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Lake restoration studies: Failures, bottlenecks and prospects of new ecotechnological measures

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Abstract

This paper critically reviews the published works on lake restoration in north-western Europe, with the aim to highlight the causes of failures of lake biomanipulation, and to identify the main bottlenecks that have impeded progress. More importantly, we explore the prospects of applying new ecotechnological measures to lakes with a focus on shallow lakes. These complementary measures are: (1) reduction of sediment resuspension; (2) water-level management; and (3) the use in shallow lakes of bivalves as effective grazers on lake seston, especially when cyanobacteria are dominant. If the sustainability of the positive effects of biomanipulation is considered over a decade, there are probably more cases of failures than successes. The failures can be ascribed to several bottlenecks that include: (1) inadequate reduction of allochthonous phosphorus (P) and an increase in autochthonous P inputs, i.e. release of P from the lake sediments following reductions of external P inputs; (2) poor edibility of filamentous and colonial cyanobacteria to daphnids; (3) inadequate coverage of the lake area by macrophytes partly due to foraging on the macrophytes by both fish and birds; (4) ineffective reduction of planktivorous fish biomass and our inability to maintain the fish mass to a 'low level' for longer periods; and (5) failure of northern pike (*Esox lucius*) after its transplantation to the lakes to develop a population level that can control planktivorous fish to desired low levels. Three potentially complementary ecotechnological measures are discussed. The first such measure concerns prevention of sediment resuspension in lakes by creating islands in order to minimise the wind fetch to reduce the wave amplitude. The second measure involves allowing greater water-level fluctuations (WLF) in lakes as planned in lowland countries like the Netherlands; WLF are likely to allow more space for water, and may lead to improved water quality and higher biodiversity. The third ecotechnological measure relates to grazer populations that complement herbivorous zooplankton to regulate phytoplankton, particularly to control cyanobacterial blooms. For this, the bivalve *Dreissena polymorpha* appears to be a good potential candidate for grazing on phytoplankton, especially in shallow eutrophic lakes that are dominated by filamentous and toxic cyanobacteria (e.g. *Planktothrix agardhii* and *Microcystis aeruginosa*).

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Introduction

Research on freshwater ecosystems since the 1970s has focused increasingly on combating and reducing the

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effects of many man-made perturbations. Several studies have been carried out on lake restoration and management in north-western Europe and North America (Cooke et al., 2005). The implementation of the EU Water Framework Directive (European Commission, 2000: WFD) in the EU countries requires freshwater rivers and lakes to achieve a good ecological state or potential by 2015. The state-of-the-art reviews on restoration of shallow, eutrophic lakes in Europe (Gulati and Van Donk, 2002; Søndergaard et al., 2007) have drawn several generalisations about the progress of lake rehabilitation works in NW Europe. These reviews are based on numerous studies on temperate lakes carried out mostly in Denmark, the Netherlands, Germany and Sweden (Gulati et al., 1990; Lammens et al., 1990; Jeppesen et al., 1990; Hansson et al., 1998; Meijer et al., 1999; Benndorf et al., 2002; Mehner et al., 2002; Van Donk and Van De Bund, 2002; Jeppesen et al., 2005). Many of these studies covered both whole-lake, enclosure and laboratory scale experiments and advanced our knowledge of theory and mechanisms behind the food-chain processes.

Analyses of data

A more recent example of data analysis is that of Søndergaard et al. (2007, Table 3). The authors examined in detail the effects of fish removal in 34 biomanipulated lakes in Denmark and the Netherlands. In 20 of the 34 lakes analysed, the Secchi-disc depth increased by 50% within 1–3 years after the fish removal compared with the Secchi-depth in 1–3 years before the measures. In 25 of these 34 lakes, where the macrophyte development was monitored, 18 lakes showed no increase in percentage of macrophyte cover. Thus, the improvement in light climate may not per se be attributed to increase in macrophyte biomass. The effect of food web or biomanipulation measures is generally difficult to predict precisely. This is primarily because many of the restoration measures, both nutrient reduction and biomanipulation, were carried out simultaneously so that their resultant effect does not allow us to separate the responses to ascribe them to the individual measures. Moreover, the feasibility and success of biomanipulation measures have been questioned (DeMelo et al., 1992; Phillips and Moss, 1994; Reynolds, 1994; Gulati and Van Donk, 2002). Thus, the lake restoration studies have contributed only to a limited extent to advance theory forming based on food web interrelationships (see for example Carpenter et al., 1985; Carpenter and Kitchell, 1993; Scheffer, 1990; Moss et al., 1996). Gulati and Van Donk (2002) critically analysed the variety of restoration techniques that have been employed in the Dutch lakes. These included hydrological management, reduction of

P in the external loads, reduction of in-lake P by sediment removal or by immobilisation of P in lake sediments, and by food web manipulation i.e. lake biomanipulation.

The above-mentioned studies revealed several bottlenecks that delayed the response to rehabilitation measures or could explain the failures. In view of these difficulties, complementary, ecotechnological measures need to be developed and tested experimentally. We consider here three of these measures: (1) reduction of sediment resuspension; (2) water-level management; and (3) use of bivalves as effective grazers on lake seston. The main objective in this paper is to briefly highlight the main bottlenecks of lake biomanipulation and to explore and discuss the above-mentioned new approaches of lake restoration and management. Thus, we aim at emphasising gaps in our present knowledge and explore the prospects that these new strategies offer based on literature. The experiences acquired from restoration measures, together with new strategies should pave the way for developing more enduring strategies for sustainable restoration of our lake ecosystems.

Lake biomanipulation: successes vs. failures and bottlenecks

Examples of early successes

Most successful biomanipulation studies were carried out in small (<25 ha) and shallow (<3 m) lakes in north-western Europe. Drenner and Hambright (1999) in a review of methods and successes of biomanipulation experiments estimated the success rate to be 61%. However, there appears to be a bias in the literature in favour of the more successful studies (see e.g. Gulati and Van Donk, 2002; Søndergaard et al., 2007). The success of such restoration measures, defined in most cases as a sustained improvement in the light climate, was attributed in shallow lakes to an increase in the macrophyte cover following the measures. The Dutch studies reveal that the increased development and cover of macrophytes occurs after the reduction of biomass of planktivorous fish, predominantly bream (*Abramis brama*) (Gulati and Van Donk, 1989, 2002; Meijer et al., 1999; Van Donk and Gulati, 1989; Van Donk et al., 1989, 1990a). The fish mass reduction results in a discernible increase in the density of large-bodied grazers *Daphnia* spp. and an increase in their grazing pressure on seston. Subsequently, a clear-water phase occurred and macrophyte development increased (e.g. in Lake Zwemlust and Wolderwijd: Gulati, 1989, 1990, 1995; Gulati and Van Donk, 1989, 2002; Hosper, 1997; Meijer and Hosper, 1997). The transient clear-water phase that usually lasted from two to four weeks was

considered to stimulate growth and development of macrophytes so that high water clarity could be prolonged. The macrophytes successfully competed with phytoplankton for the macronutrients, especially N (e.g. Van Donk et al., 1993; Ozimek et al., 1993; Van Donk and Van De Bund, 2002). In both Lake Wolderwijd and Lake Zwemlust, these changes contributed to the success of lake biomanipulation measures (Meijer, 2000; Meijer and Hosper, 1997; Gulati and Van Donk, 2002).

The importance of macrophytes

We now know that macrophytes exert their positive influence in the lakes in several ways (Fig. 1; Kornijow et al., 1990; Ozimek et al., 1993; Van de Bund and Van Donk, 2002; Van Donk and Van De Bund, 2002; see also in Moss et al., 2004). The macrophytes act as a major nutrient sink and a refuge for zooplankton as well as provide protection to young northern pike (*Esox lucius*) against predation by adult pike. They also produce allelopathic substances against phytoplankton (Mulderij et al., 2003) and reduce wind- and fish-induced resuspension of bottom sediment (Gulati and Van Donk, 2002). Interestingly, the optimal light climate, which initially acts as a trigger to initiate the macrophyte growth and development, is prolonged by the presence of macrophytes. Thus, most lake restoration accomplishments in shallow lakes in recent years have been attributed to the successful development of aquatic macrovegetation.

The successes versus failures

It is difficult to generalise how successful biomanipulation is for the success of lake restoration and management of lakes (Cooke et al., 2005), particularly in north-western Europe, e.g. in the Netherlands and Denmark (Gulati and Van Donk, 2002; Jeppesen et al., 1991, 2003, 2007; Søndergaard et al., 2007). There are probably more cases of failure than success (Meijer et al., 1999; Gulati and Van Donk, 2002), especially if the sustainability of the positive effects is considered over 8–10 years (Gulati and Van Donk, 2002). If the restoration measures were discontinued after 2, 3 or more years, i.e. the standing crop of fish was neither monitored nor managed, invariably the biomass of planktivorous fish increased, turbid conditions returned and macrophyte vegetation virtually disappeared. The failures are generally ascribed to: (1) an insufficient or no decrease at all of autochthonous P due to an increase in in-lake P loadings from sediments; (2) an inadequate reduction in the standing stock of planktivorous fish, as well as a rapid increase in their growth rates and standing stock in the years following their reduction; and (3) inability of the piscivorous fish, mainly northern pike, to establish in these lakes and control the planktivorous fish.

The factors that contribute to the failure of pike to establish and control planktivorous fish have not been systematically investigated (see in Søndergaard et al., 2007). However, Jeppesen et al. (1991) showed in

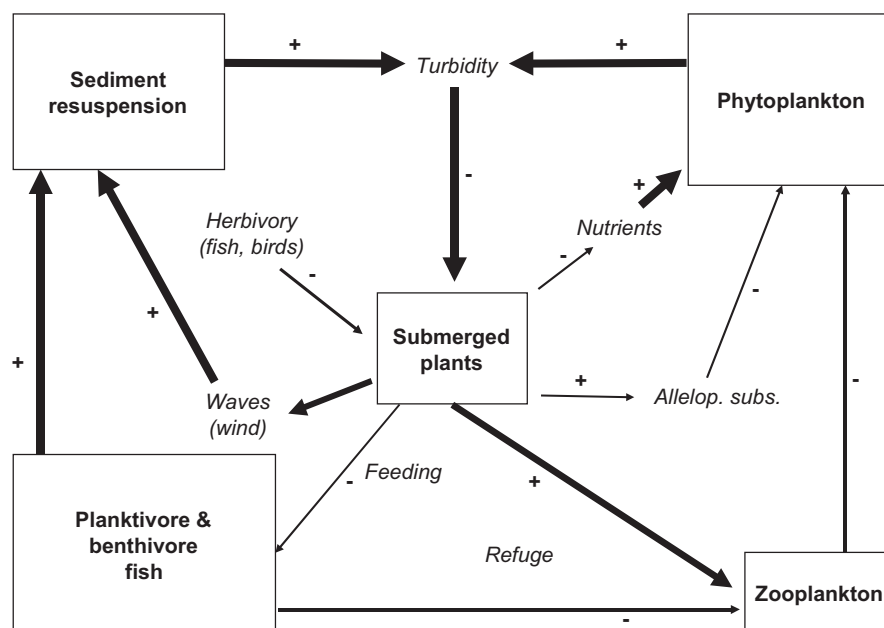


Fig. 1. Schematic representation of the mechanisms and factors causing sediment resuspension and turbidity in shallow lakes in relation to macrophytes (submerged plants). After lake restoration the increase in macrophytes plays an important role in reducing sediment resuspension and turbidity and improving the underwater light climate. Feed back mechanisms and their strength are indicated with arrows. (Allel. Subs. = allelopathic substances). From Gulati and Van Donk (2002).

300 Danish lakes that at total P concentrations $< 50 \mu\text{g L}^{-1}$, macrophytes were abundant and piscivorous fish were common in the fish community, and that at total P concentrations between 80 and $150 \mu\text{g L}^{-1}$, the planktivores (cyprinids) were common, and macrophytes scarce. Moreover, in addition to the difficulty of creating clear water, also bottom-feeding species of fish cause resuspension of sediment particles (Lammens, 1989; Meijer et al., 1990), resulting in an increase in turbidity and deterioration of conditions for macrophyte development. Resuspension of the P-rich bottom sediment also increases P availability in the water column. Both, the extra P-loading and the higher turbidity in deeper layers favour growth of algae over macrophytes.

The criteria for the efficacy of biomanipulation measures and the bottlenecks

Our understanding of the food web theory is essential for applying lake biomanipulation measures to lake restoration. Our predictions, however, have sometimes been thwarted by the incomplete insight into the food web processes and ecosystem functioning. The criteria for evaluating if the rehabilitation measures in a lake

were successful are generally based on long-term monitoring of lakes after the measures. The success criteria are: (1) a sustained increase in Secchi-depth; (2) a discernible reduction in cyanobacterial biomass and blooms; (3) an increase in densities of the large-bodied grazers, *Daphnia* spp.; and (4) an increased cover by macrophytes. An increase in Secchi-disc transparency and a decrease in chlorophyll levels would generally point to the role of grazers and macrophytes. There are several bottlenecks that hamper or even annul the effects of lake restoration measures. We discuss here the most significant of these bottlenecks (Fig. 2), irrespective of their chronological importance.

Potential bottlenecks

Firstly, in many cases it was not possible to adequately reduce the available P in lake water resulting both from excessive external and internal (release from sediment) P inputs. Thus, it might be necessary to reduce P load to a “biomanipulation efficiency threshold of P-loading” which may be in the range of 0.6–0.8 g Total-P $\text{m}^{-2} \text{yr}^{-1}$ as hypothesised by Benndorf and Miersch (1991). Only then a sustained reduction of phytoplankton

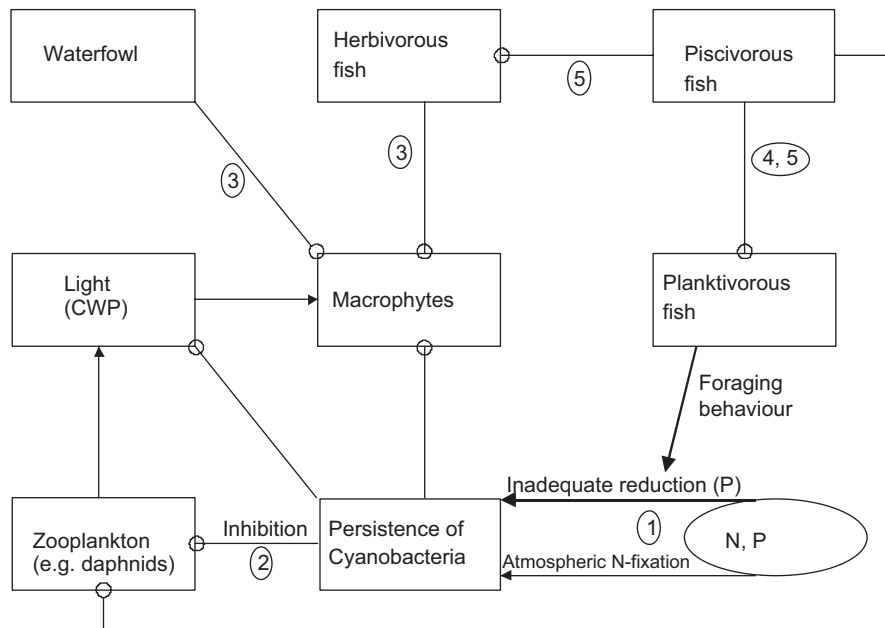


Fig. 2. Schematic view of the bottlenecks (indicated from 1 to 5 small circles) in food webs, that prevent the success of biomanipulation measures in the restoration of shallow lakes. They are: (1) the inadequate reduction of allochthonous P and the increase of autochthonous P, (2) the poor edibility of filamentous and colonial cyanobacteria to zooplankton, (3) an inadequate coverage of the lake area by macrophytes due to predation by both waterfowl and herbivorous fish, (4) the ineffective reduction of planktivorous fish biomass and the inability to maintain it at low levels for longer periods, and (5) the failure of introduction of northern pike to develop a population at the level that can control planktivorous fish. See text for a further explanation on the bottlenecks. Lines with black arrow heads represent a positive influence of one parameter on the other (e.g. zooplankton grazing has a positive effect on light). Lines with white circles represent a negative (inhibitory) influence of one parameter on another (e.g. waterfowl depress macrophytes through predation). CWP in box for light = clear water phase, N = nitrogen, P = phosphorus. The lines and arrows from Planktivorous fish to P and from N,P to Persistence of Cyanobacteria are thicker than other lines because nutrient reduction and fish removal are the most severe bottlenecks.

via top-down control might be possible due to both direct (grazing) and indirect (top-down induced P reduction) mechanisms (Benndorf et al., 2002). Such a ‘threshold’ level of P loading may however vary from lake to lake. Thus, both insufficient reduction of external P load to the lake after the restoration measures, and an increased rate of P release from the lake sediment into the overlying water would be crucial factors in offsetting the success of measures. Reduction of N, if needed, is even more complex since cyanobacteria possessing heterocysts, e.g. *Anabaena* spp., have been reported to directly fix nitrogen from the atmosphere (Van der Molen et al., 1998: Fig. 2).

Secondly, in biomanipulated lakes grazing by zooplankton in the spring period acts as an initial trigger for creating clear-water conditions (Lampert et al., 1986; Sommer et al., 1986; Gulati, 1990), which may stimulate macrophyte development. However, the grazing efficacy of larger-bodied daphnids is severely hindered by larger inedible algae, particularly both colonial and filamentous cyanobacteria, adversely affecting growth and reproduction of daphnids (Dawidowicz et al., 1988). In Dutch lakes, the daphnids are generally food-limited, soon after their grazing maximum is achieved in late spring or early summer. Because of the seston minimum, the daphnid populations collapse, and grazing is reduced to negligible levels (Gulati, 1989, 1990). Also, concomitant predation by young-of-the-year (YOY) fish may drastically reduce *Daphnia* densities during late spring or early summer (e.g. Wagner et al., 2004). Dionisio Pires et al. (2005a) suggest that such losses may be more important than the negative effects of toxic blooms. Thus, the *food limitation* of zooplankton and *predation* by fish fry on zooplankton are closely occurring events in time that contribute to wipe out the *Daphnia* spp. more than the smaller-bodied zooplankters.

Thirdly, thanks to biomanipulation research, we now know that macrophytes play a crucial role in maintaining long, clear-water periods in lakes (Carpenter and Lodge, 1986; Jeppesen et al., 1990; Gulati and Van Donk, 2002; Houser et al., 2005). However, in addition to factors that prevent macrophytes to establish in many water bodies under restoration, macrophytes fail to keep pace in their growth with their mortality due to the fish and birds that graze on the macrophytes (Prejs, 1984; Van Donk and Otte, 1996). Prejs (1984) estimated roach (*Rutilus rutilus*) and rudd (*Scardinius erythrophthalmus*) to reduce biomass of submerged plant *Elodea canadensis* by >30% in a Polish lake. In Lake Zwemlust the birds flocked to the lake when macrophyte vegetation markedly increased following the restoration measures (Van de Bund and Van Donk, 2002). It was estimated that the birds and fish daily consumed comparable amounts of macrophytes which led to a marked decline in the vegetation. In contrast to this study, Perrow et al.

(1997) provide experimental evidence of the limited role of birds in limiting macrophytes in both spring and summer. Also, Marklund et al. (2002) consider that “in shallow temperate, eutrophic lakes, a naturally occurring fish assemblage rarely reduces submerged vegetation” and that “the risk of severe reduction of submerged vegetation as a result of waterfowl or fish grazing, should thereby be low”.

Fourthly, in most cases where fish reduction was the main biomanipulation measure applied, fish removed was expressed as a percentage of the fish standing crop, irrespective of the absolute standing crop biomass at the start or after reduction. The fish standing crop in eutrophic lakes, although quite variable, roughly ranges between 100 and 400 kg ha⁻¹. In most lake biomanipulation studies, the fish stock reduction can vary from <50 to up to 75% or more (Meijer, 2000; see also reviews in Gulati and Van Donk, 2002; Søndergaard et al., 2007). Thus, we can only crudely estimate the fish mass actually removed (kg ha⁻¹) for maintaining a certain desired level after the measures. To sustain a low standing crop of planktivorous/benthivorous fish mass after its reduction (Gulati and Van Donk, 2002) continues to be the lake restorers’ dilemma. We are not aware of published literature that shows long-term success of lake rehabilitation by fish reduction unless such measures were periodically repeated. More importantly, it is often difficult to achieve an optimal fish reduction within a very short period in order to prevent the mitigating effects of recruitment. An increased recruitment of young fish, between the successive fish reduction measures, is very likely – probably because of increased food availability due to the reduced fish mass. This can considerably offset the effect of fish stock reduction measures, thereby nullifying the desired reduction in standing crop.

Lastly, there are only a few European studies (Gulati and Van Donk, 2002; Søndergaard et al., 2007), where northern pike have done well after fry have been transplanted into lakes as a biomanipulation measure. The pike stockings are done with the aim to increase predation on YOY bream and roach. However, the pike generally fail to develop a population large enough to regulate the abundant planktivorous bream (Houser et al., 2005). Several factors probably contribute to the failure of the piscivores: first, a suitable biocoenosis for their optimal and sustained growth apparently did not exist. Northern pike being cannibalistic, the larger individuals predate upon their young ones, preventing the pike population to increase. Therefore, the survival of younger pike virtually depends on availability of refuges provided by the aquatic vegetation. The conditions prevailing in our lakes are, however, not conducive for pike to develop and to sustain an adequate population. This is especially true for larger-sized pike, which are needed in the biomanipulated lakes to

regulate planktivorous fish as bream. In addition to cannibalism, the gape of the larger pike does not allow them to feed on the laterally compressed fish, bream – the main planktivorous/benthivorous fish in lakes being restored in the Netherlands. In this respect, the works of [Hambricht \(1991\)](#) and [Hambricht et al. \(1991\)](#) quite convincingly show that planktivorous and benthivorous fish grow to sizes beyond the mouth gape of piscivores. Furthermore, in view of a recent evaluation by [Skov and Nilsson \(2007\)](#) “the efficacy of pike stocking as an appropriate and reliable tool for restoration programmes in shallow lakes’ is questionable”. Finally, our knowledge relating to long-term effects of extreme enhancement of piscivore biomass in lakes ([Benndorf et al., 2000](#)) is limited because there are no published reports of lakes e.g. in the Netherlands where piscivores survived long enough to carry out studies like those by Benndorf and his associates in Gräfenhain Lakes in Germany. In the moderately deep Bautzen Reservoir, a combination of piscivore (mostly zander, *Sander lucioperca*) stocking and catch restrictions was successful in long-term restructuring of the fish stock ([Benndorf, 1995](#); [Kasprzak et al., 2007](#)). However, in this biomanipulation experiment, due to continuously high nutrient levels, total phytoplankton biovolume was not reduced but only the edible fraction.

New ecotechnological approaches

Restoration strategies in the future should typically visualise lake ecosystems as integral parts of their landscape, to pave the way for their ‘nature development’. Such an appraisal and philosophy also implies that a lake is an integral part of its larger catchment area. Lake hydrology- and morphology-related factors, i.e. water-level fluctuations (WLF), sediment structure, littoral vegetation and shoreline erosion and development are crucial parameters that facilitate interactions between lakes and their surrounding catchment. In the preceding discussion, we have attempted to critically assess the causes for failures of lake restoration research. It is logical that we also explore new methodologies that have been infrequently attempted but may offer possibilities in future studies. We discuss here the methodologies that could complement the traditional restoration approaches.

Prevention of sediment resuspension

In large, wind-exposed, shallow lakes, loose sediments and strong resuspension can prevent the re-establishment of submerged vegetation ([Hamilton and Mitchell, 1996](#); [Schutten et al., 2005](#)). Phytoplankton dominance promotes accumulation of the highly organic, unconsolidated

sediments with low cohesive strength. This is an important aspect of the sediment, affecting the distribution and abundance of submerged macrophytes, which has been largely neglected ([Schutten et al., 2005](#)). Both shallowness of lakes and exposure to wind are important causal factors for resuspension of suspended matter from the sediment. In very shallow lakes (mean depth < 1.5 m), resuspension seems to occur most commonly at wind speeds ranging from 4 to 6 m s⁻¹ ([Arfi and Bouvy, 1995](#)), which prevail commonly in many coastal countries, e.g. the Netherlands. For such shallow lakes in the Netherlands, e.g. Loosdrecht lakes ([Van Liere and Gulati, 1992](#)), the failure of restoration studies is partly attributed to the wind-induced turbid conditions, i.e. poor light climate to which cyanobacteria are well adapted.

In the Netherlands, pilot studies were carried in some shallow lakes to reduce the effects of sediment resuspension. It has been proposed to *create artificial islands* in the lakes to reduce the wind-fetch factor and thus also the resuspension of sediment particles ([Gons et al., 1986](#); [Van Donk et al., 1990b](#)). There are also plans for creating deeper pits in some shallow, eutrophic lakes, assuming that these ‘burial pits’ will function to trap the wind-induced, resuspended sediment and will curtail P release from the sediment to the overlying water column ([Van Liere and Jonkers, 2002](#)). However, we do not know of lakes where the success of such measures, as creating islands and burial pits, has been demonstrated.

Water-level management

Water-level fluctuations emerge as the decisive element of hydrology, especially in shallow lakes that are particularly sensitive to any rapid change in water level. Therefore, WLF may have an overriding effect on the ecology, functioning and management of shallow lakes. Water levels in shallow lakes naturally fluctuate both seasonally but also from year to year depending largely on regional climatic conditions (e.g. temperate, semi-arid and arid) and human activities ([Blindow, 1992](#); [Gafny and Gasith, 1999](#); [Beklioglu et al., 2001](#)). Some studies suggest that WLF may be disastrous for submersed plant communities. Extremely high water levels in the vegetation period usually reduce light availability, and a low water level may damage plants due to ice and wave action during winter and to desiccation during summer.

Some plant communities may exhibit large shifts in response to small water-level changes: high water levels in spring may prevent submersed plants from expansion inducing a shift to a sparsely vegetated state. In contrast, a marked reduction in the spring lake level may lead the submersed plants to expand. In a whole-lake manipulation experiment involving a water level draw down in

winter, McGowan et al. (2005) reported a 2.5-fold increase in macrophyte abundance and a shift from a community dominated by *Ceratophyllum demersum* to *Potamogeton pectinatus*. That “such lower levels during winter are likely to promote buffer mechanisms that reinforce a macrophyte-rich, clear-water state in shallow prairie lakes”, is crucial for lake management work involving water-level manipulations. Deegan et al. (2007) showed a significant response of both *Typha domingensis* and *Phragmites australis* to amplitude of WLF. *P. australis* appeared to prefer moderate WLF (± 30 cm) based on biomass increment. In addition, WLF can enhance species richness and diversity in the lakes (Coops et al., 2003; Coops and Havens, 2005).

According to Coops and Houser (2002) water-level management may serve as a useful tool for the restoration of shallow lake ecosystems in the Netherlands, especially because the WLF are strictly regulated. This regulation is needed to reduce risks of flooding and for agricultural uses of water. The natural WLF are considered beneficial because of their impacts on nutrient dynamics, phytoplankton development and turbidity. The present government policy to allow more space for water offers new opportunities to integrate it with flood control measures and ecological restoration. Restoring natural water-level regimes is likely to lead to improvement of water quality and biodiversity in two ways: first, by expanding the critical range within which the water level is allowed to fluctuate annually; and second, by incidental recession or draw down of the water level, or both.

Van Geest et al. (2005) examined WLF in some 100 floodplain lakes during non-flooded conditions in the Lower Rhine in the Netherlands. They found the shallow, moderately isolated lakes with occasional bottom exposure to have the highest potential for creating macrophyte-rich floodplain lakes along large lowland rivers. Moreover, Van Geest et al. (2005) found higher species richness for submerged macrophytes in lakes that experienced draw down but not for floating-leaved and emergent macrophytes. The authors consider it essential that the decline in amplitude of the lake water level with lake age is compensated by deepening lakes for conserving the successional sequence of floodplain water bodies including conditions of high biodiversity.

Havens (2002) used ecosystem conceptual models during planning for the Comprehensive Everglades Restoration Program (CERP). This Programme is expected to reduce the occurrence of damaging high and low WLF and to increase the occurrence of spring water-level recessions that benefit native biota. Johnson et al. (2007) studied the response to hydrological variations in Lake Okeechobee of both vegetation and fisheries. The study indicates that water level > 5.1 m mean sea level (MSL) and prolonged flooding are likely

to cause a substantial loss of aquatic and wetland plants as well as negatively impact fish at Lake Okeechobee. In contrast, water levels < 3.7 m MSL on a regular basis were considered to favour expansion of the native plants and some grasses. Water-level variations ranging from 3.7 to 4.6 m MSL were expected to stimulate widespread stands of emergent and submerged aquatic vegetation in most years. Consequently, habitat structure and food resources for largemouth bass (*Micropterus salmoides*), other fish species, alligators, wading birds and snail kites would improve.

Bivalve mussels as grazers of phytoplankton

Failure of cladoceran zooplankton

Bio-manipulation studies in the Netherlands have mainly been restricted to reducing standing crop of zooplanktivorous fish in order to stimulate the increase of larger-bodied filter-feeding zooplankton like *Daphnia* spp. (Houser and Jagtman, 1990; Meijer, 2000). In fact, this is generally true for the literature on bio-manipulation in most temperate, eutrophic lakes in Europe. The main ‘short-term’ or the more immediate effect of removal or reduction of planktivorous fish is an increase in zooplankton biomass dominated by larger-sized zooplankters. Particularly important among these are *Daphnia* spp., which immediately trigger a marked increase in the grazing by zooplankton in spring period. Consequently, a clear-water phase occurs and stimulates macrophyte development. However, this high grazing activity of the larger, herbivore zooplankters is transient, often lasting only a few weeks. This is because of the perennial presence and increase in early summer in these eutrophic lakes of cyanobacteria, both filamentous and colonial forms, especially *Planktothrix agardhii* (formerly *Oscillatoria agardhii*) and *Microcystis* spp. The daphnids, being severely hindered in their growth due to food limitation, sharply decline and generally disappear. Moreover, in many lakes, the zooplankton grazers are generally food-limited in early summer, as in Dutch lakes, even before cyanobacteria have developed a sizable population (Gulati, 1989, 1990). Thus, limited grazing capability of zooplankters is often suggested as an explanation for a shift to cyanobacterial dominance following the spring grazing maximum of zooplankton (Sommer et al., 1986; Sarnelle, 1993; see also in Gragnani et al., 1999).

Prospects of using mussels as grazers

There have been several attempts between the late 1980s and early 1990s to investigate if mussels can serve as complementary grazers to crustacean zooplankton, in

lakes dominated by cyanobacteria. In the Netherlands, Reeders and Bij de Vaate (1990) proposed the use of zebra mussels (*Dreissena polymorpha*) as substitute grazers to control algal populations. However, contemporary studies on grazing by zebra mussels in North America do not unambiguously demonstrate the grazing effects on lake phytoplankton in Lake Erie (e.g. Wu and Culver, 1991). Wu and Culver (1991) concluded that despite that *D. polymorpha* being abundant in Lake Erie in 1989, *Daphnia* grazing still controlled edible algal density and water transparency. This study is in contrast with some other works from the US and Europe. MacIsaac et al. (1992) estimated the impact of grazing activities of settled zebra mussels on phytoplankton stocks to be '1162 times greater than' that exerted by veliger populations in western Lake Erie. In addition, the reef-associated *Dreissena* populations in the lake possessed a great potential to filter a water column up to $132 \text{ m}^3 \text{ m}^{-2} \text{ d}^{-1}$ ($= 13.3\% \text{ d}^{-1}$) at 7-m depth, and to relocate energy from the pelagic to the benthic food web. Chlorophyll *a* concentration appeared to be strongly depleted ($< 1 \mu\text{g L}^{-1}$) above *Dreissena* beds in western Lake Erie.

In another study, Lavrentyev et al. (1995) measured direct effects of grazing activities of *D. polymorpha* on a natural assemblage of planktonic protozoa and algae from Saginaw Bay (Lake Huron). They observed that the mussels lowered protozoan numbers by 70–80% despite the latter's high growth rates. Also, *Dreissena* selectively removed nanoplanktonic *Cryptomonas* and *Cyclotella*, but did not significantly affect *Microcystis*, the predominant cyanobacterial species. Idrisi et al. (2001) reported that the most dramatic change associated with dreissenid grazing in Oneida Lake, New York, was increased water clarity. They found no evidence of a negative impact of zebra mussels on fish or other trophic levels or on fish (*Perca flavescens*) growth, biomass or production. Thus, despite the order of magnitude increase in grazing rates and associated decrease in algal biomass, pelagic production at primary, secondary and tertiary levels did not decline in association with zebra mussels. In another study on Oneida Lake, Mayer et al. (2002) indicate zebra mussels to provide a structural refuge to benthic invertebrates from predation. Moreover, a dramatic increase in light penetration led to an increase in benthic primary production and an extension of macrophytes to a greater depth in post-invasion years.

Studies dealing with mussel grazing on cyanobacteria show discrepancies of results. Horgan and Mills (1999) assume that zebra mussels clear particles over a wide size range and are, therefore, not very selective. Baker et al. (1998) present some evidence from their work on the Hudson River relating to the decline of cyanobacteria (*Microcystis*) after the invasion of zebra mussels. In addition, some other studies show that the highest

clearance rates of zebra mussels are on single cells of the cyanobacterium *Microcystis* (Baker et al., 1998; Bastviken et al., 1998). Contrary to Baker et al. (1998) and Bastviken et al. (1998), Vanderploeg et al. (2001) believed that *Dreissena* promoted the return of *Microcystis* blooms in Lake Huron and Lake Erie, because they found the mussels to selectively reject colonies of *Microcystis*. This observation is supported by Lavrentyev et al. (1995), who did not observe any filtering impact of zebra mussels on *Microcystis*, and by Nicholls et al. (2002) who reported a 13-fold increase in *Microcystis* biovolume after zebra mussels established in 1995 in the Bay of Quinte, Lake Ontario. However, such an increase in *Microcystis* was only observed in 1998, and thereafter the *Microcystis* biovolume decreased to the levels prevailing in the pre-*Dreissena* invasion period. Fernald et al. (2007), however, found no evidence of an association of *Microcystis* dominance and high zebra mussel grazing activity. Naddafi et al. (2007) showed that selective feeding of zebra mussels differed seasonally. This may reflect seasonal differences in the algal properties: concentrations, quality, toxicity and size spectrum.

In conclusion, serious discrepancies exist between studies on the impact of zebra mussels on lake phytoplankton. In a recent attempt to clarify some of the inconsistencies of published data, Dionisio Pires et al. (2004, 2005a) demonstrated that zebra mussels not only preferentially filter cyanobacteria, mainly *Microcystis*, from the water column but also ingest these (Dionisio Pires et al., 2005a). In the same study, using ambient phytoplankton from lakes in the catchment area of the River Rhine, The Netherlands, the clearance rates of *Dreissena* on *Microcystis* from Lake IJsselmeer were higher than the clearance rates of *Daphnia galeata* (Fig. 3). In another set of experiments, Dionisio Pires et al. (2005b) used laboratory reared strains of *Microcystis aeruginosa* and *Planktothrix agardhii*, both a microcystin-producing and a microcystin-free strain. In these experiments, the mussels were able to feed on both types of strains, irrespective of the microcystin content. A recent study by Dionisio Pires et al. (2007) shows that *D. galeata* fed on only *Scenedesmus* if a mixture of *Planktothrix* and *Scenedesmus* was offered, but *D. polymorpha* fed on both these algae in the mixture (Fig. 4). These findings have opened the prospects of using these mussels as a biofilter in the reduction or removal of harmful cyanobacterial blooms in shallow lakes, e.g. many Dutch lakes where the mussels are already present but usually in low densities. More recent studies in the Netherlands, and also in some other countries, confirm the important role of zebra mussels as biofilters (Lammens et al., 2004; Ibelings et al., 2007; Orlova et al., 2004). Return of zebra mussels in Lake Veluwe led to the expansion of *Chara* beds in this lake (Lammens et al., 2002; Lammens et al., 2004).

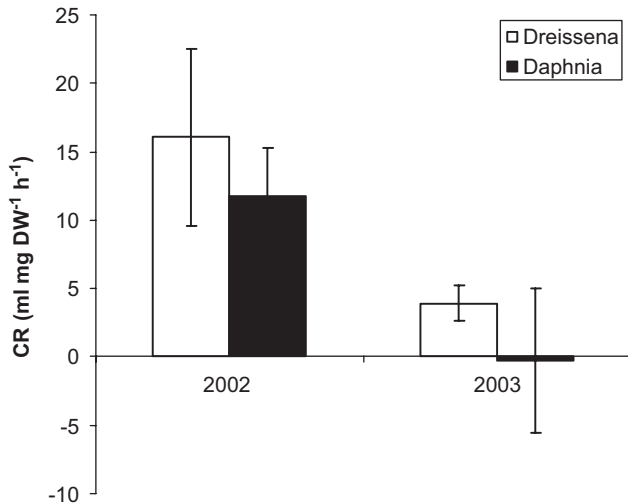


Fig. 3. Mean clearance rates ($\text{ml mg DW}^{-1} \text{h}^{-1} \pm \text{SE}$) of zebra mussels (*Dreissena polymorpha*, white bars) and *Daphnia galeata* (black bars) on the *Microcystis aeruginosa* fraction of the summer seston from Lake IJsselmeer in 2002 and 2003. Modified from Fig. 3 in Dionisio Pires et al. (2005a).

The mussels stabilized the lake-wide clear water (Secchi-depth >1 m) for long periods (Ibelings et al., 2007). These authors concluded that proper management of fish stocks (mainly bream), *Chara* and *Dreissena* should allow Lake Veluwe to maintain the clear-water phase even under high TP concentrations.

As mentioned above, studies in Oneida Lake in North America showed clear improvement of light climate and macrophyte vegetation extending to deeper areas in the presence of zebra mussels (Idrisi et al., 2001; Mayer et al., 2002). The mussels have also recently been reported to be responsible for an increase in the diversity of macrophytes in Oneida Lake (Zhu et al., 2006). Several other studies indicate an increase of water transparency due grazing by zebra mussels based both on empirical and theoretical evidence (e.g. Caraco et al., 1997). This may result in reduced zooplankton densities due to competition, as suggested for Oneida Lake (Horgan and Mills, 1999). The decline of cyanobacteria (*Microcystis*) has also been attributed to the invasion of zebra mussels (Baker et al., 1998; Smith et al., 1998). These studies reveal that zebra mussels appear to be a promising tool in biomanipulation of lakes. In the Netherlands, the zebra mussels also have a high nature value as they are the main food source of overwintering diving ducks, e.g. the tufted duck *Aythya fuligula* (De Leeuw et al., 1999).

The role of zebra mussels in shallow lakes in the Netherlands is schematically depicted in Fig. 5. Due to their powerful filtration capacity they may directly and indirectly (filtration leading to improved light conditions) depress cyanobacteria. Macrophytes may profit from the improved light conditions (seed germination

because light reaches the bottom). As a result, stems of macrophytes may serve as a substrate for the settlement of *Dreissena* larvae (Noordhuis et al., 2002), which contributes to the expansion of zebra mussels. However, as the infestation of the macrophyte stems by the mussels increases, this may cause the macrophytes to drop and sink. The mussels expel the particles that are not ingested and digested, in the form of faeces and pseudofaeces which sink to the bottom. As a result, the mussels transfer energy from the water column to the bottom. In addition to their role as biofilters, the mussels also serve as food for diving ducks and certain fish species, like roach (*Rutilus rutilus*).

Disadvantages of using bivalves in lake restoration research

There are also certain disadvantages of using bivalves in lake restoration. First, the substrate for settlement of mussel larvae is not always adequate. This could be overcome by placing stones or shells on the lake bottom but we do not know if this in some way will affect the ecosystems adversely. However, we do know that these shallow lakes serve as a recreation area and any hard substrate on the bottom together with the sharp shells of the mussels may injure swimmers. This disadvantage might be circumvented by exposing artificial substrates in the open water (Kusserow et al., in press).

Secondly, the zebra mussels may spread and expand their territory to connecting waterbodies where they may cause problems due to their settling on hard substrates (Berkman et al., 2000), including clogging of water intake pipes or settlement on the shells of unionid mussels, which eventually die (Ricciardi and Atkinson, 2004). Lastly, invasive species as zebra mussels may also negatively affect the biodiversity of native fauna through competition for food resources and habitat.

Prospects of using native mussels as grazers

The potential disadvantages of using zebra mussel have led researchers to focus on native mussels as a filtering tool in lake restoration and management programmes instead of the zebra mussel. Large unionid mussels, like *Anodonta* sp. en *Unio* sp. inhabit many lakes. Different studies (Strayer et al., 1994; Vaughn et al., 2004; Welker and Walz, 1998) have shown that unionid mussels can filter large amounts of the water column, as long as their biomass is high (Vaughn et al., 2004). According to Vaughn et al. (2004) (Fig. 1) about 34 mussels m^{-2} ($\text{DW} = 160 \text{ g}$) would deplete all the chlorophyll ($20 \mu\text{g L}^{-1}$) of a system in about 4 days. A density of 34 mussels m^{-2} is not high and commonly encountered in the field (Weber, 2005). For more productive systems, however, a higher mussel biomass will be needed. We are, however, unable to estimate the

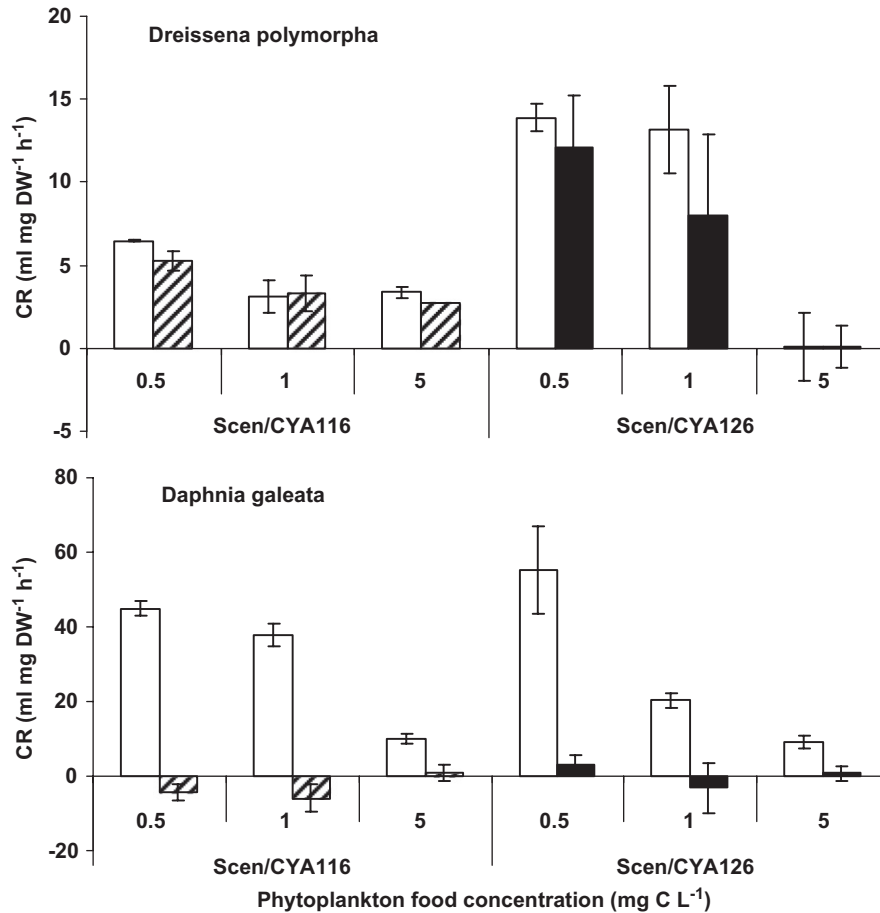


Fig. 4. Mean clearance rates ($\text{ml mg DW}^{-1} \text{h}^{-1} \pm \text{SE}$) of the zebra mussel *Dreissena polymorpha* (upper panel) and the cladoceran *Daphnia galeata* (lower panel) on 50:50% mixtures (based on carbon content) of the green alga *Scenedesmus obliquus* and the cyanobacterium *Planktothrix agardhii* at three different food concentrations (0.5, 1 and 5 mg C L^{-1}). *Planktothrix* was either provided as a microcystin-free (CYA116) and a microcystin-containing (CYA126) strain. Scen = *Scenedesmus*. White bars show clearance rates on *Scenedesmus*, dashed bars on CYA116, and black bars on CYA126. Modified from Fig. 2 in Dionisio Pires et al. (2007).

needed areal densities of mussels for highly productive systems. Bontes et al. (2007) and Dionisio Pires et al. (2007) examined if unionid mussels are also capable of filtering cyanobacteria, e.g. colony forming *M. aeruginosa* and filamentous *P. agardhii*. *Anodonta anatina* shows a slight preference for green algae like *Scenedesmus*, but filters and ingests both *Microcystis* and *Planktothrix*, causing a net loss of these cyanobacteria from the water column. Current research also shows that another unionid bivalve, *Unio pictorum*, is able to filter and ingest *Planktothrix* (Dionisio Pires, unpublished data). These mussels are, therefore, a promising tool in lake restoration and should be a good alternative for the use of exotic species like *Dreissena*.

Concluding remarks

Literature on restoration of shallow, eutrophic lakes, especially from north-western Europe, reveals that in

many cases the feasibility and success of the biomani-pulation measures are debatable. The rehabilitation and management studies are skewed towards improving water quality rather than to obtaining a deeper insight into intricacies of food web interrelationships, and to advance theory forming. In most cases where the measures were successful, a sustained improvement in the light climate played a crucial role in promoting macrophyte development following reduction of planktivorous fish biomass. Considering the sustainability of the positive effects over 8–10 years, the cases of success are very limited. The main bottlenecks in most failed attempts have been due to: (1) inadequate reduction of the allochthonous phosphorus (P) inputs and increased rate of in-lake P release from sediments; (2) inability of daphnids to feed effectively on filamentous and colonial cyanobacteria; (3) failure of development of a stable macrophyte vegetation; (4) our inability to reduce planktivorous fish biomass and maintain it at a consistently 'low standing level'; and (5) failure in

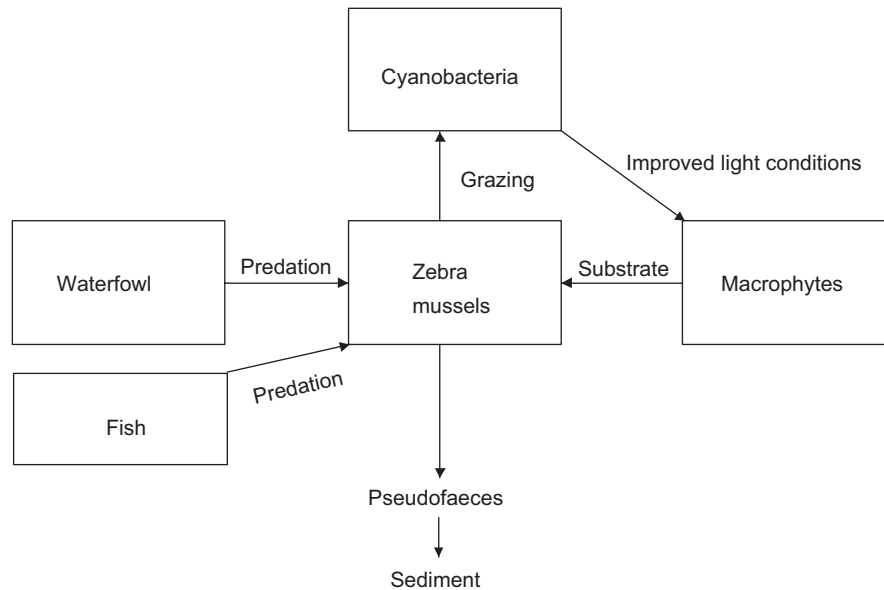


Fig. 5. Diagram of the “central role” of zebra mussels in the food web of temperate shallow lakes. Through grazing, zebra mussels may depress the cyanobacterial biomass (and of other seston). This in turn leads to improved light conditions in a lake, which is beneficial for the development and establishment of macrophytes. Macrophytes in turn, may become substrate for the settlement of mussel larvae (although it is not clear what happens when the stems and leaves die off). The mussels also aid in the transfer of energy from the water column to the benthos by filtering particles from the water and depositing a part of it on the sediment as faeces and pseudofaeces. In addition to these biofilter functions, the mussels are also an important food source for waterfowl (diving ducks), especially in the Netherlands. To a lesser extent, they also serve as food for some fish, as roach (*Rutilus rutilus*).

establishing piscivores, mainly northern pike (*Esox lucius*), to regulate planktivorous fish standing crop biomass to the desired low levels.

We propose three relatively new ecotechnological, complementary measures for future studies: (1) reduction of sediment resuspension in the shallow lakes through a decrease in wind-fetch factor; (2) water-level management, which is going to play a more crucial role in view of the climatic changes relating to a rise in the sea level; and (3) use of bivalve mussels including prospects of using zebra mussels (*Dreissena polymorpha*), as grazers on lake seston dominated by colonial cyanobacteria.

Acknowledgments

We thank the guest editors of this special issue for inviting us to submit a review paper on the occasion of the retirement of Prof. Dr. Jürgen Benndorf. It is an honour to contribute a paper to this special issue of *Limnologia* dedicated to Jürgen. The first and the last author have pleasant memories of Jürgen’s visits to Nieuwersluis in the late 1980s and of our visits to Dresden on invitation from Jürgen. On his retirement, Jürgen will enter a new phase in life; we wish him all happiness and joy. This is publication number 4312 of

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