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Long-term responses to fish-stock reduction in small shallow lakes: interpretation of five-year results of four biomanipulation cases in The Netherlands and Denmark

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Abstract

The effects of fish stock reduction have been studied in 3 Dutch lakes (Lake Zwemlust, Lake Bleiswijkse Zoom and Lake Noorddiep) and 1 Danish lake (Lake Væng) during 4–5 years. A general response is described. The fish stock reduction led in general to a low fish stock, low chlorophyll-*a*, high Secchi-disc transparency and high abundance of macrophytes. Large *Daphnia* became abundant, but their density decreased, due to food limitation and predation by fish. The total nitrogen concentration became low due to N-uptake by macrophytes and enhanced denitrification. In Lake Bleiswijkse Zoom the water transparency deteriorated and the clear water state was not stable. The fish stock increased and the production of young fish in summer was high. Clear water occurred only in spring. Large daphnids were absent in summer and the macrophytes decreased.

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

Introduction

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

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

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

Study areas

All four lakes are small and shallow, but their phosphorus levels differ from 0.15 mg P l^{-1} (Lake Væng) to 1.0 mg P l^{-1} (Lake Zwemlust) (Fig. 1g). In the three Dutch lakes the fish stock was drastically reduced during one winter (85–100%), in Lake Væng the fish stock reduction was 50% in 1.5 year. In Lake Væng and Lake Zwemlust no additional fish removal has occurred, in Lake Noorddiep and Lake Bleiswijkse Zoom two and three years after the fish reduction a small additional fishery has been carried out on behalf of the anglers (maximum 3–10% of the original fish stock). In Lake Zwemlust and Lake Bleiswijkse Zoom almost every year young pike were introduced to increase the predation pressure on young-of-the-year cyprinids.

Table 1. Main characteristics of the studied lakes.

Lake	Surface area (ha)	Mean depth (m)	Max. depth (m)	Fish reduction (%)
Væng	15	1.2	2.0	50
Noorddiep	4.5	1.5	2.5	85
Bleiswijk	3.5	1.1	1.5	85
Zwemlust	1.5	1.5	2.5	100

Methods

The summer averages (Denmark: May–October; The Netherlands: April–September) of *Daphnia* (>0.8 mm), Chlorophyll-*a* concentration, Secchi-disc transparency, % macrophytes cover, total N-, total P-concentration and the estimates of the fish stock at the end of the summer are compared with the previous reference state. In Lake Væng, Lake Zwemlust and Lake Noorddiep, data for the year before the fish reduction are used as reference, in Lake Bleiswijkse Zoom the data of the lake part without a fish reduction are used as a reference.

Concentrations of nitrogen, phosphorus and chlorophyll-*a* (ethanol extraction) were measured according to International standards (ISO). *Daphnia* biomass was calculated using a L-DW relationship from Bottrel *et al.*, (1975). In the Dutch lakes and in 1986 in Lake Væng the fish biomass was estimated with the adjusted Petersen mark-recapture method (Ricker, 1975). In Lake Væng a standardized test fishing was undertaken in August each year using multiple gillnets with 14 different mesh-sizes. Results are expressed in Catch per unit effort (CPUE, kg net^{-1}). For details about method and results see Meijer *et al.*, 1990; Van Donk *et al.*, 1990, Søndergaard *et al.*, 1990; Jeppesen *et al.*, 1990, 1991.

General responses

A general pattern can be found based on the average of the four lakes. In all lakes the fish stock

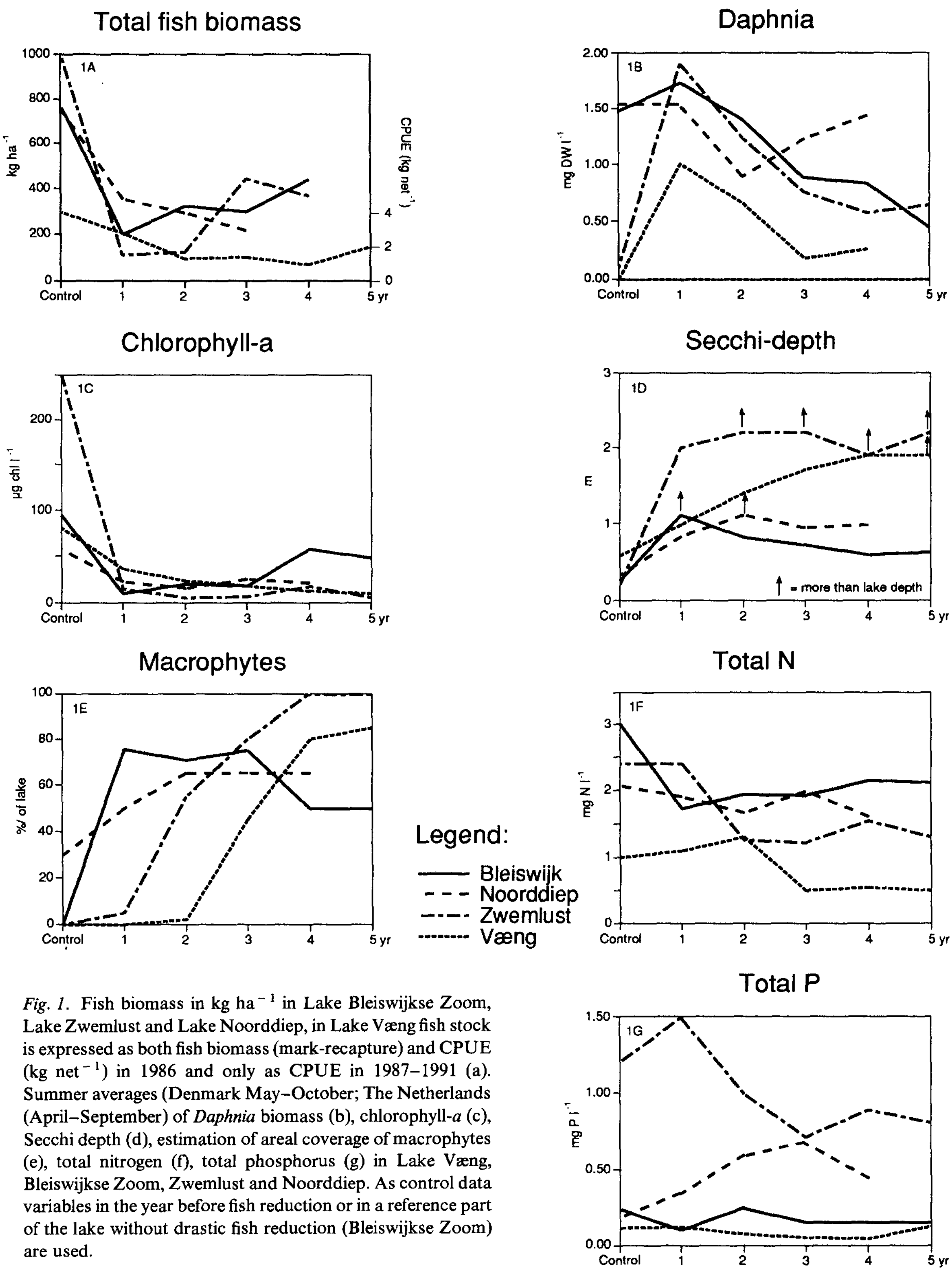


Fig. 1. Fish biomass in kg ha^{-1} in Lake Bleiswijkse Zoom, Lake Zwemlust and Lake Noorddiep, in Lake Væng fish stock is expressed as both fish biomass (mark-recapture) and CPUE (kg net^{-1}) in 1986 and only as CPUE in 1987–1991 (a). Summer averages (Denmark May–October; The Netherlands (April–September)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

has drastically been reduced (Fig. 1a). In two lakes the *Daphnia* biomass was high in the first year after the fish reduction, and afterwards the biomass decreased due to food limitation and predation by fish (Fig. 1b). In the two other lakes, the *Daphnia* biomass was already high before the fish reduction. The Secchi depth increased to maximum values (to the bottom) and the chlorophyll-*a* concentrations became very low (Figs 1c and 1d). As a consequence the lake surface became covered with submerged macrophytes (Fig. 1e). In all lakes the total nitrogen concentration started decreasing not in the year that the fish reduction took place, but in the year that macrophytes covered more than 50% of the lake surface area (Figs 1e and 1f), indicating that macrophytes caused this decrease. The total nitrogen concentration remained low due to uptake by macrophytes and enhanced denitrification (Ozimek *et al.*, 1990; Van Donk *et al.*, 1993, Moss, 1990). Total phosphorus concentration did not show a general pattern (Fig. 1g).

Differences between the lakes

Lake Væng

In Lake Væng the relative fish stock reduction was less drastic than in the Dutch lakes. This might explain why most responses were more gradual in Lake Væng than in the other lakes. In Lake Væng the increase of the Secchi depth to the bottom took 3 years, while in the Dutch lakes this was reached in the first year after the fish reduction. Also the decrease of chlorophyll-*a*, total P and the increase in macrophytes progressed more slowly. The delay in recovery of the macrophytes in Lake Væng was probably caused by the slower increase in Secchi transparency and macrophyte grazing by water fowl (Lauridsen *et al.*, 1994). A drastic decrease in total N was found in the third year when the macrophytes became abundant. The decrease in *Daphnia* biomass was mainly caused by a decrease in *Daphnia* length. The amount of fish caught in the test fishing (CPUE) did not increase in the course of the years, possibly due to the lower nutrient concentration and the high percentage of piscivorous fish (Fig. 4). The water remained continuously clear during these five years.

Lake Zwemlust

The response of Lake Zwemlust was very similar to the general pattern as described above. A strong response in Secchi depth, chlorophyll-*a* and *Daphnia* biomass was found in the first year after the very drastic fish stock reduction. The *Daphnia* biomass decreased in the following years, due to a shift to small *Daphnia* species. A strong increase in macrophytes occurred in the second year, followed by a decrease in nitrogen concentration. The water remained continuously clear during the five years. Incidently large colonies and bluegreen cyanobacteria were found for short periods (van Donk *et al.*, 1990). A small decrease of the coverage of the macrophytes was found, starting in 1990, probably caused by the increased herbivory by birds and rudd (Van Donk *et al.*, in press). The fish stock gradually increased, combined with an increase in planktivorous fish and a decrease in percentage of piscivores (Fig. 4).

Lake Noorddiep

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

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

Lake BLeiswijkse Zoom

Lake Bleiswijkse Zoom is the only lake in which a deterioration can be found during the five years. In the first year Lake Bleiswijkse Zoom was in a clear water state, thereafter a deterioration was found, probably triggered by a repeated inlet with turbid water. The fish stock increased, chlorophyll-*a* concentration increased, Secchi depth decreased and the macrophytes became less abundant.

Detailed observations showed that in Lake Bleiswijkse Zoom the water became turbid only in summer; in spring the water was often clear, due to abundance of large *Daphnia* (Fig. 2).

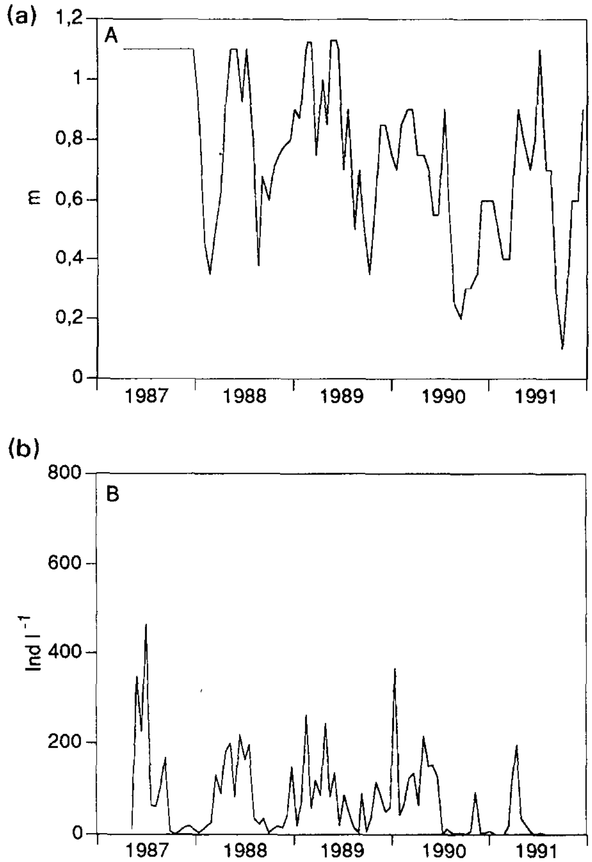


Fig. 2. Individual data on Secchi depth (a) and *Daphnia* density (b) in Lake Bleiswijkse Zoom. In March 1987 the fish stock was drastically reduced. In March and June 1988 and in June 1989 inflow of turbid water (rich in algae and suspended sediment) occurred.

Hypothesis on the change in seasonal cycle

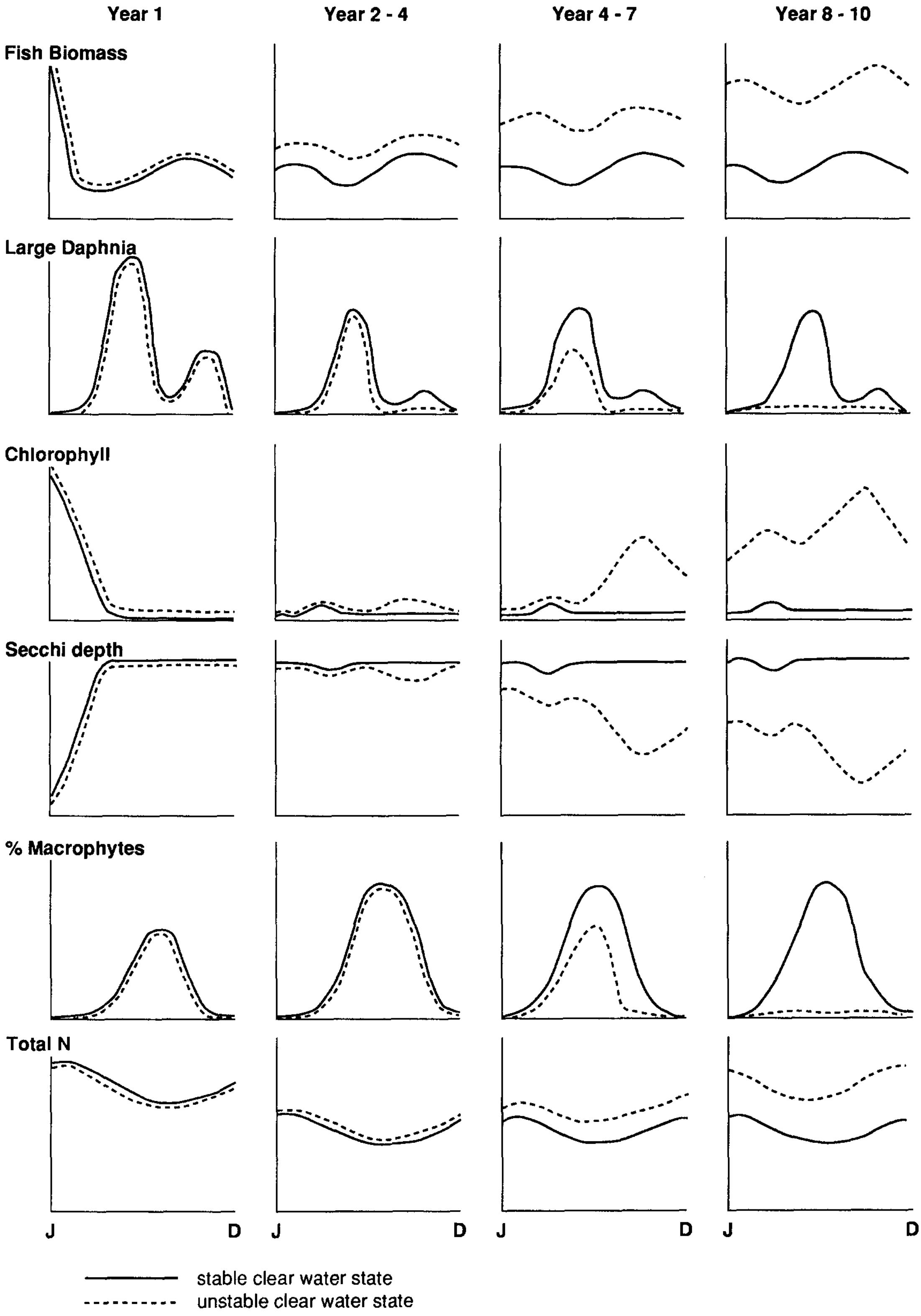
Results from Lake Bleiswijkse Zoom show that the seasonal cycle is important. We formulate a hypothesis on the change in the seasonal cycle in the years after the fish stock reduction. A stable clear water state is compared with a system going back to the turbid state, with emphasis on differences in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

First two years

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

Later years

Around the third year after the fish reduction differences start to develop between lakes establishing a stable clear water state, and lakes that are returning to the turbid state (Fig. 3).


Year 1
Year 2 - 4
Year 4 - 7
Year 8 - 10
Fish Biomass
Large Daphnia
Chlorophyll
Secchi depth
% Macrophytes
Total N
J
D
stable clear water state
unstable clear water state

To a stable clear water state

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

Return to a turbid state

In spring of the first year or two large *Daphnia* is still able to develop exponentially and control the algal biomass, because the fish predation on zooplankton is relatively low until the end of June. From then onwards the young-of-the-year fish start feeding on large *Daphnia*.

In summer the production of 0 + fish can reach such high levels that the planktivorous fish stock exceeds a threshold level and large *Daphnia* might disappear in summer (e.g. Lake Bleiswijkse Zoom, Fig. 2). In the first years macrophytes compete with phytoplankton for nitrogen and thus keep the algal biomass low and the transparency high. In later years the Secchi depth gradually decreases during this period. Eventually macrophytes may disappear due to e.g. periphytic growth (Phillips *et al.*, 1978), abrupt dieback of a monoculture of macrophytes (Lauridsen *et al.*, 1994) or external disturbances such as water inlet (Meijer *et al.*, 1990) or increased herbivory (Van Donk *et al.*, in press) and the water becomes turbid. The first years with turbid water in summer, are still followed by clear water in spring (e.g. Bleiswijkse Zoom, Figs 2 and 3). But at some point due to a low percentage of piscivorous fish the planktivorous fish stock will become so high that large *Daphnia* can not reach high densities in spring anymore and the water may remain turbid throughout the year. Also the biomass of benthivorous fish increases, causing higher resuspension of the sediment.

Some lakes may alternate between the turbid and clear water stage over decades (Jeppesen *et al.*, 1990; Perrow *et al.*, 1994). The mechanisms behind the alterations at those lakes are not yet clear.

Signals of deteriorating stability

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

Fig. 3. Hypothesized generalization of developments of fish, *Daphnia*, chlorophyll-*a*, Secchi depth, macrophytes and nitrogen in the long term in stable and unstable clear water states.

- increase of total fish stock, decrease of percentage of predatory fish and an increase of 0+ fish (Fig. 4)
- decrease of mean length of *Daphnia* in August (Lake Bleiswijkse Zoom and Lake Zwemlust, Gulati, 1990)
- increase of periphyton on macrophytes and decrease of areal coverage of macrophytes (Lake Bleiswijkse Zoom, pers. comm. R. W. Doef, RIZA Zwemlust, Van Donk *et al.*, in press)

In Lake Væng and Lake Noorddiep less signs of instability are present (Table 2). According to the Danish data which show that clear water can occur at P-levels of *ca* 0.10 mg P l^{-1} (Jeppesen *et al.*, 1990) only Lake Væng (Fig. 1) seems suitable for a stable clear water state. Indeed in Lake Væng none of the above mentioned indications for a deterioration are observed in first 5 years. However in 1992 also in Væng the water became turbid (Table 2) after the macrophytes almost disappeared in spring, probably reflecting a sudden die-back of a monoculture of *Elodea* sp (Lauridsen *et al.*, 1993). However this return was only temporary (1.5 month) and the percentage piscivorous fish remained high, both in numbers and biomass. In Lake Noorddiep and Lake Bleiswijkse Zoom the surface area and P-levels are close to the range in which stable clear water might be expected (lakes <3 ha at P-levels of 0.35 mg P l^{-1}). However, the latter lake is deteriorating, probably triggered by a repeated inlet of turbid water. However, in 1990 hardly any and in 1991 no water inlet had taken place, but still the water became turbid in summer due to a decrease of macrophytes and an increase in algal biomass. The production of 0+ fish was very high and large cladocerans were absent in summer (Figs 2 and 4). Each spring the water became clear again. In Lake Noorddiep with the same morphology and nutrient level as in Lake Bleiswijkse Zoom, the increase of the fish stock was much lower. It is not exactly known why in Lake Noorddiep the fish stock is not increasing. The total P-concentrations even increased after the measure, probably due to P-release from the sediment under a dense cover of filamentous macroalgae, and the total nitrogen concentration did not decrease much. Possibly the natural pike population (composed of small individuals) was better able to control planktivorous 0+ recruitment. The nutrient levels, especially P, in Lake Zwemlust were so high that no stable clear water state was expected. Nevertheless the water remained clear for over five years (Van Donk *et al.*, 1993, in press). One reason for the remarkably long period of high transparency might be that in Lake Zwemlust all fish were removed and the lake was stocked with piscivorous fish and some rudd. In addition young pike were added throughout the investigation period. The increasing fish stock and the absence of large *Daphnia* in summer are indications that the clear water situation might not continue, although the results show that the water can stay clear with those high planktivorous fish densities. As in Lake Væng the water became turbid in summer 1992 (Table 2). Here the turbid period lasted longer (still turbid in October 1992) than in Lake Væng,

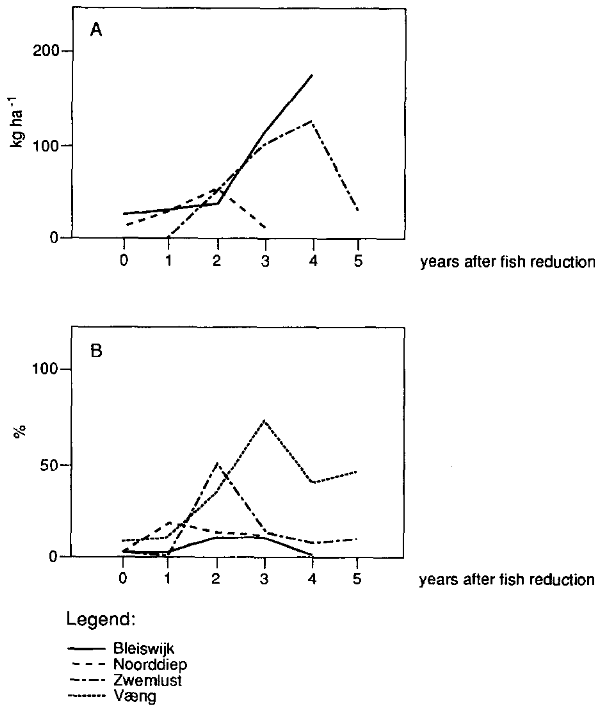


Fig. 4. Total biomass of 0+ planktivorous fish (a) and percentage of piscivores (b) in Lake Væng, Zwemlust, Bleiswijkse Zoom and Noorddiep.

Table 2. Presence of signs of instability in the summer 4–5 years after the fish stock reduction in lake Væng, Noorddiep, Bleiswijkse Zoom and Zwemlust. + = yes, – = no.

	Secchi 4–5 years high	Fish stock decreases	Few 0 + fish	High % pisciv. fish	Daphnia length stays high	Secchi depth Summer 1992 stays high
Væng	+	+	+	+	+	–
Noorddiep	+	+	±	–	±	+
Bleiswijk	–	–	–	–	–	–
Zwemlust	+	–	–	–	–	–

possibly because of the higher biomass of planktivores due to a lower % of piscivorous fish.

Especially in Lake Zwemlust and Lake Bleiswijkse Zoom the amount of small planktivorous fish is increasing (Fig. 4), despite the repeated introduction of 0 + pike in the lakes. In Lake Væng and Lake Noorddiep where the development of planktivorous fish has been less explosive, pike was already present before the fish reduction. There the conditions were already favourable for pike. It seems that a natural pike population is better able to control 0 + fish than a population of stocked 0 + pikes. One explanation for the limited success of introduced pike may be that pike needs a high abundance of emergent vegetation (Grimm & Backx, 1990) and apparently this vegetation does not develop automatically after a fish reduction measure.

An abrupt return to the turbid state, as can be seen in summer in Lake Væng, Lake Zwemlust and Lake Bleiswijkse Zoom seems more related to a decrease in macrophytes than to a high predation by planktivorous fish. However, a high percentage of piscivores associated with a low density of planktivorous fish, makes it more likely that the turbid stage will not last long. An increase in planktivorous fish causing the disappearance of large *Daphnia*, makes the system more vulnerable to sudden changes in macrophyte populations and can lead to a gradual decrease in transparency. Although in Lake Bleiswijkse Zoom, the water becomes clear again in each spring, the transparency in later years was lower than in the first year after the fish removal.

Conclusions

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

- The results indicate that macrophytes play a key-role in keeping the water clear in the lakes included in the present analysis. All studied lakes are small and shallow and therefore suitable for abundant growth of submerged macrophytes. Vegetation cannot develop to the same extent in deeper lakes and larger lakes. We, therefore, expect the long-term effects of fish stock reduction described here are only valid for small and shallow lakes.

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