



Bio-manipulation in shallow lakes in The Netherlands: an evaluation of 18 case studies

Marie-Louise Meijer¹, Ingeborg de Boois¹, Marten Scheffer², Rob Portielje¹ & Harry Hoser¹

¹*Institute of Inland Water Management and Waste Water Treatment, P.O. Box 17, 8200 AA Lelystad, The Netherlands*

²*Agricultural University, Department of Aquatic Ecology and Water Quality Management, P.O. Box 9101, 6700 HB Wageningen, The Netherlands*

Key words: bio-manipulation, shallow lakes, fish stock reduction, macrophytes, *Daphnia* grazing

Abstract

Eighteen shallow lakes in The Netherlands were subjected to bio-manipulation, i.e. drastic reduction of the fish stock, for the purpose of lake restoration. The morphology and the nutrient level of the lakes differed, as did the measures applied. In some lakes bio-manipulation was accompanied by reduction of the phosphorus loading. In all but two lakes, the Secchi disk transparency increased after the fish removal. Eight lakes (no phosphorus loading reduction, except for one lake) showed a strong and quick response to the measures: the bottom of the lake became visible ('lake bottom view') and there was a massive development of submerged macrophytes. In eight other lakes the water transparency increased, but lake bottom view was not obtained. In the bio-manipulated lakes the decrease in total phosphorus and chlorophyll *a* and the increase in Secchi disk transparency were significantly stronger than the general trend occurring in Dutch lakes where no measures had been taken. The improvement in the Secchi depth and chlorophyll *a* was also stronger than in lakes where only the phosphorus load was reduced. The critical factor for obtaining clear water was the extent of the fish reduction in winter. Significant effects were observed only after >75% fish reduction. Success seems to require substantial fish manipulation. In such strongly bio-manipulated lakes, wind resuspension of the sediment never prevented the water from becoming clear. No conclusion can be drawn with respect to the possible negative impact of cyanobacteria or *Neomysis* on grazing by *Daphnia* and consequently on water clarity. In all lakes where there had been a high density of cyanobacteria or years with a high density of *Neomysis* other factors such as insufficient fishery may explain why lake bottom view was not obtained. In all lakes with additional phosphorus loading reduction the fish stock has been reduced less drastically (15–60%). In these lakes the effects on transparency were less pronounced than in the lakes with > 75% fish removal. *Daphnia* grazing seems responsible for spring clearing in all clear lakes but one. In three lakes the reduction of benthivorous fish also increased the transparency. The factors that determine water clarity in summer are less obvious. In most clear lakes a low algal biomass coincided with a macrophyte coverage of more than 25% of the lake surface area. However, it was not clear what mechanism caused the low algal biomass in summer, although inorganic nitrogen concentrations were regularly found to be very low. *Daphnia* grazing in open water seemed to be of little importance for suppressing the algal biomass in summer. Although in most lakes the total phosphorus concentration decreased after the bio-manipulation, the dissolved phosphorus concentration remained too high to cause phosphorus limitation of the algal growth. In four out of six clear lakes for which there are long-term data the transparency decreased again after 4 years. In one lake with lower nutrient levels the Secchi disk transparency increased over the years. However, the number of lakes with low nutrient levels is too small for conclusions to be drawn regarding the impact of nutrient levels on the stability of the clear water state.

Introduction

Bio-manipulation as a possible method of lake restor-

ation was introduced by Shapiro in 1975 (Shapiro et al., 1975). It is only in the past ten years that the technique of bio-manipulation has become more gener-

ally applied in water quality management (Carpenter & Kitchell, 1993; Hansson et al., 1999; Meijer et al., 1994; Hosper, 1997; Jeppesen, 1998; Perrow et al., 1997; Philips & Moss, 1994; Van Berkum et al., 1995). The first experiments with biomanipulation were performed in relatively deep lakes (Benndorf et al., 1984; Carpenter & Kitchell, 1993) and were concerned with the removal of all fish with rotenon or with stocking of predatory fish (Benndorf et al., 1988; Henrickson et al., 1980; Shapiro & Wright, 1984). In The Netherlands, biomanipulation measures usually involve the substantial reduction of planktivorous and benthivorous fish in shallow lakes. A reduction of the overwintering planktivorous fish stock cause large filter-feeding zooplankton to exert a higher grazing pressure on phytoplankton, thus forcing a spring clear water phase. Reduction of benthivorous fish further supports the clearing of the lake, as the resuspending of the sediment and the release of nutrients in the water due to these bottomfeeders will be reduced (Breukelaar et al., 1994; Havens, 1993). Clear water during spring allows the submerged vegetation to grow and creates a sustainable clear water state. Stocking of the lakes with pike fingerlings (*Esox lucius* L.) may help to reduce the young-of-the-year fish during summer. In The Netherlands, the first biomanipulation experiments were conducted in 1986 in small drainable ponds of 0.1 ha, where the impact of 0+ fish on zooplankton was investigated (Meijer et al., 1990a). Since 1987 experiments have also been carried out in natural lakes and ponds (Driessen et al., 1993; Meijer et al., 1990b; Van der Vlugt et al., 1992; Van Donk et al., 1990). Later, guidelines were formulated for the assessment of chances for clear water and macrophytes, based on the results of nine biomanipulation cases (Hosper & Meijer, 1993). Five out of these nine cases were successful: in those five lakes biomanipulation led to clear water and a rich submerged vegetation (Hosper, 1997). Several factors may prejudice successful biomanipulation in the other cases: insufficient fish reduction, wind-induced resuspension, inedible cyanobacteria and predation of *Daphnia* by invertebrates (Hosper, 1997; Hosper & Meijer, 1993).

The number of projects involving biomanipulation, whether or not accompanied by P load reduction, has increased considerably during the past 10 years. In this paper we evaluate the results of 18 cases, which differ in morphology, nutrient level and the measures applied. We compare the effect of biomanipulation with the effects of phosphorus loading reduction in

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

Sites studied

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

Methods

Zooplankton

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

Table 1. Lake characteristics

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

*Fish migrated into the lake directly after biomanipulation.

** Only large fish, percentage removal of small fish is unknown, total fish removal <75%.

¹Additional fish removal in later years.

d, dredging; f, flushing; i, isolation; p, reduction external phosphorus load.

2.52 ln(L) (Bottrell et al., 1976), L being the length in mm.

In six lakes the length of *Daphnia* was measured, in other lakes only data on the species composition of *Daphnia* were available. Here, the following average lengths per species were assumed: *Daphnia magna* (2.75 mm), *Daphnia cucullata* (0.8 mm), *Daphnia*

longispina/pulex (1.5 mm), *Daphnia hyalina/galeata* (1.0 mm). Although Schriver et al. (1995) used the total biomass of *Daphnia* and *Bosmina*, we used only the biomass of *Daphnia*, because in the observed lakes the potential grazing pressure of *Bosmina* and copepods was negligible compared to that of *Daphnia* (Meijer & de Boois, 1998). Because of expected dif-

ferences between spring and summer, we considered the periods May–June and July–September separately. In The Netherlands the highest *Daphnia* density and the highest transparency are generally found in May–June.

Macrophytes

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

Fish

Long-term quantitative data on fish biomass and species composition were available for only six lakes. In this paper the data on total fish biomass, benthivorous fish, piscivorous fish and biomass of 0+ fish are presented. In Noorddiep, Galgje and Zwemlust the fish biomass was estimated in December/January with a mark-recapture method (Meijer et al., 1995). In Lake Waay, Wolderwijd and Duinigermeer the biomass was estimated with a catch per unit effort method in September/October (Grimm & Backx, 1994).

Perch > 0+ and all pike and pikeperch were assumed to be predatory fish. The biomass of 0+ fish is based on the estimation of the young-of-the-year (YOY) fish at the end of the growing season (in September or December).

Trend analysis

Trends for biomanipulation cases were compared with the general development in the water quality in 160 lakes where no measures were taken. Also trends in lakes in which specific phosphorus reduction measures had been taken but no biomanipulation had been applied were compared with the general trend (Portielje & van der Molen, 1999).

Trend analysis was performed for lakes for which there were at least 8 years of data. The Mann–Kendall test was used for the trend analysis. In this non-parametric test the trend is estimated by the median of the set of the slopes (Theil slope estimator, Theil, 1950; KIWA, 1994) that are calculated from all possible pair-wise combinations of the summer mean

Table 2. Average of Secchi depth (summer mean) after the measures divided by the average Secchi depth before the measures

| | |
|-----------------------------|-----|
| <i>Successful</i> | |
| Zwemlust | 9.4 |
| Waay | 2.6 |
| Noorddiep 3 | 2.6 |
| Duinigermeer | 2.2 |
| IJzeren Man | 8.4 |
| Bleiswijkse Zoom; Galgje | 3.3 |
| Wolderwijd | 8.4 |
| Zuidlaardermeer | 1.6 |
| <i>Partially successful</i> | |
| Nanneviid | 1.6 |
| Boschkreek | 1.7 |
| Hollands Ankeveense Plas | 1.5 |
| Oude Venen: 40-Med | 2.5 |
| Oude Venen: Tusken Sleatten | 1.5 |
| Oude Venen: Izakswiid | 1.6 |
| Klein Vogelenzang | 1.4 |
| Sondelerleien | 1.4 |
| <i>Failures</i> | |
| Breukeleveense Plas | 1.1 |
| Deelen | 1.2 |

Successful, >1.3 and bottomview; partially successful, >1.3, no bottom view; failures, <1.3.

concentrations. An effect of measures can be calculated if data are available for at least 2 years before and 2 years after the measures. The instantaneous effect of a measure is thus incorporated in the calculated trend. Sufficient data were available from eight biomanipulation cases (Figure 1). In Hollands Ankeveense Plas extra phosphorus reduction measures were taken, but they did not lead to a decrease in the phosphorus concentration in the lake in the observed period of biomanipulation. The analysis was based on relative trends, where a relative trend was defined as the absolute trend divided by the historical means.

Results

Transparency

In all but two lakes the Secchi depth improved after the measures. The extent of the improvement differed from lake to lake (Figure 1, Table 2). Before the measures the average Secchi depth was ca. 0.2–0.4 m. After the measures lake bottom view was achieved in eight

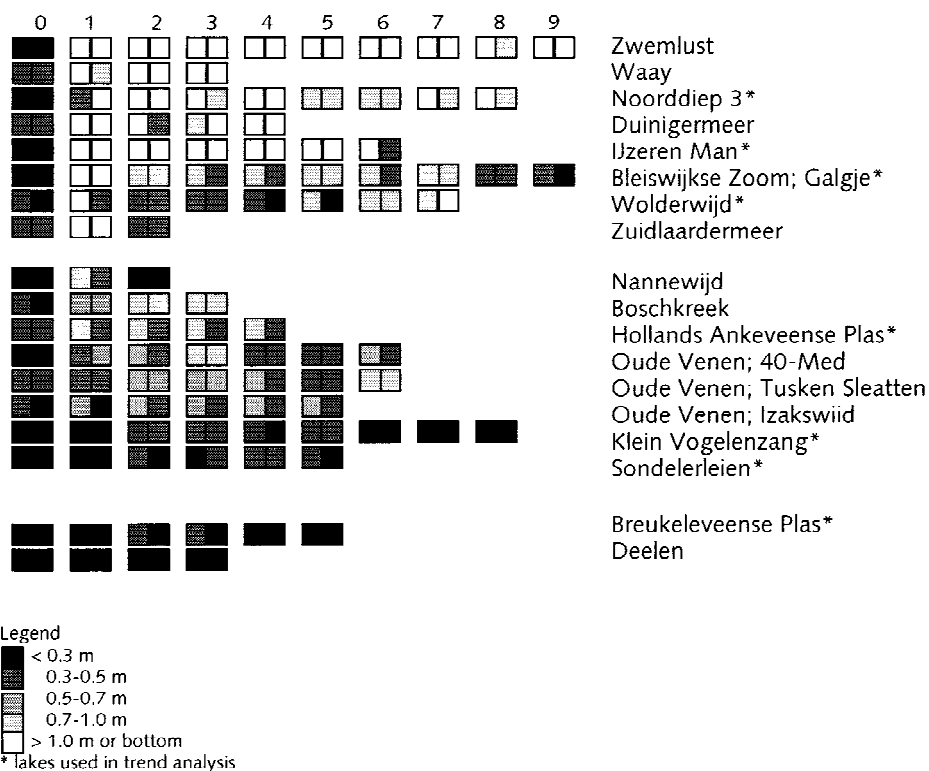


Figure 1. Secchi depth in all lakes in years after biomanipulation (first square is average of May–June, second square is average of July–September).

lakes. In those lakes the biomanipulation is called successful. In five of these eight lakes, the bottom view was achieved in the spring directly after the fish removal. In the other lakes the process took several months (Platform Ecologisch Herstel Meren, 1997). In Lake Wolderwijd in the first year the water remained clear only for about 6 weeks in May–June (Meijer & Hosper, 1997), but 6 years later the Secchi depth remained high (>1 m) during the summer. In most lakes with long-term data the average Secchi depth starts to decrease after 3–4 years, with the exception of Lake Wolderwijd where the Secchi depth starts to increase after 5 years (Figure 2). In the lakes with lake bottom view the Secchi depth improved considerably (60–800%). In eight other lakes the transparency improved also (40–150%), but the lake bottom did not become visible. In those lakes the biomanipulation is called partially successful. The Secchi depth often reached 0.5–0.9 m in spring, but decreased in summer. In two lakes (Deelen and Breukeleveense Plas) there was no significant improvement in water transparency (improvement <25%) (Figure 1, Table 2).

Chlorophyll a

In 13 out of 18 lakes the chlorophyll *a* concentration decreased. In lakes with bottom-view the summer average chlorophyll *a* concentration generally became lower than $15 \mu\text{g l}^{-1}$ (Figure 3). In the lakes where the Secchi depth improved without lake bottom view the chlorophyll *a* concentration was often low in spring (May–June) but increased from July onwards. In Klein Vogelenzang and Sondelerleijen the chlorophyll *a* concentration remained quite high, despite improvement of the Secchi depth.

Daphnia

In general the *Daphnia* biomass increased slightly after the measures (Figure 3). In one lake (Noorddiep) there was a decrease of the *Daphnia* biomass (Meijer et al., 1990b). However, the potential grazing pressure (PGP) became larger after the measures due to a simultaneous reduction in algal biomass in most lakes. The highest PGP was found in lakes with the highest Secchi depth (Figure 4). In all lakes with bottom view the PGP is high in May–June and decreases

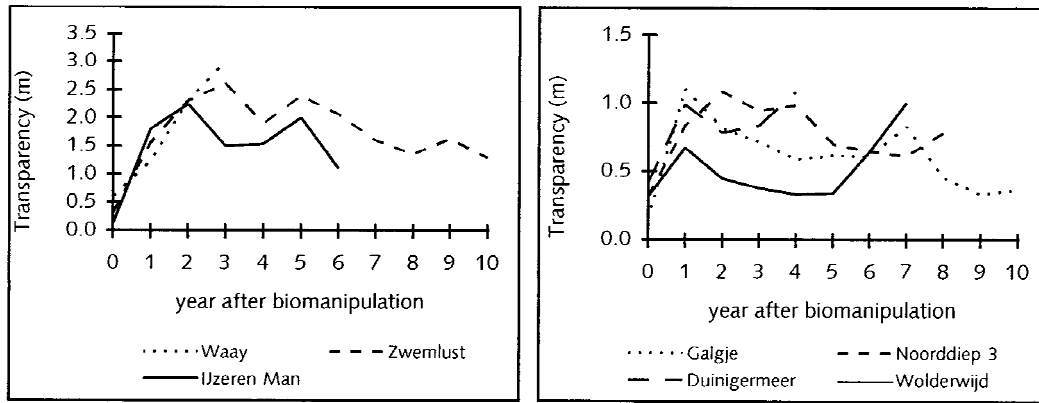


Figure 2. Summer mean Secchi depth in seven successfully biomanipulated lakes.

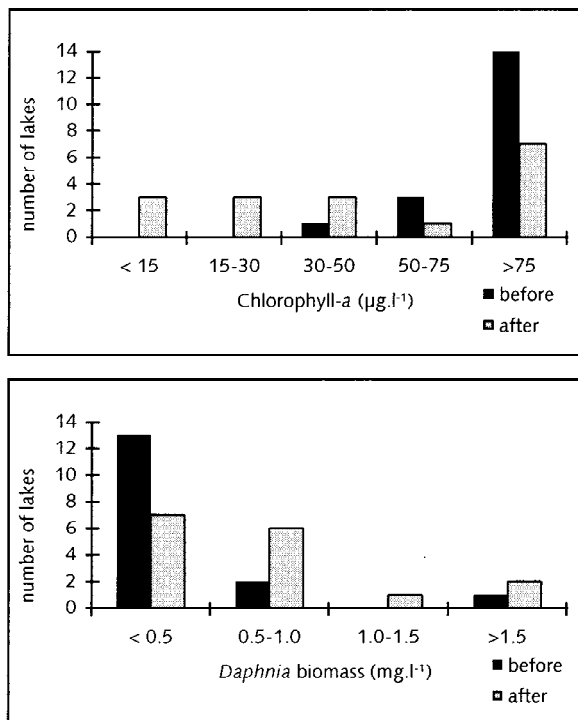


Figure 3. Distribution of summer average chlorophyll *a* concentration and summer average *Daphnia* biomass before and after the measures.

in July–September. Only in three out of 16 lakes with zooplankton data could a high PGP of *Daphnia* also be found in summer.

Both the chlorophyll *a*: total-P ratio ($P < 0.01$) and the chlorophyll *a*: total-N ratio ($P < 0.001$) were significantly lower at a PGP of *Daphnia* of $>1.0 \text{ day}^{-1}$ compared to lower potential grazing pressures (Figure 5).

Macrophytes

In all eight lakes with bottom view macrophytes developed. The colonization by Characeae was very rapid. In three small lakes (Galgje, IJzeren Man, Duinigermeer) more than 50% of each lake was colonized within 2 months. In the large Lake Wolderwijd it took 3 years for 40% of the lake to become covered with dense vegetation. The species composition of the macrophytes changed from a dominance of *Potamogeton* sp. to a dominance of *Chara* sp. In Zwemlust and Noorddiep *Chara* hardly developed at all, but species like *Elodea* sp. and *Ceratophyllum* sp. colonized the lake more gradually (Figure 6). In Zuidlaardermeer the macrophytes developed during the first 2 years in very low densities (<15%). In the third year densities of more than 20% were found at 80% of the surface area. In Noorddiep submerged macrophytes developed only in the shallow part of the lake (ca. 45% of the lake surface).

In the lakes without bottom view macrophytes occurred after the biomanipulation only in Hollands Ankeveense Plas (25% of the lake surface area); in all other lakes macrophytes remained absent. The chlorophyll *a*:total-P ratio seems to be lower when > 25% of the surface area of the lake is covered with macrophytes ($P < 0.001$). The chlorophyll *a*:total-N ratio seems to become lower with decreasing abundance of macrophytes (Figure 7), as is found in a comparable analysis of a larger data set (Portielje & van der Molen, 1999). A strong decrease is found at a coverage of >25% (Figure 7) ($P < 0.001$).

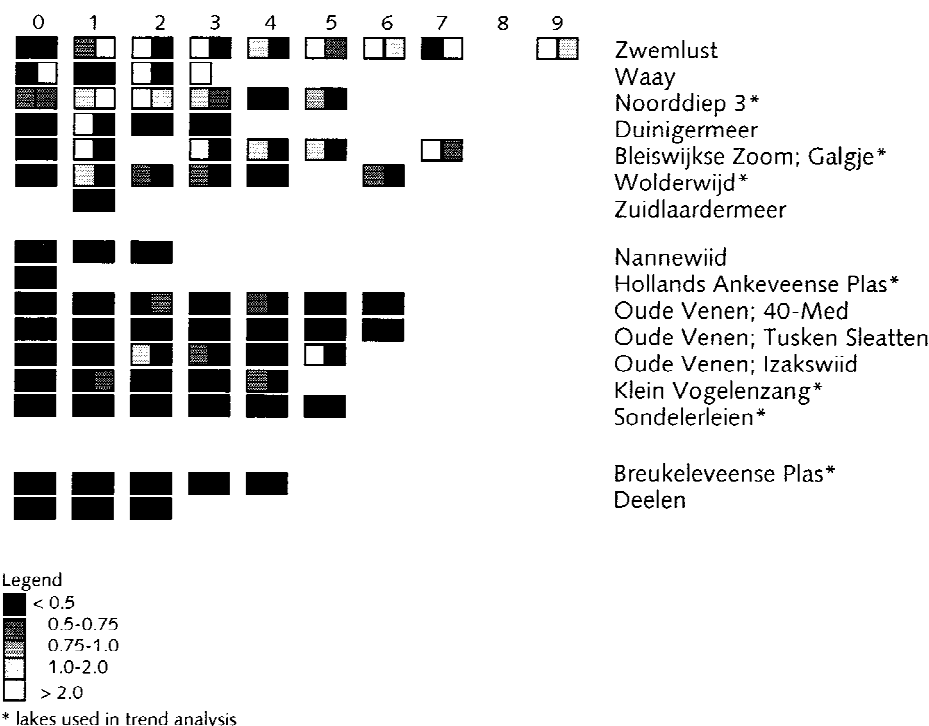


Figure 4. Potential grazing pressure (PGP) of *Daphnia* in years after biomanipulation (first square is average of May–June, second square is average of July–September).

Fish

In two out of six lakes with long-term fish data the fish biomass gradually decreased after the fish reduction (Waay, Wolderwijd), whereas in all other lakes the fish stock increased (Figure 8). In Zwemlust and Noorddiep the increase seemed to stabilize at a level of about half the original biomass. The biomass of 0+ fish is high ($> 100 \text{ kg ha}^{-1}$) in Zwemlust and Bleiswijkse Zoom/Galgje, and in the first year in the Waay. In the other lakes the biomass of YOY fish remains below 40 kg ha^{-1} . The biomass of 0+ fish seems to increase after the measures, whereas the benthivorous fish stock is reduced. The percentage of predatory fish is low in all lakes except in the first years in lake Zwemlust from which all fish had been removed and only pike and rudd had been stocked.

Trend analysis

In the biomanipulation cases a significantly stronger decrease in concentrations of phosphorus ($P < 0.05$) and chlorophyll *a* ($P < 0.05$) and increase in Secchi depth ($P < 0.01$) was found compared to the general trend occurring in lakes where no specific measures

had been taken (Figure 9). Although the total-N concentration decreased in most biomanipulation cases, the decrease was not significantly stronger (at $P < 0.1$) than the general trend. Lake-specific measures that reduced the phosphorus load led only to a significantly stronger decrease in the total-P concentration ($P < 0.01$) compared to the general trend, but not with respect to transparency, chlorophyll *a* and total-N (Van der Molen & Portielje, 1999). Strong decreases in total-P were found in lakes with biomanipulation, whereas an additional P-reducing measure (dredging) was applied only in one biomanipulated lake.

Discussion

How does successful biomanipulation work?

In all lakes with successful biomanipulation the algal biomass dropped to very low levels, leading to a strong increase in transparency. In only three lakes had benthivorous fish been a major cause of turbidity (Table 3). In those lakes more than 150 kg/ha of benthivorous fish had been removed, which led to a reduction in the resuspended sediment (Havens,

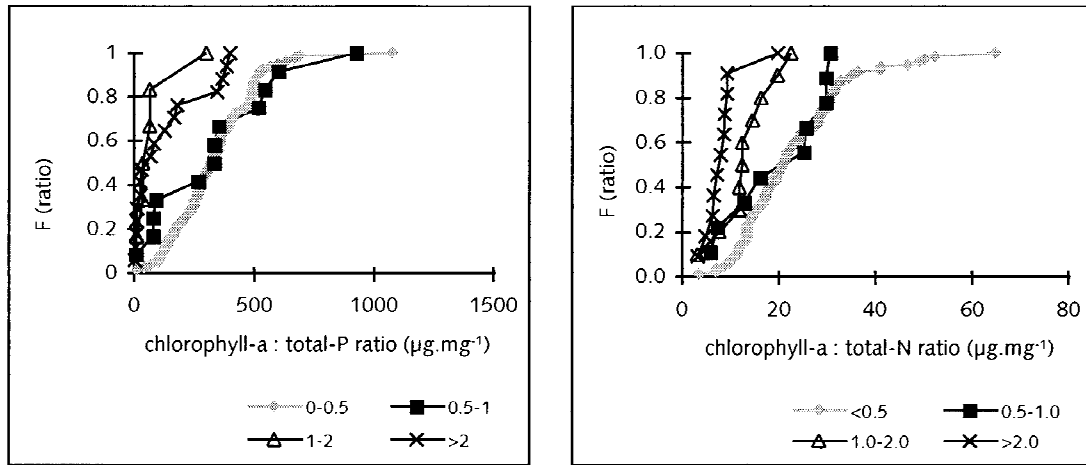


Figure 5. Impact of the potential grazing pressure on the chlorophyll *a*:nutrients ratio. *F* (ratio) is the distribution function of the chlorophyll *a*:nutrients ratio).

1993; Meijer et al., 1990a). In the other lakes the benthivorous fish stock was relatively low before the measures.

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

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

In spring the potential grazing pressure (PGP) of *Daphnia* was high in almost all clear lakes, indicating that *Daphnia* is an important initiator of the spring clearing of the water (Table 3). The biomass of *Daphnia* did not always increase after the measures, possibly because the food for *Daphnia* became limited when the algal biomass dropped to low levels. The PGP, however, is a better criterion than *Daphnia* biomass for determining the possible impact of *Daphnia* on algae. Also low dissolved nitrogen concentrations were found regularly in spring (Table 3). This suggests nitrogen limitation of the algal growth, but it is not conclusive because part of the nitrogen may have been recycled.

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

Macrophytes are considered to be important for keeping the water clear in summer. Macrophytes generally appeared quite rapidly after the clearing of the

lake. Only in lake Zuidlaardermeer, the Waay and Lake Wolderwijd did it take 3 years to get a substantial macrophyte growth. Our results show a strong reduction in the chlorophyll *a*:nutrients ratio at a coverage of >25% of the lake surface area. This corresponds to the reduction in algal biomass found in Denmark at a PVI (plant volume infested) of 20% (Schriver et al., 1995; Sondergaard & Moss, 1997). In the Danish experiments zooplankton grazing seems to be the major mechanism involved. However, it is not clear which mechanisms cause the increase in transparency or the reduction in the algal biomass in the presence of macrophytes in the Dutch lakes. Several mechanisms are possibly involved, e.g. increased sedimentation and reduced resuspension of the sediment (Scheffer, 1998; Van den Berg et al., 1997), which provide refuge for zooplankton (Moss, 1990), competition with algae for nutrients, especially nitrogen (Ozimek et al., 1990; Van Donk et al., 1993) and allelopathy (Wium-Anderson et al., 1982). We have no data on increased sedimentation or reduced resuspension in the lakes studied, but these aspects were shown to be important in *Chara* meadows in lake Veluwe, which is comparable to Lake Wolderwijd in many respects (Van den Berg, et al., 1997). In the early biomanipulation cases an increase in macrophytes coincided with a decrease in total nitrogen (Zwemlust, Galgje, Noorddiep) (Meijer et al., 1994; Scheffer, 1998). In those lakes N-limitation could be confirmed with bioassays (Meijer et al., 1990b; Van Donk et al., 1993). In the other successful biomanipulation cases low dissolved nitrogen concentrations occurred regularly too, but

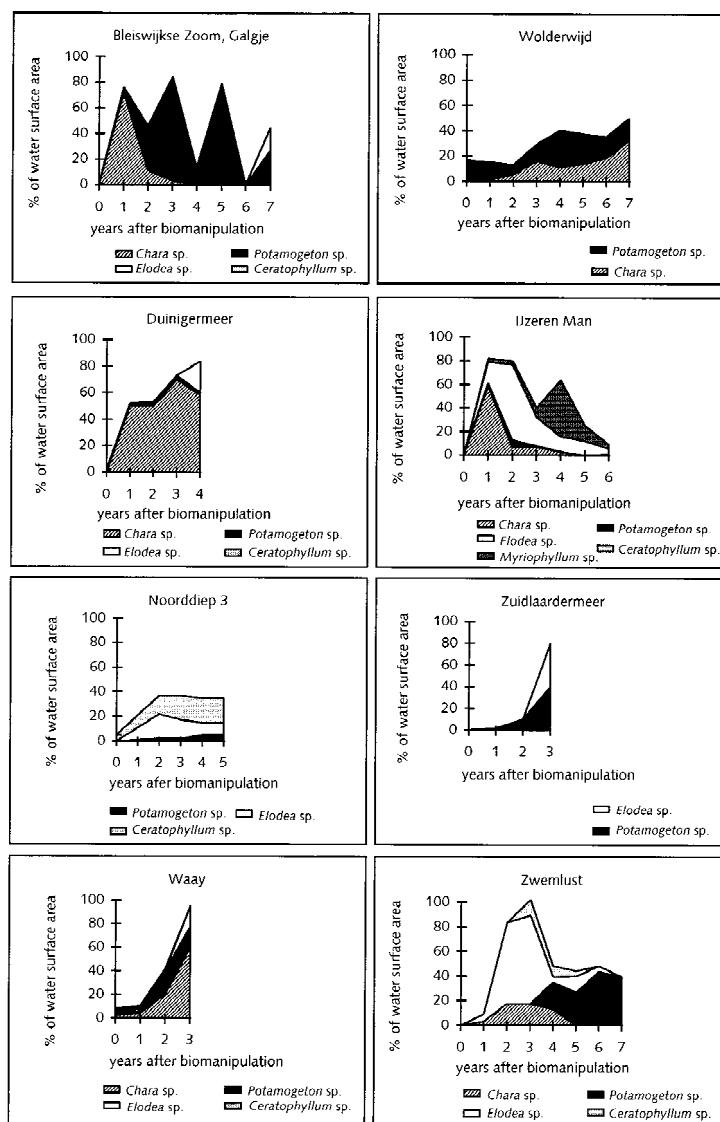


Figure 6. Abundance and species composition of macrophytes in eight successfully biomanipulated lakes.

this does not necessarily imply nitrogen limitation of the algal growth.

Although in most lakes the total-P concentration decreased, the dissolved-P concentration never reached very low values, except in lake Wolderwijd. Thus phosphorus limitation of the algal growth is unlikely to have played a role in the cases studied.

Our results suggest that in summer *Daphnia* grazing is not really important (Table 3). This is not in line with the dominant role of zooplankton in Danish lakes (Jeppesen et al., 1997; Schriver et al., 1995). This discrepancy may be due to a better sampling method for

zooplankton in Denmark, where the sampling is often done during the night. In The Netherlands, sampling of zooplankton is carried out during the day. *Daphnia* is difficult to sample in daytime particularly in clear water, since the species tend to hide against predation of fish near the bottom and between the macrophytes (Lauridsen & Buenk, 1996; Schriver et al., 1995). Often the sampling for zooplankton in Dutch lakes is carried out in the open water only, and consequently zooplankton densities may have been underestimated. Also macrophytes associated zooplankton (e.g. *Simocephalus*, *Sida*, *Eurycercus*) are not sampled, so the

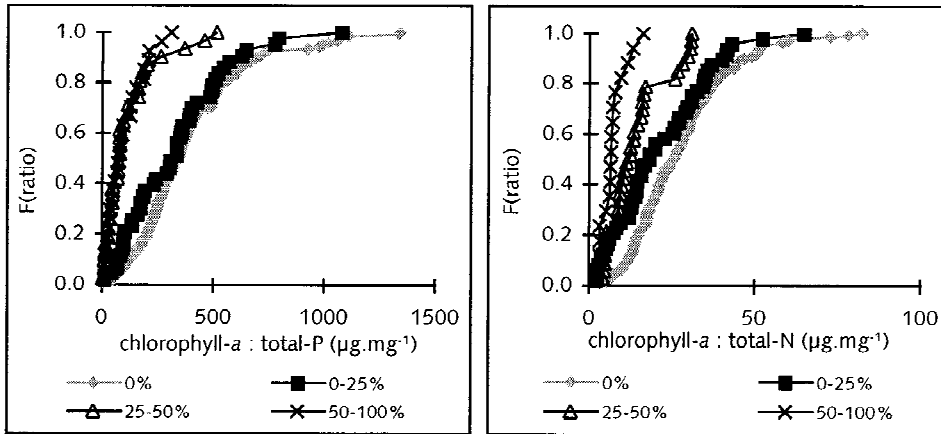


Figure 7. Impact of a high coverage of macrophytes on the chlorophyll a:nutrients ratio. *F*(ratio) is the distribution function of the chlorophyll a:nutrients ratio.

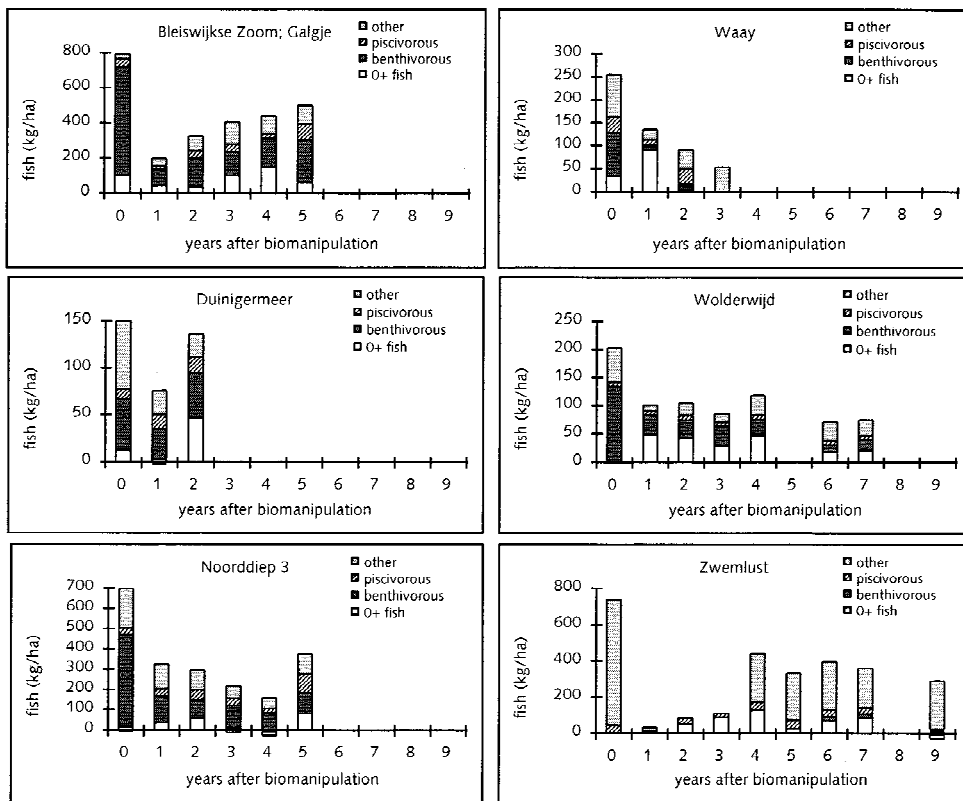


Figure 8. Development of the fish community in six lakes.

impact of these zooplankton species among the macrophytes is not known. No data were available on allelopathic effects.

An evaluation of 20 biomanipulation cases in the USA and Europe had led to the conclusion that in many cases the increased water clarity could not be

related to increased zooplankton grazing (De Melo et al., 1992). They suggested that the results are often a consequence of changes in the nutrient levels due to the fish removal. Also for lake Pohjalampi it was suggested that the high transparency in the lake after fish reduction was caused not by increased *Daphnia*

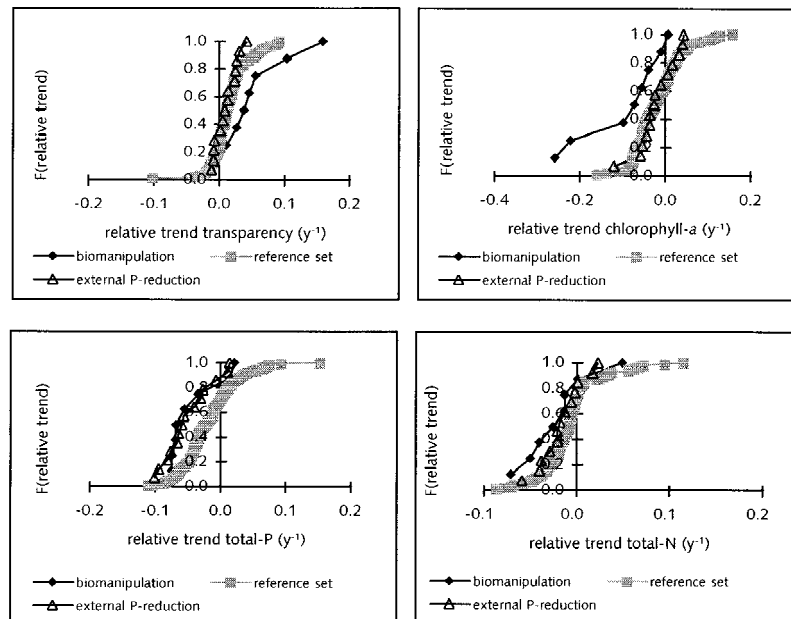


Figure 9. Comparison of trends in Secchi depth, nutrients and chlorophyll *a* in manipulated lakes (biomanipulation or reduction of the phosphorus load) with lakes without measures.

grazing, but by a reduction in nutrient due to the removal of benthivorous fish (Karjalainen pers. comm.). However, most observations on the impact of *Daphnia* were based on *Daphnia* biomass, whereas the potential grazing pressure is a better instrument for determining the impact of *Daphnia* on algae. Our results show that in spring *Daphnia* grazing is important. No conclusions can be drawn from our results with regard to nitrogen limitation, but phosphorus limitation of the algal growth does not seem to be important. However, the decrease in total nutrient concentrations confirm the idea that the change in nutrient fluxes due to the manipulation of the food chain may play a role in the success of the biomanipulation (Carpenter et al., 1992; Jeppesen, 1998).

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

In the 10 lakes without lake bottom view, the goal of high transparency and macrophytes was not achieved, but only the two lakes where no improvement of the transparency was found at all can be called real failures. The eight lakes where an improvement of the transparency was found, but no bottom view and no macrophytes occurred, are not fully successful, but cannot be regarded as complete 'failures'. As we have seen in Lake Wolderwijd a relatively small increase in transparency may lead in the shallow parts of the

lake to a development of macrophytes and clear water (Meijer & Hosper, 1997). The part with macrophytes and clear water may gradually expand and after a number of years the whole system may change to a clear water system (Figure 2).

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

(i) Insufficient fish removal (Carpenter & Kitchell, 1992; Hosper & Meijer, 1993)

Substantial (more than 75%) reduction of the fish stock is thought to be important for getting clear water in spring. This drastic reduction should take place in one winter and no fish must be able to migrate into the lake afterwards.

(ii) Presence of peat (Portielje & van der Molen, in press)

In lakes with peaty sediment a high transparency may be hard to achieve, because of the presence of a higher back-ground (non-algal, humic) turbidity.

(iii) High wind resuspension (Hosper & Meijer, 1993)

When a lake is turbid because of resuspension of the sediment by wind, it may be difficult to get clear water by biomanipulation. The criteria for high windresuspension are based on fetch in prevailing wind direction

(WSW-ENE in the Netherlands), water depth and absence/presence of sandy bottom.

(iv) *High surface area* (Benndorf, 1995; Reynolds, 1994)

A lower chance of high transparency in large lakes may occur because of higher susceptibility to wind resuspension and because drastic fishery may be more difficult to achieve in larger lakes.

(v) *High nutrient concentration* (Benndorf, 1995; Reynolds, 1994; Jeppesen et al., 1990)

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

(vi) *High density of cyanobacteria* (Gliwicz, 1990; Hosper & Meijer, 1993)

At densities of cyanobacteria of $> 80\,000$ ind/ml *Daphnia* may not be able to consume the algae and reproduction of *Daphnia* may be reduced.

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

A 75% reduction in the fish stock seems critical for achieving lake bottom view. In fact, in all but two instances the percentage of fish removal may explain which cases are successful and which are not (Figures 10 & 11). Other evaluations have also shown that substantial (more than a 75%) fish reduction is required for success (Hansson et al., 1999). Nonetheless, some comments can be made concerning the other 'risk factors' too:

A high Secchi depth is rarely achieved in lakes with *peaty sediment* (Figure 10), but we cannot conclude that this has hampered recovery, since these lakes also appear to have been subjected to a relatively low fish reduction (Table 1). In The Netherlands a drastic fish stock reduction is generally more difficult to achieve in peaty sediment than in other lakes, as peat digging created many small canals and ditches where small fish can concentrate during winter and escape the fish nets.

Resuspension by wind did not prevent a high transparency in the lakes with $>75\%$ fish stock reduction (Figure 10, Table 4). Resuspension by wind occurred

before the measure was taken in Zuidlaardermeer, Duinigermeer and, to a lesser extent, in lake Wolderwijd, but this did not prevent the lakes from becoming clear. In Zuidlaardermeer the construction of a large enclosure (75 ha) reduced the wind resuspension (Torenbeek & de Vries, 1997), whereas in lake Duinigermeer wind resuspension was decreased by an explosive growth of *Chara* (Van Berkum et al., 1995).

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

A logistic regression showed no significant relation between the occurrence of bottom view and *the total-P concentration*. Jeppesen et al. (1990) stated that biomanipulation is best carried out in lakes with a phosphorus concentration of $<0.08-0.15$ mg P l⁻¹. This may guarantee the stability of the clear water state, but it is probably not necessary for achieving clear water (Fig. 10).

No relation was found between occurrence of bottom view and *surface area* of the treated lakes either (Figure 10). After analysing 33 biomanipulation cases all over Europe and the USA Reynolds (1994) concluded that the best chances for successful biomanipulation are in lakes covering an area of <4 ha. This is not confirmed in this study.

A *high density of cyanobacteria* seems to reduce the chances of lake bottom view (Figure 10). However, in all lakes with a high density of cyanobacteria an insufficient fish reduction may also explain the lack of lake bottom view (Table 4). In Lake Breukeleveen not only insufficient fish stock reduction and a high density of cyanobacteria, but also the presence of *Leptodora*, and resuspension of the sediment by wind could have prevented the clearing of the water (Van Donk et al., 1990b; Table 4). In Klein Vogelenzang the increase in transparency was probably due not only to the high density of cyanobacteria, but also to insufficient fish reduction. In winter 1990 when the young fish migrated from the lake, the blue-green algae disappeared (after a high peak of *Bosmina*) *Daphnia*

Table 3. Mechanisms that keep the water clear

| | benthic fish reduction >150 kg ha ⁻¹ | May–June | | | July–September | | | |
|--------------------|---|----------------|----------------------------|-----------------------------|----------------|----------------------------|-----------------------------|------------------|
| | | grazing | diss. N | ortho P | grazing | diss. N | ortho P | macro- phytes |
| | | press. >1.0 | <0.1 mg l ⁻¹ | <0.01 mg l ⁻¹ | press. >1.0 | <0.1 mg l ⁻¹ | <0.01 mg l ⁻¹ | >25% |
| Zwemlust | • | ○ | ○ | • | ∅ | ∅ | • | ○ |
| Waay | | ○ | ○ | • | • | ∅ | • | ○ |
| Noorddiep 3 | ○ | ∅ | ○ | • | • | ∅ | • | ○ |
| Duinigermeer | • | • | • | • | • | • | ∅ | ○ |
| IJzeren Man | ○ | | ○ | • | • | ∅ | • | ○ |
| Bleisw. Z.; Galgje | ○ | ○ | ∅ | • | • | ∅ | • | ○ |
| Zuidlaardermeer | • | ∅ | • | • | • | • | • | • |
| Wolderwijd | • | ○ | • | • | • | ○ | • | ∅ |

benthivorous fish reduction > 150 kg ha⁻¹ ○, yes; ∅, •, no
for the other criteria ○ > 60 ∅ 30–60 • 0–30 % of clear period that the criterion is valid.

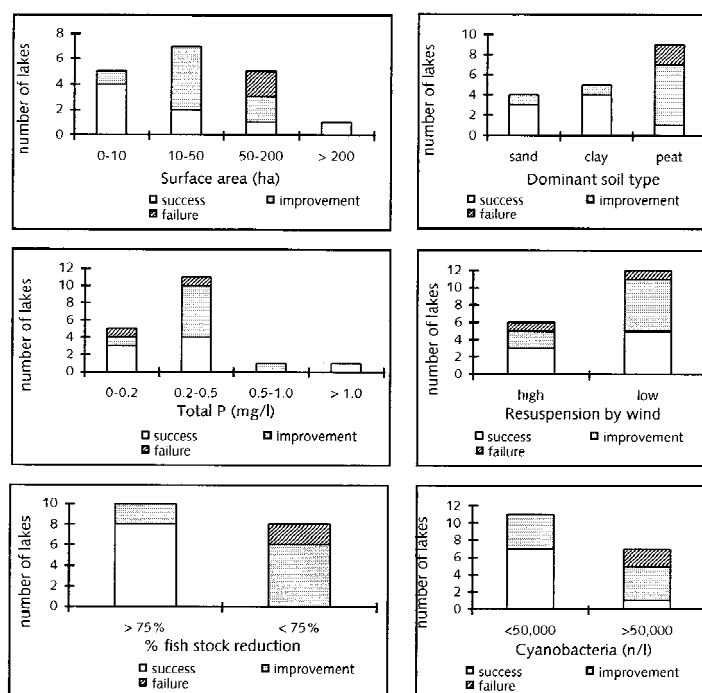


Figure 10. Occurrence of bottom view in relation with surface area, phosphorus level, sediment type, cyanobacteria abundance, wind resuspension and fish reduction.

came up and the water became clear. However, the clear water phase did not last long, and the water became turbid again during the growing season when the fish returned to the lake (Van der Vlugt et al., 1992).

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

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

In two lakes (Izakswiid and Sondelerleien) the water remained relatively turbid, despite a fairly substantial fish reduction. In Izakswiid the 75% limit was only just met (76%) and probably the lake did not clear completely, because the remaining fish consisted ex-

Table 4. Factors which might prejudice successful biomanipulation (after the name of the lake the years which have been taken into consideration)

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

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

L: *Leptodora* instead of *Neomysis*
 * reduction >75%, but fish immigration

clusively of small planktivorous fish. This case shows that it is best to reduce considerably more than 75% of the original fish stock, (especially of planktivorous fish). In Sondelerleien the turbidity of the water was caused not by algae, but by resuspended matter, probably coming from the inflow of turbid water. The lake had a very short retention time (< 20 days) and the inflow water contained very high concentrations of suspended matter (Claassen & Maasdam, 1995). In this lake it is likely that biomanipulation will never lead to clear water. This is in line with the idea of Reynolds (1994), namely that success of biomanipulation is higher in lakes with a long residence time.

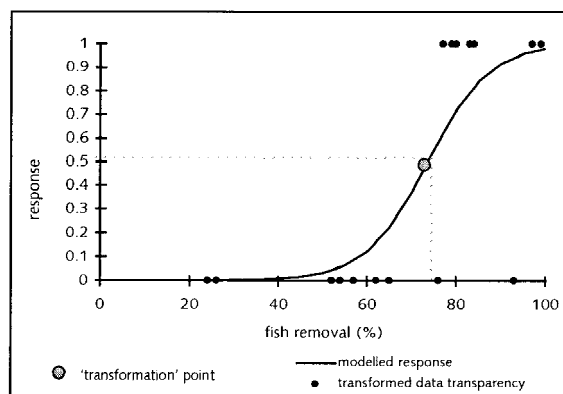


Figure 11. Logistic regression on percentage of fish reduction and the occurrence of bottom view.

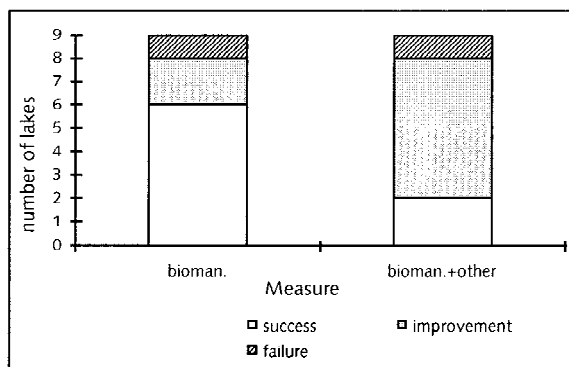


Figure 12. Occurrence of bottom view in relation to additional measures.

In the present set of cases bottom view was found more often in lakes where only biomanipulation had been carried out than in lakes where additional phosphorus reduction measures had been applied as well (Figure 12). This was probably caused by the relatively low fish reduction in the lakes where phosphorus reduction measures had been taken prior to the biomanipulation measures. Biomanipulation probably received less attention in these lakes than in lakes where it was applied as the only measure.

What factors determine long-term stability?

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

(a) In the present study in almost all lakes with long term results the *Secchi depth* decreased over the years, but after 6 years the *Secchi depth* was still 5–8 times higher than before the measures were taken. In only one lake (Wolderwijd) did the *Secchi depth* gradually increase. This was related to the gradual increase in the abundance of *Characeae* in this lake (Meijer & Hoesper, 1997). In the first year the transparency was only high above the *Chara*, but in later years the area with *Chara* and clear water expanded dramatically and the whole system changed. The nutrient concentra-

tions decreased dramatically, more mussels appeared and the fish composition changed (Lammens, Perrow & Meijer, unpubl. results).

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

(c) The biomass of 0+ *fish* after the measures is high in most hypertrophic (total-P concentration >0.25 mg P/l) lakes (>100 kg ha⁻¹), but lower in lakes with lower nutrient concentrations (Waay, Duinigermeer and Wolderwijd, Table 1). Noorddiep is an exception in that it has a relatively high phosphorus concentration and a relatively low 0+ fish biomass, which may be caused by a relatively good foraging conditions for pike (Meijer et al., 1995; Walker, 1994).

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

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

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

centrations. The current results, however, do point to a deterioration at higher nutrient concentrations.

The signs of stability chosen in the earlier work (Meijer et al., 1994) are related mainly to fish and Secchi depth. Later results have shown that the presence of macrophytes is probably even more important for stability than the presence of piscivorous fish. In our study we found that when more than 25% of the lake surface is covered with submerged macrophytes the algal biomass is repressed by the macrophytes. In almost all successfully biomanipulated lakes we found a strong decline in overall macrophyte abundance several years after the manipulation (Figure 7). However, the species composition of the macrophytes community may also be important. *Chara* can keep the water clear for a long period during the year, but for example *Potamogeton bertholdii* may die off early in the summer, and will cause turbid water again in August (Van Donk & Gulati, 1995). The species composition of the macrophytes was not stable in all lakes (Figure 6). It seems that a higher instability is found in lakes with a high phosphorus concentration, but more research needs to be done on this aspect.

Conclusions

Biomanipulation can be a very effective method for increasing the transparency of the water in a lake. In The Netherlands 90% of the biomanipulation cases resulted in an improvement in water transparency.

The greatest improvement was found in lakes with the highest fish stock reduction. All but two successes could be attributed to drastic fish stock reduction.

The improvement in Secchi depth and chlorophyll *a* concentrations in biomanipulated lakes is stronger than in lakes where only phosphorus reduction measures were taken.

Clear water in spring is probably caused by *Daphnia* grazing, whereas in summer *Daphnia* grazing in open water is not important. Low nitrogen concentrations occurred, but nitrogen limitation of the algal growth could not be proved. Macrophytes that covered more than 25% of the surface area coincided with low algal biomasses.

Despite high nutrient levels, after more than 5 years the Secchi depth is still much higher than before the measures, although the transparency is decreasing.

Acknowledgements

We want to thank all Dutch water quality managers and researchers from the Dutch Platform on Lake Restoration who let us evaluate their data relating to their restoration projects: D. de Vries (Provincial Water board of Groningen) and R. Torenbeek (Waterboard of Drenthe) for data on Zuidlaardermeer; E. Van Donk (NIOO) and P. Heuts (Waterboard Stichtse Rijnlanden) for data on Lake Zwemlust; Y. van Scheppingen (Waterboard 3 Ambachten) for data on the Boschkreek; E. Van Donk (NIOO) for data on Lake Breukerveen; T. Claassen (Waterboard Fryslan) for data on Lake Deelen, Sondelerleien and the Oude Veenen; R. Veenigen (Waterboard of Fryslan) for data on Lake Nanneiid; I. Barten (Waterboard Rijn & IJssel) for data on Lake de Waay; Y. Scheffer-Ligtermoet (Watermanagement and Sewage Service) for data on Lake Hollands Ankeveense Plas; O. Driessen & M. Talsma (Waterboard Limburg) for data on Lake IJzeren Man; J.A. Van Berkum (Waterboard of Groot Salland) for data on Lake Noorddiep and Lake Duinigermeer; G. de Jong (Waterboard of Schieland) for data on Lake Bleiswijkse Zoom; F. Zant (Directorate IJsselmeer area) for data on Lake Wolderwijld; Van der Vlugt (Institute for Public Health and Environment) and B. van der Veer (Waterboard of Rijnland) for data on Lake Klein Vogelenzang. We also want to thank T. Mehner for his useful suggestions for the improvement of the manuscript.

References

- Barten, I., 1997. De Waay. In I. de Boois, T. Slingerland & M-L. Meijer (eds), Actief Biologisch Beheer in Nederland, Projecten 1987-1996, Institute for Inland Water Management and Waste Water Treatment, Lelystad, report 97.084: 145-152.
- Benndorf, J., 1995. Possibilities and limits for controlling eutrophication by biomanipulation. *Int. rev. ges. Hydrobiol.* 80: 519-534.
- Benndorf, J., H. Kneschke, K. Kossatz & E. Penz, 1984. Manipulation of the pelagic food web by stocking with predacious fishes. *Int. Rev. ges. Hydrobiol.* 69: 407-428.
- Benndorf, J., H. Schultz, A. Benndorf, R. Unger, E. Penz, H. Kneschke, K. Kossatz, R. Dumke, U. Hornig, R. Kruspe & S. Reichnel, 1988. Food-web manipulation by enhancement of piscivorous fish stocks: long-term effects in the hypertrophic Bautzen reservoir. *Limnologica* 19: 97-110.
- Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygiered, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larsson & T. Weglenska, 1976. A review of some problems in zooplankton production studies. *Norw. J. Zool.* 24: 419-456.
- Breukelaar, A. W., E. H. R. R. Lammens & J. G. P. Klein Breteler, 1994. Effects of benthivorous bream (*Abramis brama*) and carp

- (*Cyprinus carpio*) on sediment resuspension and concentrations of nutrients and chlorophyll *a*. *Freshwat. Biol.* 32: 113–121.
- Carpenter, S. R. & J. F. Kitchell, 1992. Trophic cascade and biomanipulation: interface of research and management: a reply to the comment by De Melo et al. *Limnol. Oceanogr.* 37: 208–213.
- Carpenter, S. R. & J. F. Kitchell, 1993. *The Trophic Cascade in Lakes*. Cambridge University Press: 386 pp.
- Carpenter, S. R., K. L. Cottingham & D. E. Schindler, 1992. Biotic feedbacks in lake phosphorus cycles. *TREE* 7: 332–336.
- Claassen, T. H. L., 1994. Eutrophication and restoration of a peat ponds area, De Deelen, in the northern Netherlands. *Verh. int. Ver. Limnol.* 25: 1329–1334.
- Claassen, T. H. L., 1997. Ecological water quality objectives in The Netherlands especially in the province of Friesland. *Eur. Wat. Poll. Control* 7: 36–45.
- Claassen, T. H. L. & M. Clewits, 1995. Actief Biologisch Beheer in de Sondelerleien: een meer met een korte verblijftijd. *H₂O* 28: 805–808.
- Claassen, T. H. L. & R. Maasdam, 1995. Restoration of the broad-area Alde Feanen, The Netherlands: measures and results. *Wat. Sci. Tech.* 31: 229–233.
- De Melo, R., R. France & D. J. McQueen, 1992. Biomanipulation: hit or myth? *Limnol. Oceanogr.* 37: 192–207.
- Driessen, O., P. Pex & H. H. Tolcamp, 1993. Restoration of a lake: First results and problems. *Verh. int. Ver. Limnol.* 25: 617–620.
- Grimm, M. P. & J. J. G. M. Backx, 1990. The restoration of shallow eutrophic lakes and the role of northern pike, aquatic vegetation and nutrient concentration. *Hydrobiologia* 200/201: 557–566.
- Grimm, M. P. & J. J. G. M. Backx, 1994. Mass-removal of fish from lake Wolderwijd (2700 ha), The Netherlands. Part I: Planning and strategy of a large scale biomanipulation project. In Cowx, I. G. (ed.), *Rehabilitation of Freshwater Fisheries*, Fishing News Books, Hull, UK: 390–400.
- Gliwicz, Z. M., 1990. Why do cladocerans fail to control algal blooms? *Hydrobiologia* 200/201: 557–566.
- Henrikson, L., H. G. Nyman, H. G. Oscarson & J. A. Stenson, 1980. Trophic changes without changes in the external nutrient loading. *Hydrobiologia* 68: 257–263.
- Hansson, L.-A., H. Annadotter, E. Bergman, S. F. Hamrin, E. Jeppesen, T. Kairesalo, E. Luokkanen, P. Å. Nilson, M. Søndergaard, 1999. Biomanipulation as an application of food chain theory: constraints, synthesis and recommendations for temperate lakes. *Ecosystems* 1: 13–23.
- Havens, K. E., 1993. Responses to experimental fish manipulations in a shallow, hypertrophic lake: The relative importance of benthic nutrient cycling and trophic cascade. *Hydrobiologia* 254: 73–80.
- Hosper, Harry, 1997. *Clearing Lakes. An ecosystem approach to the restoration and management of shallow lakes in The Netherlands*. Thesis, Agricultural University, Wageningen: 168 pp.
- Hosper, S. H. & M.-L. Meijer, 1993. Biomanipulation, will it work for your lake. A simple test for the assessment of chances for clear water, following drastic fish-stock reduction in shallow eutrophic lakes. *Ecol. Eng.* 2: 63–72.
- Jeppesen, E., 1998. The ecology of shallow lakes, trophic interactions in the pelagial. D.Sc. Thesis, NERI Tech. Report no. 247, Silkeborg, Denmark, 420 pp.
- Jeppesen, E., J. P. Jensen, P. Kristensen, M. Søndergaard, E. Mortensen, O. Sortkjær & K. Olrik, 1990. Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes 2: threshold levels, long-term stability and conclusions. *Hydrobiologia* 200/201: 219–227.
- Jeppesen, E., T. Lauridsen, T. Kairesalo & M. R. Perrow, 1997. Impact of submerged macrophytes on fish-zooplankton interactions in lakes. In Jeppesen, E., M. Søndergaard, M. Søndergaard & K. Christoffersen (eds), *The structuring role of submerged macrophytes in lakes*. Ecological Studies. Springer Verlag, New York: 91–115.
- KIWA, 1994. A protocol for trend analysis of the input of pollutants to the North Sea. SWO 93.337, 46 pp.
- Lauridsen, T. L. & I. Bøenck, 1996. Diel changes in the horizontal distribution of zooplankton in the littoral zone of two shallow eutrophic lakes. *Arch. Hydrobiol.* 137: 161–176.
- Meijer, M.-L. & S. H. Hosper, 1997. Effects of biomanipulation in the large and shallow Lake Wolderwijd, The Netherlands. *Hydrobiologia* 342/343: 355–349.
- Meijer, M.-L. & I. de Boois, 1998. Actief Biologisch Beheer in Nederland. Evaluatie Projecten 1987–1996. Institute for Inland Water Management and Waste Water Treatment, Lelystad, report 98.023: 140 pp.
- Meijer, M.-L., E. H. R. R. Lammens, A. J. P. Raat, M. P. Grimm & S. H. Hosper, 1990a. Impact of cyprinids on zooplankton and algae in ten drainable ponds. *Hydrobiologia* 191: 275–284.
- Meijer, M.-L., M. W. de Haan, A. W. Breukelaar & H. Buitenveld, 1990b. Is reduction of the benthivorous fish an important cause of high transparency following biomanipulation in shallow lakes? *Hydrobiologia* 200/201: 303–315.
- Meijer, M.-L., E. H. R. R. Lammens, A. J. P. Raat, J. G. P. Klein Breteler & M. P. Grimm, 1995. Development of fish communities in lakes after biomanipulation. *Neth. J. aquat. Ecol.* 29: 91–101.
- Meijer, M.-L., E. Jeppesen, E. van Donk, B. Moss, M. Scheffer, E. Lammens, E. van Nes, J. A. van Berkum, G. L. de Jong, B. A. Faafeng & J. P. Jensen, 1994a. Long-term responses to fish stock reduction in small shallow lakes: interpretation of five-year results of four biomanipulation cases in The Netherlands and Denmark. *Hydrobiologia* 275/276: 457–466.
- Meijer, M.-L., E. H. R. R. Lammens, R. D. Gulati, M. P. Grimm, J. J. G. M. Backx, P. Hollebeek, E. M. Blaauw & A. W. Breukelaar, 1994b. The consequences of a drastic fish reduction in the large and shallow lake Wolderwijd, The Netherlands. Can we understand what happened? *Hydrobiologia* 275/276: 31–42.
- Moss, B., 1990. Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. *Hydrobiologia* 200/201: 367–377.
- Ozimek, T., R. D. Gulati & E. van Donk, 1990. Can macrophytes be useful in biomanipulation of lakes? The Lake Zwemlust example. *Hydrobiologia* 200/201: 399–407.
- Perrow, M. R., M.-L. Meijer, P. Dawidowicz & H. Coops, 1997. Biomanipulation in shallow lakes: state of the art. *Hydrobiologia* 342/343: 355–365.
- Persson, L. & L. B. Crowder, 1997. Fish-habitat interactions mediated via ontogenetic shifts. In Jeppesen, E., M. Søndergaard, M. Søndergaard & K. Christoffersen (eds), *The structuring role of submerged macrophytes in lakes*, Ecological Studies. Springer Verlag, New York: 3–24.
- Platform Ecologisch Herstel Meren, 1997. Actief Biologisch Beheer in Nederland. In de Boois, I., T. Slingerland & M.-L. Meijer (eds), *Projecten 1987–1996*. Institute for Inland Water Management and Waste Water Treatment, Lelystad, report 97.084: 184 pp.
- Philips, G. & B. Moss, 1994. Is biomanipulation a useful technique in lake management? National Rivers Authority, UK, R&D note 276: 48 pp.
- Portielje, R. & D. van der Molen, 1999. Relationships between eutrophication variables: from nutrient loading to transparency. *Hydrobiologia*, 408/409: 375–387

- Reynolds, C. S., 1994. The ecological basis for successful biomanipulation of aquatic communities. *Arch. Hydrobiol.* 130: 1–33.
- Scheffer, M., 1998. Ecology of shallow lakes. In *Population and Community Biology Series 22*. Chapman & Hall, London: 357 pp.
- Scheffer-Ligtermoet, Y., 1997. Holland Ankeveense Plas. In de Boois, I., T. Slingerland & M.-L. Meijer (eds), *Actief Biologisch Beheer in Nederland, Projecten 1987–1996*. Institute of Inland Water Management and Waste Water Treatment, Lelystad, report 97.084: 73–81.
- Schriver, P., J. Bogestrand, E. Jeppesen & M. Søndergaard, 1995. Impact of submerged macrophytes on fish–zooplankton interactions: large-scale enclosure experiments in a shallow lake. *Freshwat. Biol.* 33: 255–270.
- Shapiro, J. & Wright, D. I., 1984. Lake restoration by biomanipulation: Round Lake Minnesota, the first two years. *Freshwat. Biol.* 14: 371–383.
- Shapiro, J., V. Lamarra & M. Lynch, 1975. Biomanipulation: an ecosystem approach to lake restoration. In Brezonik, P. L. & J. L. Fox (eds), *Proceedings of a symposium on water quality management through biological control*. Univ. of Florida, Gainesville: 85–96.
- Søndergaard, M. & B. Moss, 1997. Impact of submerged macrophytes on phytoplankton in shallow freshwater lakes. In Jeppesen, E., M. Søndergaard, M. Søndergaard & K. Christoffersen (eds), *The structuring role of submerged macrophytes in lakes*. Ecological Studies, Springer Verlag, New York: 115–133.
- Theil, H., 1950. A rank-invariant method of linear and polynomial regression analysis, 1, 2 and 3. *Ned. Akad. Wetensch. Proc.* 53: 386–392, 521–525, 1397–1412.
- Torenbeek, R. & D. de Vries, 1997. Zuidlaardermeer. In de Boois, I., T. Slingerland & M.-L. Meijer (eds), *Actief Biologisch Beheer in Nederland, Projecten 1987–1996*. Institute for Inland Water Management and Waste Water Treatment, Lelystad, report 97.084: 169–176.
- Van Berkum, J. A., M. Klinge & M. P. Grimm, 1995. Biomanipulation in the Duinigermeer, first results. *Neth. J. aquat. Ecol.* 29: 81–90.
- Van Berkum, J. A., M.-L. Meijer & J. H. Kemper, 1996. *Actief Biologisch Beheer in het Noorddiep*. H₂O 29: 308–313.
- Van den Berg, M. S., H. Coops, M.-L. Meijer, M. Scheffer & J. Simons, 1998. Clear water associated with a dense *Chara* vegetation in the shallow and turbid lake Veluwemeer, The Netherlands. In Jeppesen, E., M. Søndergaard, M. Søndergaard & K. Christoffersen (eds), *The structuring role of submerged macrophytes in lakes*. Ecological Studies, Springer Verlag, New York: 339–352.
- Van der Molen, D. T. & R. Portielje, 1999. Multi-lake studies in The Netherlands: trends in eutrophication. *Hydrobiologia*, 408/409: 359–365.
- Van der Vlugt, J. C., P. A. Walker, J. van der Does & A. J. P. Raat, 1992. Fisheries management as an additional lake restoration measure: biomanipulation scaling up problems. *Hydrobiologia* 233: 213–224.
- Van Donk, E. & R. D. Gulati, 1995. Transition of a lake to turbid state six years after biomanipulation: mechanisms and pathways. *Wat. Sci. Tech.* 32: 197–206.
- Van Donk, E., M. P. Grimm, R. D. Gulati & J. P. G. Klein Breteler, 1990a. Whole-lake food-web manipulation as a means to study community interactions in a small ecosystem. *Hydrobiologia* 200/201: 275–289.
- Van Donk, E., M. P. Grimm, R. D. Gulati, P. G. M. Heuts, W. A. de Kloet & E. van Liere, 1990b. First attempt to apply whole-lake food-web manipulation on a large scale in The Netherlands. *Hydrobiologia* 200/201: 291–302.
- Van Donk, E., R. D. Gulati, A. Iedema & J. T. Meulemans, 1993. Macrophyte-related shifts in the nitrogen and phosphorus contents of the different trophic levels in a biomanipulated shallow lake. *Hydrobiologia* 251: 19–26.
- Van Scheppingen, Y., 1997. Boschkreek. In de Boois, I., T. Slingerland & M.-L. Meijer (eds), *Actief Biologisch Beheer in Nederland, Projecten 1987–1996*, Institute for Inland Water Management and Waste Water Treatment, Lelystad, report 97.084: 29–36.
- Veeningen, R., 1997. Restoration of the lake Nanneviid: first results. In Royackers, R., R. H. Aalderink & G. Blom (eds), *Eutrophication Research, State-of-the-art, Proceedings of a symposium for Prof. Lyklema*. University of Wageningen: 273–279.
- Walker, P. A., 1994. Development of pike and perch populations after biomanipulation of fish stocks. In Cowx, I. C. (ed.), *Rehabilitation of freshwater fisheries*. Fishing News Books, Blackwell Scientific Publications: 376–389.
- Wium-Andersen, S., U. Anthoni, C. Christophersen & G. Houen, 1982. Allelopathic effects on phytoplankton by substances isolated from aquatic macrophytes Charales. *Oikos* 39: 187–190.