (Fig. 7.8), may be a favorable source for flushing, for example the Friesland lakes or lakes in the western provinces. Small lakes in the Netherlands can possibly be flushed with clear water from adjacent deep sandpits (e.g. Reeuwijk lakes with water from the sandpit Broekvelden-Vettenbroek, or Holland-Ankeveen lakes with water from the sandpit Spiegelpolderplas).

How can P release from sediments be reduced?

Phytoplankton blooms may promote the P release from sediments by creating high sediment oxygen demand (SOD) and high pH. Such a self-perpetuating process (algal blooms, P release, more algal blooms) can be interrupted by flushing with water, which is low in TP and algae, but rich in Ca^{2+} and HCO_3^-. The manipulation of the carbonate system proved to be particularly successful in Veluwemeer (chapter 4). Following 'hard water' winter flushing, the internal P loading strongly decreased, and algal growth was P-limited throughout the summer. For other lakes with high summer P release (apparent from high summer TP peaks), the significance and technical possibilities should be further evaluated. It has been suggested that the inlet of external water, which may be relatively rich in macro-ions such as bicarbonate, sulfate and chloride, into formerly isolated peat lakes, could enhance P release from the sediments (Smolders & Roelofs, 1995; Beltman & Van der Krift, 1997). For many peat lakes in the Netherlands, however, the naturally inflowing (ground)water already has relatively high concentrations of these macro-ions (see for example Van Liere *et al.*, 1989; Rip *et al.*, 1992; Hessels, 1995). Therefore, for these lakes the effects of the inlet of outside water on macro-chemistry are probably less dramatic than suggested, and the significance of altered macro-chemistry on P release may be questioned. Eiseltová (1994) concluded from work in the Swedish lake Trummen that dredging and removal of P-rich sediments from the lake system, though expensive, seemed to be the final answer to the problem of internal loading. However, sediment removal (25-100 cm loose top layer) from the Dutch peat lake Geerplas, after severely reducing the external P loading, failed to result in the desired TP and phytoplankton levels (Van der Does *et al.*, 1992; Frinking & Van der Does, 1993). Initially, the sediment top layer in this lake was solid, but shortly afterwards a new loose mud layer had been formed. It has been demonstrated that P release after dredging was not significantly lower than before. Apparently, the new top layer shows the same P release characteristics as before the dredging (Van der Does & Frinking, 1993). Dredging is no panacea, and it seems wise to focus on external loading reduction and other more appropriate in-lake measures.

How can Daphnia grazing and macrophytes be restored?

Algae-dominated turbid lakes are usually rich in planktivorous and benthivorous fish, poor in piscivorous fish and practically devoid of submerged macrophytes. All these factors contribute to an unhindered development of algal blooms and stability of the turbid water state (Table 7.1). A single substantial reduction of planktivorous fish during winter may trigger a *Daphnia*-mediated clear water phase in spring, followed by a shift to a stable macrophyte-dominated clear water state. Benthivore reduction, particularly in productive clay-bottom lakes, further supports the clearing of the lake. 'Inedible' filamentous cyanobacteria and the possible development of invertebrate predators (e.g. *Neomysis*), consuming the zooplankton grazers, are uncertain factors for spring clearing. Toxic compounds may also block the way to recovery and the lake water should be checked for acute or chronic toxicity to *Daphnia*. The formerly heavily polluted Rhine river has shown a dramatic recovery and currently toxic effects on *Daphnia*, reported for the 1970s (Sloof *et al.* 1985), can no longer be observed (Hendriks, 1995). Locally, however, particularly in intensively used agricultural areas, small water bodies (ditches) can still be acutely toxic (Gorter *et al.*, 1996). After fish stock reduction and clearing, rapid colonization of submerged macrophytes has been demonstrated in small lakes (< 30 ha). In large lakes recolonization takes more time and therefore repeated intensive fishing over several years may be necessary. In large lakes, and particularly in networks of interconnected lakes, it is more difficult to achieve a drastic reduction of the fish stock. Less drastic, but permanent winter fishing may be promising then, but case studies are needed for further evaluation. As noted above, prerequisites for successful biomanipulation are low TP levels (TP < 100 mg m^{-3}, or higher TP levels for very small lakes), and low numbers of inedible algal species, such as *Oscillatoria*. The chances for biomanipulation are improving, as in many large lake areas TP is approaching the indicated levels (Fig. 7.8). Furthermore, *Oscillatoria*-type algae are losing ground in large lake areas, including Veluwemeer (Fig. 7.3) and Wolderwijd (chapter 6), De Wieden (Moonen, pers. comm.) and some of the Friesland lakes (Maasdam, pers. comm.). Uncertainties remain, however, particularly for large shallow lakes. It should be noted that complete case studies covering the whole process of recovery from the stable turbid water state to the stable clear water state, are not available. Therefore, only tentative guidelines could be presented and several questions remain unanswered, such as: (1) the role of resuspended sediments in windswept lakes in preventing submerged vegetation from developing; (2) the role of submerged vegetation in maintaining clear water, not just in restricted areas, but throughout large shallow lakes and (3) the efficacy of repeated winter fishing in large and complex lake systems, for promoting *Daphnia*.

Priorities in lake restoration

Several authors have suggested radical measures for lake restoration, including the restoration of the original groundwater flow systems by reflooding adjacent polders (Engelen *et al.*, 1992; Verstraelen *et al.*, 1992; Barendrecht *et al.*, 1992), the construction of large-scale pike nursery habitats (Grimm, 1994; Klinge *et al.*, 1995), and restoring the former 'legakker' structure (see chapter 2) in peat lakes by constructing islands and dams (Lürling *et al.*, 1995; Everards, pers. comm.). Emulating the original natural processes, unquestionably, is the best guide to lake restoration. However, it will be clear that current economic and public interests may oppose to this approach and the lake manager has to look for more realistic tools (Table 7.2).

	Reduction external P loading	**Washout *Oscillatoria* by flushing**	**Promoting spring clear water phase by fishing**	**Additional measures**
Veluwemeer	**	*	**	continue 'hard water' flushing
Wolderwijd	**	*	**	continue 'hard water' flushing
Friesland lakes	***	**	***	-
De Wieden	**	*	**	protect cormorant colony
Loosdrecht lakes	*	***	**	-
Nieuwkoop lakes	*	***	**	-
Reeuwijk lakes	**	***	**	-

Table 7.2 *Priorities suggested for the restoration of some shallow Dutch lakes (* * * high, * * moderate, * low priority).*

For many shallow lakes, including the Loosdrecht lakes, the Nieuwkoop lakes and the Reeuwijk lakes, it is obvious that the persistent bloom of *Oscillatoria*-type algae is the main bottleneck for recovery. Therefore, priority should be given to fighting the *Oscillatoria* blooms. Essentially, the options for eliminating *Oscillatoria* include (1) further reduction of external P loading or (2) improving the light conditions in the lake, so more favorable (edible) algal species could outcompete *Oscillatoria*, which prefers dim-light conditions. For the Loosdrecht lakes for example, it is feasible to bring the external loading further down from 0.35 to 0.10 g P m^{-2} y^{-1} (De Ruiter, 1992). Model calculations indicated that TP and chlorophyll *a* will decrease as a result, but that filamentous cyanobacteria will still be dominant (Janse *et al.*, 1992). The light conditions in the Loosdrecht lakes might be improved either by washout of the *Oscillatoria* (by flushing), or by reduction of non-algal turbidity.

Wind-induced resuspension of sediments is the main cause of non-algal turbidity in the Loosdrecht lakes (Gons *et al.*, 1991) and would be extremely difficult to control. Radical (and costly) changes in the morphometry of the lake would be necessary (e.g. creating islands, dams or deep sediment accumulation basins). What remains is the option of flushing with water low in *Oscillatoria* and TP. Van Liere & Janse (1992) already evaluated the feasibility of flushing for the Loosdrecht lakes and concluded that the existing infrastructure does not allow an effective lake flushing. It is suggested here to explore new possibilities for flushing, including the use of mobile pumping engines to overcome infrastructural problems. Flushing possibilities should also be investigated for other persistent *Oscillatoria* lakes, such as the Nieuwkoop lakes and the Reeuwijk lakes.

The original natural water level fluctuations in the Friesland lakes usually resulted in the flooding of extended grassland areas during winter and spring (Klinge *et al.*, 1995). The flooded areas (temporal wetlands) acted as sinks for nutrients and fine sediment particles and as spawning and nursery habitat for pike (chapter 2), supporting the clear water state of the Friesland lakes at that time. Restoring such a flooding scenario will only be possible on a small scale (Claassen, pers. comm.). Grimm (1994) suggested creating of large-scale 'managed marshes' with an optimal water level regime for raising young pike. However, before deciding upon this kind of costly measures in the Friesland lakes, it seems wise to focus on the further control of the (non-point) nutrient loading and appropriate in-lake measures such as flushing and fishing. Winter flushing with water from IJsselmeer could be effective in fighting the *Oscillatoria* blooms. Winter fishing on bream and large pike-perch could enhance the top-down control of algae, through planktivorous fish and *Daphnia*. For the Friesland lakes this top-down control may be most promising, as the non-point P sources for these lakes (inflow of water from agricultural areas) will be difficult to control.

It was shown above that in De Wieden lake area (e.g. Beulakerwijde), *Oscillatoria* lost ground completely after the cold winter of 1996, and that cormorants possibly contributed to the top-down control of the algae. Winter fishing may further enhance this top-down control.

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Summary

In the 1950s and 1960s, most shallow lakes in the Netherlands shifted from macrophyte-dominated clear water lakes, towards algae-dominated turbid water lakes. Eutrophication, i.e. increased nutrient loading, is the main cause of the deterioration of the lake ecosystems. Other perturbations, such as the loss of lake-marginal wetlands (nutrient filters, habitat for pike, *Esox lucius*) and chemical pollution toxic to zooplankton, will have reinforced the effects of nutrient enrichment. The lake restoration strategy has been concentrated on the reduction of the external phosphorus (P) loading. However, so far this approach did not result in the water quality (in terms of transparancy, phytoplankton species, fish stock etc.) desired. A more comprehensive approach to lake ecosystem functioning may provide additional tools for lake restoration. Algal blooms in lakes will develop when the algal production is high and the algal losses are low. Production is controlled by the supply of nutrients and light. Consumption of algae by zooplankton is a major loss process. In this thesis attention is focused on both sides of the algal balance: (1) the control of the external and internal (from the sediments) P loading, and (2) biomanipulation, the manipulation of fish communities aiming at increased consumption of algae. Reduction of the planktivore fish stock may enhance the zooplankton and thus the grazing on algae. Bream (*Abramis brama*) and roach (*Rutilus rutilus*) are among the major fish species in many turbid Dutch lakes. Large bream feeds on zooplankton, as well as benthic organisms. Reduction of the benthivore fish stock results in reduced sediment resuspension and P release and less disturbance of rooted macrophytes.

Development of the lake restoration strategy (chapter 1)
The strategy for lake restoration gradually evolved from solely P stripping from sewage, towards a more comprehensive and ecosystem-based approach. In the Netherlands, P removal at sewage treatment plants is common practice and polyphosphates in household detergents have been replaced by less harmful compounds. TP levels in surface waters (including the Rhine river) are going down, however, in lakes algal blooms persist. Presently, additional measures directed at the reduction of non-point sources, treatment or removal of P-rich sediments and fish stock management come into focus. Other negative influences such as the ongoing loss of lake-marginal wetlands and (locally) the chemical pollution toxic to zooplankton, should be reversed as well.

Shallow lakes in the Netherlands: searching for lake restoration objectives (chapter 2)
Shallow lakes which are not, or only slightly, influenced by man, may provide clues to define key variables and processes expressing ecological sustainability. Historical studies may therefore be useful for finding specific objectives for lake restoration. One natural peat lake (Naardermeer) and two lake areas resulting from peat mining (Reeuwijk lakes and Oude Venen) were selected for such a reference study. It is well-known that many lakes in the Netherlands showed major changes in water transparency in the 1950s and 1960s. The

information collected refers mainly to the period 1930-1950. At that time, all three lakes were clear with abundant submerged vegetation. Naardermeer, with its extremely low nutrient loading, showed the strongest indications for a stable clear water state (a high diversity of *Chara* species). Nutrient loading of the other two lakes was probably higher. It is speculated that the intensive commercial fishing in the Reeuwijk lakes (by 30-50 families), and the excellent pike habitat in the Oude Venen (due to natural water level fluctuations), played a significant role in maintaining the clear water state in these two lakes.

Multi-lake studies: external nutrient loading and lake response (chapter 3)

Multi-lake studies proved to be helpful in developing management criteria for eutrophication control. In 1976-1977, the first national eutrophication survey of the shallow eutrophic lakes of the Netherlands was conducted, including ca. 65 lakes, of which 14 lakes with reliable water- and nutrient budgets. More up-to-date relationships for lake management were derived by including the results of the eutrophication surveys for 1983-1985 and 1980-1988. According to the steady-state loading-response models, the in-lake TP concentration shows a proportional or 'somewhat' less than proportional response to a decrease in TP loading. Secchi depth-chlorophyll relationships and upper limits for chlorophyll in relation to TP, TN and underwater light climate could be established. Lakes with an excess of TP will show a 'threshold response', after P loading reduction: algal biomass only goes down if the TP concentration approaches the limitation line, CHL = -24 + 1.04 TP (CHL and TP in mg m^{-3}). *Oscillatoria*-dominated lakes may produce more algal biomass per unit P (CHL = 1.54 TP). Objectives for Secchi depth were derived, (1) for triggering a collapse of *Oscillatoria* blooms, and (2) for creating proper light conditions for the restoration of submerged vegetation. However, due to the highly variable non-algal turbidity, only upper limits can be given for the chlorophyll and TP levels necessary.

Whole-lake study of Veluwemeer: lake flushing for control of *Oscillatoria* blooms and internal phosphorus loading (chapter 4)

Lake Veluwemeer (3,356 ha, mean depth 1.25 m) has suffered from a year-round *Oscillatoria* bloom from 1971 onwards. Early in 1979, the P loading of the lake was reduced from 2.7 to 1.5 g P $m^{-2}y^{-1}$. Monthly TP budgets, however, showed a substantial net P release from the sediments during summer and therefore the prospects for recovery were poor. Summer peaks in TP coincided with extremely high pH (pH 9-10) and it was hypothesized that the *Oscillatoria* bloom supported a self-perpetuating process of algal activity, high pH, P release and even more algal activity. Winter flushing with water that was low in TP and high in Ca^{2+} and HCO_3- could interrupt this vicious cycle. The effects were spectacular. After the first winter flushing in 1979-80, summer pH dropped by one whole unit, TP and chlorophyll more than halved and summer algal growth has been P-limited ever since. However, Secchi depth only increased from 0.20 to 0.30 m. This disappointing transparency could be explained by reduced chlorophyll content per unit algal biovolume. *Oscillatoria*, which prefers dim light conditions, lost its dominant position after the cold winter of 1985. After the species shift, summer transparency was still limited to 0.40-0.50 m. Model calculations showed a decrease of summer internal P loading from 1.0-8.4 before to 0.0-1.7 mg m^{-3} d^{-1}

after the measures. Low summer pH values could be explained by the enhanced $CaCO_3$ precipitation during the spring. Apparently, the low pH resulted in reduced P release from the sediments and P-limited algal growth during summer. The reduced algal biomass and consequently lower sediment oxygen demand, and maybe also increased NO_3^- levels during early spring, will have reinforced the better binding of P to the sediments. Manipulation of the carbonate system proved to be an effective tool in controlling internal P loading. During winter, conservative behavior (net growth = 0) of the *Oscillatoria* population may be assumed. Therefore, *Oscillatoria* blooms can be effectively (> 95%) removed from well-mixed lakes by flushing in November-February, with three times the lake volume.

Biomanipulation in shallow lakes: concepts, case studies and perspectives (chapter 5)

High fish stocks in algae-dominated lakes tend to impose a homeostasis on the lake ecosystem, which then resists the recovery of the lake. In today's turbid lakes, the common phenomenon of the 'spring clear water phase', induced by zooplankton grazers, fails to appear. Large numbers of planktivorous bream and roach, throughout the year, as well as high densities of 'inedible' filamentous cyanobacteria, prevent the peaking in population of the efficiently grazing large-bodied *Daphnia*. Submerged macrophytes play a key role in maintaining the clear water state throughout the summer. For the reestablishment of the submerged vegetation, it is necessary to restore the spring clear water phase. Biomanipulation, i.e. a substantial fish stock reduction, could trigger a shift from a stable turbid water state to an alternative stable clear water state. Nine case studies were evaluated for testing the applicability and perspectives of biomanipulation. It was concluded that a single substantial fish stock reduction (> 75%) during winter, offers good chances for achieving clear water in the next spring. The filamentous cyanobacteria and the possible development of invertebrate predators (*Neomysis, Leptodora*) on *Daphnia* are uncertain factors for successful biomanipulation. Rapid colonization of submerged macrophytes, stabilizing the clear water state, has been demonstrated in small lakes (< 30 ha). High nutrient levels, ultimately (in two cases, after five and seven years), lead to a shift back to the turbid water state. Top-down control by the predatory fish (pike and perch, *Perca fluviatilis*) seems restricted to small lakes, with a high degree of 'patchiness' (patches of macrophytes and open water). An alternative stable clear water state may be expected in the TP range of 50-100 mg m-3 (or higher TP levels for very small lakes). More and more lakes in the Netherlands approach these TP levels, so the chances for biomanipulation are improving. Fish control is more difficult in large lakes, and particularly in networks of interconnected lakes. Additionally, in large lake areas the reestablishment of vegetation takes more time. Winter fishing on a regular basis (rather than a single fish stock reduction) may then be promising, but case studies are needed for further evaluation.

Whole-lake study of Wolderwijd: biomanipulation for promoting the clear water state (chapter 6)

Lake Wolderwijd (2,555 ha, mean depth 1.60 m) has suffered from *Oscillatoria* blooms, turbid water and a poor submerged vegetation as a result of eutrophication since the early 1970s. From 1981-1984 the lake was flushed (via Veluwemeer) during winter, with water low in TP and high in Ca^{2+} and HCO_3^-. TP and chlorophyll *a* in the lake more than halved, but Secchi depth in summer only increased from 0.20 to 0.30 m. 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 1990-91. The fish stock, mainly bream and roach, was reduced from 205 to 45 kg ha^{-1}. In May 1991, 575,000 (217 ind ha^{-1}) pike fingerlings were introduced. From 1989 onwards, lake flushing was intensified in order to reduce TP and the *Oscillatoria* bloom. In spring 1991, the lake water cleared as a result of grazing by *Daphnia galeata*. The clear water phase lasted for only six weeks. Macrophytes did not respond as strongly as was expected on the basis of the results from the small-scale case studies (ch. 5). Most of the young pike died. However, from 1991 to 1993, the submerged vegetation has gradually changed. 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 within these areas and reduced mixing between (clear) water from vegetated areas and (turbid) water from non-vegetated areas. It is hypothesized that expansion of the *Chara* meadows might ultimately result in a shift of the whole lake to a long-lasting clear water state. In order to promote the *Chara*, the fish stock reductions, which aimed at a spring clear water phase, should be continued.

Guiding lake restoration and management (chapter 7)

The relationships between nutrient loading and shallow lake response are complex and tend to be different for the process of eutrophication and the reverse process of oligotrophication. The bottom line is that both clear water lakes and turbid water lakes resist changes in nutrient loading, showing the phenomenon of hysteresis. In shallow lakes of moderate productivity, the submerged vegetation plays a key role in stabilizing the clear water state. In turbid water lakes, algal blooms and particularly *Oscillatoria* blooms (resistant to low P and low light, reduced edibility for *Daphnia*), are self-reinforcing and therefore resistant to restoration efforts. Additionally, resuspension of sediments by wind and benthivorous fish may contribute to the stability of the turbid water state. Exceptional weather conditions or special actions ('switches') may trigger a shift from the one state into the other. The external nutrient loading should first of all be reduced in lake restoration. Furthermore, negative trends such as pollution with chemicals, toxic to *Daphnia* or macrophytes, should be reversed. The rehabilitation of lake-marginal wetlands will also contribute to a sustainable clear water state. However, as the turbid water state is extremely stable, additional measures may be necessary. Certain 'blockages' have to be removed to get the recovery process started:

(1) the Oscillatoria bloom

After external loading reduction, eliminating the *Oscillatoria* bloom should be the first priority in lake restoration. For many lakes it will be difficult to achieve TP < 20-50 mg m^{-3}, which is needed for a collapse of the bloom. Therefore, additional switches are needed. Washout by flushing during winter is a promising tool (flushing with at least three times the lake volume, during November-February).

(2) the bloom-mediated P release from the sediments

Manipulation of the carbonate system through flushing with water low in TP, but rich in Ca^{2+} and HCO_3^-, was successful in Veluwemeer. Sediment removal in the Dutch peat lake Geerplas failed to produce the desired results. Obviously, dredging is no panacea for solving problems of P release in shallow Dutch lakes. It seems wise to focus on external loading reduction and more appropriate in-lake measures.

(3) the abundance of fish, preventing Daphnia and macrophytes from developing

After fish stock reduction (> 75%) and clearing of the lake water, rapid colonization of submerged macrophytes has been demonstrated in small lakes (< 30 ha). In large lakes and particularly in networks of interconnected lakes the fish stock is more difficult to control. Additionally, in large lake areas the reestablishment of submerged vegetation takes more time. Winter fishing on a regular basis, rather than a single fishing operation, may be promising then. However, case studies are needed for further evaluation of the efficacy of repeated fishing for promoting *Daphnia.* Prerequisites for successful biomanipulation are low TP levels ($TP < 100$ mg m^{-3}, or higher TP levels for very small lakes) and low numbers of inedible algal species, such as *Oscillatoria.*

Samenvatting

In de jaren '50 en '60 veranderden vele ondiepe, Nederlandse meren en plassen van heldere wateren met veel ondergedoken waterplanten, in troebele wateren met veel zwevende algen. Eutrofiëring, dat is de verhoogde belasting met plantenvoedende stoffen (nutriënten, met name fosfaat en stikstof), is de belangrijkste oorzaak van deze verslechtering in waterkwaliteit. Andere verstoringen, zoals het voortgaande verlies van moerassige oeverlanden (filters voor nutriënten, habitat voor snoek) en de chemische verontreiniging met stoffen die giftig zijn voor het zoöplankton, hebben de effecten van eutrofiëring versterkt.

De strategie voor bestrijding van de eutrofiëringsproblemen concentreert zich op het terugdringen van de externe fosfaatbelasting. Hoewel deze aanpak op veel plaatsen heeft geleid tot lagere fosfaatgehalten, is de gewenste waterkwaliteit (in termen van helderheid, algensoorten, visstand e.d.) tot nu toe niet bereikt. Een bredere benadering van het eutrofiëringsprobleem waarin de relevante fysische, chemische en biologische factoren in samenhang worden bestudeerd, kan effectieve aanvullende maatregelen opleveren voor het ecologisch herstel.

Algenbloei (een hoge concentratie aan algen in het water) is het resultaat van hoge algenproductie, en tegelijkertijd lage algenverliezen. De algenproductie wordt behalve door de temperatuur en de beschikbaarheid van zonlicht, bepaald door de toevoer van nutriënten. Belangrijke verliesprocessen zijn de consumptie van algen door zoöplankton (vooral *Daphnia*, watervlooien), de bezinking van algen naar de bodem en de sterfte door bijvoorbeeld voedselgebrek of parasieten. In dit proefschrift richt de aandacht zich op beide zijden van de algenbalans: (1) de reductie van de externe en interne (vanuit de waterbodem) fosfaatbelasting en (2) de bevordering van de algenverliezen door watervlooien. De consumptie van algen kan worden vergroot door het uitdunnen van zoöplankton-etende (planktivore) vis. Brasem (*Abramis brama*) en blankvoorn (*Rutilus rutilus*) zijn de belangrijkste vissoorten in vele troebele Nederlandse meren. Grote brasem eet niet alleen watervlooien, maar ook macrofauna organismen die in het sediment leven (benthos). Uitdunnen van de benthos-etende (benthivore) vis leidt tot minder opwoeling van bodemslib, met als positieve gevolgen: minder vertroebeling, verlaagde interne fosfaatbelasting en minder verstoring van wortelende waterplanten. Visstandbeheer in het kader van het ecologisch herstel van meren en plassen wordt internationaal aangeduid als 'biomanipulation', en in Nederland ook als 'actief biologisch beheer'.

Ontwikkeling van de strategie voor ecologisch herstel (hoofdstuk 1)
De strategie voor ecologisch herstel van meren en plassen verbreedt zich geleidelijk van uitsluitend defosfatering op zuiveringsinstallaties tot een integrale en ecosysteem-gerichte benadering. In Nederland behoort fosfaatverwijdering uit afvalwater inmiddels tot de normale procedure en de polyfosfaten in wasmiddelen zijn grotendeels vervangen door

andere stoffen. De fosfaatgehalten in de oppervlaktewateren (incl. de Rijn) dalen, maar de algenbloei duurt nog voort. Aanvullende maatregelen richten zich nu vooral op de diffuse fosfaatbronnen, behandeling of verwijdering van fosfaatrijk sediment en op visstandbeheer. Andere knelpunten die aandacht verdienen, zijn het verlies aan moerassige oeverzones en lokaal de verontreiniging met toxische stoffen voor *Daphnia*.

Meren en plassen in Nederland: op zoek naar doelstellingen voor ecologisch herstel (hoofdstuk 2)

Wateren die niet of nauwelijks zijn beïnvloed door de mens, kunnen inzicht geven in de processen die bepalend zijn voor ecologische duurzaamheid. Historisch-ecologische studies leveren aanknopingspunten voor specifieke doelstellingen voor het herstel van meren en plassen. Voor een natuurlijke veenplas (Naardermeer) en twee verveningsgebieden (Reeuwijkse plassen en Oude Venen) is een referentiestudie uitgevoerd. Veel Nederlandse meren vertoonden een sterke verslechtering in waterkwaliteit in de jaren '50 en '60. De referentiestudie richtte zich vooral op de periode 1930-1950. In die periode waren alle drie plassengebieden helder en rijkbegroeid met ondergedoken waterplanten en oeverplanten. De stabiliteit van de helder water toestand was waarschijnlijk het grootst in het Naardermeer (een hoge diversiteit aan kranswiersoorten), met name door de aanvoer van voedselarm kwelwater uit 't Gooi. De belasting met voedingsstoffen van beide ander meren was hoger. De intensieve beroepsvisserij in de Reeuwijkse plassen (door 30 tot 50 families) en de optimale habitat voor snoek (*Esox lucius*) in de Oude Venen (door wisselende peilen en ondergelopen oeverlanden) speelden mogelijk een belangrijke rol voor de duurzaamheid van helder water in deze twee plassengebieden.

Eutrofiëringsenquêtes: relaties externe nutriëntenbelasting, nutriëntenconcentraties, fytoplankton en doorzicht (hoofdstuk 3)

'Multi-lake' studies, waarbij grote aantallen meren worden vergeleken, kunnen bijdragen aan de ontwikkeling van grenswaarden voor de eutrofiëringsbestrijding. De eerste CUWVO eutrofiëringsenquête omvatte ca. 65 meren voor de jaren 1976-1977, waarvan slechts 14 meren met betrouwbare balansgegevens. Latere enquêtes hadden betrekking op de periode 1983-1985 en 1980-1988. Volgens de empirische evenwichtsmodellen voor belasting in relatie tot concentratie, neemt het fosfaatgehalte evenredig (of 'iets minder' dan evenredig) af met de fosfaatbelasting. Doorzicht-chlorofyl (CHL) relaties en bovengrenzen voor chlorofyl in relatie tot TP, TN en onderwater lichtklimaat konden worden vastgesteld. Meren met een overmaat aan TP, vertonen een 'drempel' respons bij afnemende fosfaatbelasting: de algenbiomassa gaat pas omlaag wanneer TP de limitatie-lijn nadert: CHL = -24 + 1.04 TP (CHL en TP in mg m^{-3}). *Oscillatoria*-gedomineerde meren kunnen meer algenbiomassa per eenheid P produceren: CHL = 1.54 TP. Doelstellingen voor het doorzicht zijn afgeleid, (1) voor het bereiken van een lichtklimaat dat leidt tot instorting van de *Oscillatoria* bloei en (2) voor het realiseren van een lichtklimaat dat geschikt is voor het herstel van de ondergedoken waterplanten. Door de grote variatie in achtergrondstroebeling (non-algal turbidity) konden slechts bovengrenzen voor chlorofyl en TP worden aangegeven.

Case study Veluwemeer: doorspoelen met polderwater ter bestrijding van de *Oscillatoria* bloei en de interne fosfaatbelasting (hoofdstuk 4)

Vanaf 1971 werd het fytoplankton van het Veluwemeer (3356 ha, gemiddelde diepte 1.25 m) gekenmerkt door een vrijwel continue bloei van *Oscillatoria agardhii*. De externe fosfaatbelasting nam begin 1979 af van 2,7 tot 1,5 g P m^{-2} j^{-1}. De vooruitzichten op herstel waren echter slecht omdat de fosfaatbalansen in de zomermaanden een aanzienlijke fosfaatafgifte door het bodemslib lieten zien. Hoge zomerpieken in TP vielen samen met extreem hoge pH waarden (pH 9-10) en de hypothese was dat de *Oscillatoria* bloei zorgde voor een zichzelf instandhoudend proces van algenactiviteit, hoge pH, fosfaatafgifte en nog meer algenactiviteit. Winterdoorspoeling met polderwater uit Flevoland, dat arm is aan TP, maar rijk aan Ca^{2+} en HCO_3^-, zou deze vicieuze cirkel kunnen doorbreken. Het effect was spectaculair. Na de eerste winterdoorspoeling in 1979/80, was de pH in de zomer een volle eenheid lager. TP en chlorofyl *a* waren meer dan de helft lager. In de latere jaren was de algengroei gedurende de zomer in het algemeen P-gelimiteerd. Het doorzicht nam slechts toe van 0,20 m tot 0,30 m. De tegenvallende helderheid van het water kon worden verklaard door een afnemend chlorofylgehalte per eenheid van biovolume *Oscillatoria*. De cyanobacterie *Oscillatoria*, die een voorkeur heeft voor troebel water, verloor zijn dominante positie pas na de koude winter van 1984/85. Na de overgang van cyanobacteriën naar groenalgen nam het doorzicht in de zomer toe tot 0,40-0,50 m. Modelberekeningen tonen aan dat de fosfaatafgifte door het bodemslib in de zomermaanden was afgenomen van 1,0-8,4 tot 0,0-1,7 mg m^{-3} d^{-1}. De lagere pH waarden in de zomer kunnen worden verklaard door een verhoogde precipitatie van $CaCO_3$ in het voorjaar. Blijkbaar leidde de lagere pH tot een verminderde fosfaatafgifte door het bodemslib, met als gevolg P-gelimiteerde algengroei. Andere factoren die mogelijk hebben bijgedragen aan een betere fosfaatbinding aan het sediment zijn de verlaagde zuurstofvraag van de bodem (door minder bezinkende algen) en het door de doorspoeling verhoogde nitraatgehalte in het vroege voorjaar. Manipulatie van het carbonaatsysteem door doorspoeling met kalkrijk water, blijkt een effectieve methode te zijn voor het reduceren van de interne fosfaatbelasting. Gedurende de wintermaanden (november t/m februari) gedraagt de *Oscillatoria* populatie zich als een conservatieve stof (d.w.z. netto groei = 0). Een bloei van *Oscillatoria* in goed gemengde meren kan daarom effectief (> 95%) worden verwijderd door doorspoeling gedurende deze maanden, met een debiet van tenminste driemaal het meervolume.

Biomanipulatie in ondiepe meren: theorie, case studies en perspectieven (hoofdstuk 5)

Een grote visstand in algen-gedomineerde meren kan het herstel van de waterkwaliteit, na de reductie van de externe fosfaatbelasting, in de weg staan. In algen- en visrijke meren treedt de 'voorjaar helder water fase', veroorzaakt door grazende watervlooien, niet meer op. De efficient grazende, grote watervlooien komen onvoldoende tot ontwikkeling door zowel grote aantallen planktivore brasem en blankvoorn, als hoge dichtheden aan slecht eetbare draadvormige cyanobacteriën. Ondergedoken waterplanten spelen een sleutelrol bij het helder houden van het water, gedurende de zomer. Voor de ontwikkeling van deze vegetaties is het nodig dat de 'voorjaar helder water fase' weer wordt hersteld. Biomanipulatie, i.c. een drastische reductie van de visstand, kan een verschuiving op gang brengen van een stabiele toestand van troebel water naar een alternatieve, stabiele toestand van helder water. De toepasbaarheid en de perspectieven van biomanipulatie zijn getest door het evalueren van 9 case studies. Een eenmalige, substantiële reductie (> 75%) van de visstand, gedurende de winter, biedt goede kansen op helder water in het volgende voorjaar. Ongunstige factoren voor het 'opklaren' zijn een hoge dichtheid aan draadvormige cyanobacteriën en de mogelijke ontwikkeling van planktivore, invertebrate predatoren (*Neomysis, Leptodora*). De kleine meren (< 30 ha) lieten een snelle rekolonisatie door waterplanten zien, gevolgd door stabilisatie van de helder water toestand. Hoge nutriëntengehalten leiden uiteindelijk (twee gevallen, na respectievelijk 5 en 7 jaar) tot terugval naar de troebel water toestand. Top-down regulatie door roofvis (snoek en baars, *Perca fluviatilis*) lijkt te zijn beperkt tot kleine wateren met een hoge mate van 'randhabitat' (overgangen tussen begroeid en onbegroeid). Een alternatieve, stabiele helder water toestand kan worden verwacht bij TP = 50-100 mg m^{-3} (of hogere TP gehalten voor zeer kleine plassen). Omdat geleidelijk meer wateren in Nederland in de buurt komen van deze lage TP niveaus, nemen de kansen voor succesvolle biomanipulatie toe. In grote meren en vooral in netwerken van met elkaar verbonden meren, is het praktisch moeilijker om de visstand in een eenmalige actie drastisch te reduceren. Bovendien kost in grote meren de rekolonisatie door waterplanten meer tijd. Voor zulke wateren zou een reguliere wintervisserij (in plaats van een eenmalige bevissing) wellicht perspectieven kunnen bieden. Case studies zijn echter nodig voor beoordeling van de effectiviteit van dergelijke visserijen voor het succes van *Daphnia*.

Case study Wolderwijd: biomanipulatie ter bevordering van de door waterplanten gedomineerde, helder water toestand (hoofdstuk 6)

Vergelijkbaar met het Veluwemeer, werd het fytoplankton in het Wolderwijd-Nuldernauw (2555 ha, gemiddelde diepte 1,60 m) vanaf het begin van de jaren '70 gedomineerd door een bloei van *Oscillatoria*. Van 1981 tot 1984 is het meer (via het Veluwemeer) in de winter doorgespoeld met polderwater dat arm is aan TP, en rijk aan Ca^{2+} en HCO_3^-. Het resultaat was dat TP en chlorofyl *a* meer dan halveerden; het zomerdoorzicht nam toe van 0,20 m tot 0,30 m. Met als doel een verschuiving teweeg te brengen van een stabiele toestand van troebel water, naar een alternatieve stabiele toestand van helder water, is biomanipulatie toegepast in de winter 1990/91. De visstand, vnl. brasem en blankvoorn, is gereduceerd van ca. 205 tot 45 kg ha^{-1}. In mei 1991 werden 575.000 jonge snoekjes uitgezet (217 ind ha^{-1}). Om TP en *Oscillatoria* zoveel mogelijk te verlagen werd vanaf 1989 de doorspoeling geïntensiveerd. Na de visserij, in mei 1991, klaarde het water op als gevolg van graas door watervlooien (*Daphnia galeata*). De helder water fase duurde 6 weken. De waterplanten vertoonden niet de snelle respons, die werd verwacht op basis van de ervaringen in de kleine proefgebieden (hoofdstuk 5). De meeste uitgezette snoekjes zijn dood gegaan. De ondergedoken vegetatie in het meer veranderde echter wel geleidelijk. Kranswieren ontwikkelden zich van 28 ha in 1991 tot 438 ha in 1993. Het water boven de kranswiervelden bleef helder, waarschijnlijk als gevolg van toegenomen netto sedimentatie in de velden, en verminderde menging tussen het (heldere) water uit de begroeide delen en het (troebele) water uit de onbegroeide delen. Uitbreiding van de kranswiervelden zal uiteindelijk leiden tot een verschuiving van het gehele meer naar een stabiele helder water toestand. Voor de gewenste uitbreiding zal het waarschijnlijk nodig zijn om door middel van herhaalde uitdunningsvisserijen, weer een nieuwe 'voorjaar helder water fase' te creëren.

Aanbevelingen voor ecologisch herstel en beheer (hoofdstuk 7)
De relatie tussen nutriëntenbelasting en algenbiomassa is ingewikkeld, en bovendien verschillend voor het proces van eutrofiëring en het omgekeerde proces van oligotrofiëring. Zowel heldere meren, als troebele meren vertonen weerstand tegen veranderingen in de nutriëntenbelasting. Er is sprake van hysterese: pas bij relatief hoge (bij eutrofiëring), respectievelijk lage (bij oligotrofiëring) belastingen, vertoont het systeem een (discontinue) respons. In matig voedselrijke, ondiepe meren speelt de ondergedoken vegetatie een sleutelrol bij het stabiliseren van de helder water toestand. In troebele meren houdt de algenbloei, en met name de bloei van *Oscillatoria* (door lage P behoefte, lage lichtbehoefte en verminderde eetbaarheid) zichzelf in stand. De resuspensie van bodemslib door wind en benthivore vis in onbegroeide meren, draagt verder bij aan de stabiliteit van de troebel water toestand. Extreme weersomstandigheden of speciale maatregelen ('switches') kunnen een verschuiving teweeg brengen van de ene toestand naar de andere toestand. Voorwaarde voor duurzaam ecologisch herstel is de aanpak van de externe nutriëntenbelasting. Verder is het (lokaal) van belang om de negatieve invloed van toxische stoffen (voor watervlooien) terug te dringen en de ontwikkeling van moerassige oeverzones te bevorderen. Daar bovenop zullen vaak nog aanvullende acties nodig zijn om het herstel op gang te brengen. Bepaalde 'blokkades' moeten worden weggenomen:

(1) de Oscillatoria bloei
Na de reductie van de externe belasting zal het elimineren van de *Oscillatoria* bloei de hoogste prioriteit moeten krijgen. Voor vele meren is het praktisch onmogelijk om TP te reduceren tot < 20-50 mg m^{-3}, nodig voor het instorten van de *Oscillatoria* bloei. Aanvullende 'switches' zullen daarom nodig zijn. Doorspoelen in de winter (november t/m februari) met debieten van tenminste driemaal het meervolume is een effectieve maatregel.

(2) de door algenbloei geïnduceerde fosfaatafgifte
De manipulatie van het carbonaatsysteem door doorspoeling met water laag in TP en rijk aan Ca^{2+} en HCO_3^-, was effectief in het Veluwemeer. Het verwijderen van de bovenste sedimentlaag in de Geerplas was niet succesvol. Baggeren is kennelijk geen panacee voor problemen van fosfaatafgifte in ondiepe Nederlandse meren. Het verdient aanbeveling om de aandacht te concentreren op andere, meer geschikte middelen.

(3) de grote visstand die zorgt voor de onderdrukking van watervlooien
Uitdunning van de visstand (> 75%) blijkt in de kleine meren (< 30 ha) te leiden tot helder water en een snelle kolonisatie door waterplanten. Rekolonisatie in grote meren verloopt trager. In grote meren en vooral in netwerken van met elkaar verbonden wateren zal een drastische uitdunning moeilijk te realiseren zijn. Minder drastische, maar reguliere visserijen kunnen dan effectief zijn. Case studies zijn nodig voor verdere evaluatie van dergelijke visserijen. Voorwaarden voor succesvolle biomanipulatie zijn lage TP (< 100 mg m^{-3}, of hogere TP gehalten in zeer kleine plassen) en lage aantallen slecht eetbare algensoorten, als *Oscillatoria*.

Met dank aan

"..En wanneer ga jij nou eens promoveren?.." vroeg professor Bert Lijklema mij terloops, vlak voor hij moest optreden als sessie voorzitter bij de IAWQ conferentie 'Living with Water' (Amsterdam, september 1994). Druk als ik toen was als programmaleider van die conferentie, ontging het mij even. Maanden later spraken wij af dat ik de 'rode draad' zou aangeven in mijn twintigjarige loopbaan bij het RIZA. Het was even zoeken, maar op 19 mei 1995 luidde het kommentaar: '..Het ziet er goed uit, je kunt aan de slag..'. Bert, dank voor je initiatief, je hebt heel wat losgemaakt. Onze inhoudelijke sessies waren pittig, maar ook gezellig en stimulerend. Paul Boers kent het klappen van de zweep (hij promoveerde in 1991 bij Lijklema) en ik heb dankbaar van zijn ervaringen gebruik kunnen maken. Paul, trouw heb je al mijn concepten doorgeworsteld. Je was kritisch, constructief en snel en je had er ook nog plezier in. De RIZA 'lake restoration' groep: Marie-Louise Meijer, Marten Scheffer, Eddy Lammens, Egbert van Nes, Diederik van der Molen, Hugo Coops, Aart Griffioen, Paul Boers, Carolien Breukers, André Breukelaar (tot 1 april 1994), Winfried Laane en Hendrik Buiteveld, bedank ik voor de samenwerking in een werk-sfeer als 'onder vrienden'. Roel Doef bedankt, je was mijn partner in PR. Vlak buiten het RIZA waren het vooral Ellen van Donk, Ramesh Gulati, Map Grimm, Lex Raat, Jo van der Vlugt en Lowie van Liere die mij op het goede spoor hielden. Iets verder weg Erik Jeppesen, Brian Moss, Dennis Cooke, Joe Shapiro, Steve Carpenter en vele anderen. Al in 1975 zei Shapiro: '..*we should treat lakes as ecosystems, rather than containers of algae and phosphorus*..'. Deze boodschap leidde in 1984 tot de opdracht voor een uitgebreide literatuurstudie aan het Limnologisch Instituut (Bert Richter en Koos Vijverberg). Samen met Geert van Urk, die helaas veel te vroeg is overleden, heb ik deze studie begeleid. Bert Steinmetz wil ik bedanken, want hij bracht mij in augustus 1985 in contact met de praktische visbiologen Map Grimm en Lex Raat, toen nog allebei werkzaam bij de Organisatie ter Verbetering van de Binnenvisserij. In datzelfde jaar waren Eric Jagtman en ik al begonnen met de eerste voorbereidingen voor de afvissing van het Wolderwijd. Eric verhuisde later naar de beheersdirectie (toen Directie Flevoland) en zorgde ervoor dat het ook inderdaad ging gebeuren. Marie-Louise zette het begeleidend onderzoek op poten. Sikko Parma en Joost de Jong lanceerden het idee voor een internationale conferentie over biomanipulatie. Deze conferentie 'Biomanipulation, tool for water management' (Amsterdam, augustus 1989) betekende een enorme impuls voor het onderzoek en het internationale netwerk. Mijn vele bazen dank ik voor het vertrouwen en de ruimte die ik kreeg voor eigen initatief. Ik noem de eerste en de huidige: Jan Koolen, dank voor je rust en inspiratie; Eric Marteijn, dank voor je steun en open houding. Joost de Jong, algemeen directeur van het RIZA (tot 1 februari 1997), wil ik bedanken voor zijn interesse in onze projecten en voor de geboden gelegenheid om dit proefschrift af te ronden. Een 'brononderzoeker' als ik, kan niet zonder de discussies met de praktische deskundigen uit het waterbeheer. Bedankt voor de zomer '96 gesprekken: Klaas Everards, Winnie Rip, Jaap Hofstra, Liz van Duin, Bart van der Veer, Linda Frinking, Wim Oosterloo, Jan-Arie van Berkum, Bert Moonen, Theo Claassen, Ruurd Maasdam en Roelof Veeningen.

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Over de auteur

Zijn passie voor helder water ontwikkelde Harry Hosper (Soest, 17 juni 1947) tijdens een praktijkstage op het Limnologisch Instituut van de Universiteit van Lund (Zweden) in 1970. In Zweden waren de effecten van eutrofiëring uitstekend waar te nemen. Schone, heldere meren (met tevreden aanwonenden) komen voor, direct naast benedenstrooms gelegen vervuilde meren met algenbloei (en boze aanwonenden). De samenwerking met Sven Björk en vele anderen in het later beroemd geworden 'Lake Trummen Restoration Project', was voor hem zeer inspirerend. Na afronding van zijn studie Waterzuivering aan de Landbouwhogeschool trad Hosper in dienst van het Rijksinstituut voor Zuivering van Afvalwater (RIZA) te Voorburg, met als speciale opdracht de beleidsvoorbereiding rond de eutrofiëringsproblematiek. Hij was trekker van de beide eerste CUWVO eutrofiëringsenquêtes (1976 en 1980) en actief betrokken bij de opstelling van de eerste beleidsnota over de eutrofiëringsbestrijding (Fosfatennota, 1979). De resultaten van de enquêtes vormden de basis voor de normstelling voor doorzicht, chlorofyl en meststoffen in latere beleidsnota's (IMP 1980-1984; IMP 1985-1989). In het begin van de jaren '80 drong het inzicht door dat alleen defosfatering van afvalwater vaak onvoldoende is voor ecologisch herstel. Hosper schetste de contouren voor een bredere aanpak in 'Aanbevelingen voor bestrijding van de eutrofiëring van de Nederlandse oppervlaktewateren' (CUWVO, 1983). In deze nota introduceerde hij het 'actief biologisch beheer', een variant op het begrip 'biomanipulation' van Joseph Shapiro (1975). Vanaf 1985 trad Hosper op als themaleider en kreeg de 'lake restoration' groep van het RIZA geleidelijk meer gestalte. Praktijkexperimenten werden opgezet, naast onderzoek gericht op theorievorming en modellering. Kennisoverdracht vond plaats zowel naar de wetenschappelijke tijdschriften, als naar de beleidsvoorbereiding en de regionale waterbeheerders. In 1987 publiceerden Hosper, Meijer & Jagtman in H_2O het met de NVA-prijs bekroonde artikel 'Actief biologische beheer, nieuwe mogelijkheden voor het herstel van meren en plassen'. Een jaar later ging de promotiefilm Actief Biologisch Beheer van Henk de Koning (regie) en Harry Hosper (scenario) in première. Een internationaal congres onder de titel 'Biomanipulation, tool for water management' werd georganiseerd te Amsterdam (Artis, augustus 1989), samen met onder meer het Limnologisch Instituut. In 1992 verscheen de praktische Handleiding Actief Biologisch Beheer, met Marie-Louise Meijer en Paddy Walker als co-auteurs. Hosper sprak regelmatig als 'invited speaker' op internationale congressen, onder meer van de Universiteit van Helsinki (1991, 1993), de American Society of Limnology and Oceanography (ASLO, 1993), de North American Lake Management Society (NALMS, 1994) en het Japanse Ministry of Construction (Tsukuba, 1994).