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EUTROPHICATION IN LAKES

Restoration of shallow lakes by nutrient control and biomanipulation—the successful strategy varies with lake size and climate

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Abstract Major efforts have been made worldwide to improve the ecological quality of shallow lakes by reducing external nutrient loading. These have often resulted in lower in-lake total phosphorus (TP) and decreased chlorophyll *a* levels in surface water, reduced phytoplankton biomass and higher Secchi depth. Internal loading delays recovery, but in north temperate lakes a new equilibrium with respect to TP often is reached after <10–15 years. In comparison, the response time to reduced nitrogen (N) loading is typically <5 years. Also increased top-down control may be important. Fish biomass often declines, and the percentage of piscivores, the zooplankton:phytoplankton biomass ratio, the contribution of *Daphnia* to zooplankton biomass and the cladoceran size all tend to increase. This holds for both small and relatively large lakes, for example, the largest lake in Denmark (40 km^2), shallow Lake Arresø, has responded relatively rapidly to a ca. 76% loading reduction arising from nutrient reduction and top-down control.
Some lakes, however, have proven resistant to loading reductions. To accelerate recovery several physico-chemical and biological restoration methods have been developed for north temperate lakes and used with varying degrees of success. Biological measures, such as selective removal of planktivorous fish, stocking of piscivorous fish and implantation or protection of submerged plants, often are cheap versus traditional physico-chemical methods and are therefore attractive. However, their long-term effectiveness is uncertain. It is argued that additional measures beyond loading reduction are less cost-efficient and often not needed in very large lakes.

J. P. Jensen was deceased.

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Eutrophication of shallow lakes with special reference to Lake Taihu, China

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Although fewer data are available on tropical lakes these seem to respond to external loading reductions, an example being Lake Paranoá, Brazil (38 km^2). However, differences in biological interactions between cold temperate versus warm temperate-subtropical-tropical lakes make transfer of existing biological restoration methods to warm lakes difficult. Warm lakes often have prolonged growth seasons with a higher risk of long-lasting algal blooms and dense floating plant communities, smaller fish, higher aggregation of fish in vegetation (leading to loss of zooplankton refuge), more annual fish cohorts, more omnivorous feeding by fish and less specialist piscivory. The trophic structures of warm lakes vary markedly, depending on precipitation, continental or coastal regions locations, lake age and temperature. Unfortunately, little is known about trophic dynamics and the role of fish in warm lakes. Since many warm lakes suffer from eutrophication, new insights are needed into trophic interactions and potential lake restoration methods, especially since eutrophication is expected to increase in the future owing to economic development and global warming.

Keywords Lake restoration · Large lakes · Recovery · Nutrient loading reduction · Climate

Introduction

Efforts in the last 20–30 years have attempted to combat eutrophication by reducing external phosphorus (P) loading in Western Europe and North America. Sewage and industrial loading has declined, whereas nutrient input from diffuse sources often remains high, particularly in countries with intensive agriculture (Van der Molen & Portielje, 1999; Kronvang et al., 2005).

Many lakes have responded positively to nutrient loading reductions (Sas, 1989; Marsden, 1989; Jeppesen et al., 2005c). An analysis of European and North American lakes based on 35 case studies, including long time-series data, revealed that, although internal P loading does delay recovery, new equilibria with respect to (total phosphorus) TP were reached in most lakes after <10–15 years, marginally dependent on lake retention time and depth (Jeppesen et al., 2005c). In comparison, response times to reduced N loading are typically <5 years. These findings also apply to shallow Danish lakes after a reduction in mainly external P loading (Søndergaard et al., 2002a, 2005; Jeppesen et al., 2002, 2005a, b). In these lakes, TP has declined during all seasons, particularly in winter, followed by spring and autumn, while weaker effects in late summer can be ascribed to internal P loading. Changes in chlorophyll *a* follow TP, indicating that nutrient constraints are important in determining seasonal behaviour. Diatoms declined precipitously in winter and spring. Non-heterocystous cyanobacteria declined throughout the summer, primarily in early summer, while heterocystous cyanobacteria increased in late summer and autumn. Green algae declined throughout the year but least so in mid-summer. In Barton Broad, a shallow lake in the UK, Phillips et al. (2005) observed a similar pattern with strong effects on diatoms in spring and a decline first in non-heterocystous cyanobacteria and secondly, albeit slower, in heterocystous genera after 15–20 years. Thus, there is clear evidence for enhanced resource control of phytoplankton after an external loading reduction.

However, enhanced top-down control by zooplankton may also play a role. Fish biomass often declined in the Danish lakes and the percentage of piscivores often increased. Similar observations were made in the study of 35 North American and European lakes in recovery (Jeppesen et al., 2005c); in 82% of the lakes for which data were available, fish biomass declined with TP, while the piscivore proportion increased in 80% of the lakes. This is surprising given the high longevity of the dominant species. While there were no changes in zooplankton biomass, the contribution of *Daphnia* to the biomass and mean individual biomass of cladocerans increased most notably during summer. Moreover, the zooplankton:phytoplankton biomass ratio, and probably phytoplankton grazing, rose. This is suggested also by the cladoceran size increase. Higher abundance of large-bodied zooplankton, particularly in summer, may reflect that increased piscivory leads to stronger predation control of young-of-the year (YOY), primarily planktivorous, fish. This reduces predation on zooplankton during summer, when YOY fish are abundant and forage in the pelagic zone. Enhanced abundance of submerged macrophytes or filamentous algae in some lakes may also enhance survival of large-bodied zooplankton as they can serve as a daytime refuge from predation (Burks et al., 2002).

A north temperate example: recovery of Lake Arresø, Denmark

The positive response to external nutrient loading reduction is not restricted to small lakes. Here we elaborate in more detail on the response of Arresø to nutrient loading reduction. Arresø (coordinates) is the largest lake in Denmark (40 km^2). It is shallow (mean depth 3.1 m, max depth 5.9 m) and has a 215 km^2 catchment area. The retention time is long (1.3–10.3 years, mean 1989–2003: 3.5 years) compared with most Danish shallow lakes. The lake is near the coast and exposed to prevailing north-westerly winds and, thus, wave-induced resuspension (Kristensen et al., 1992). Based on intensive sampling (every 2–8 h) during different seasons in 1991, and modelling, resuspension was calculated to occur 50% of the time and to reduce Secchi depth to <0.5 m on average (Kristensen et al., 1992). The lake was loaded heavily with P and N from the catchment, particularly P from the upstream city of Hillerød. TP loading decreased from 0.68 g P m^{-2} year^{-1} in 1989 to 0.16 g P m^{-2} year^{-1} for 1996–2003, and TN decreased from 13 to 11 g N m^{-2} year^{-1} (Jacobsen et al., 2004). The reduction mostly was due to improved sewage treatment, establishment of artificial lakes on the main inlet stream, and possibly to reduced fertilization in the catchment. Nutrient load reduction led to substantial improvements in the lake. TN, TP, chlorophyll *a* and the total biomass (and especially of green algae) of phytoplankton have declined markedly (Fig. 1). Diatom biomass has tended to increase with associated effects on silicate concentration, whereas the trend for cyanobacteria is ambiguous. Algal biomass changes cannot be ascribed entirely to enhanced nutrient control, since there have been marked zooplankton community changes and potential grazing, most likely due to fish community changes. Biomasses of the dominant plankti-benthivorous bream (*Abramis brama*) (Fig. 2) and benthic ruffe (*Gymnocephalus cernua*) are decreasing, whereas zander (*Sander lucioperca*), a potential predator, is increasing, implying enhanced top-down control on prey fish. Accordingly, zooplankton biomass and the share of large-sized cladocerans have increased substantially. This can be explained by reduced predation pressure on zooplankton, since the algal biomass was dominated by edible green algae when biomass was low and the zooplankton were dominated by small forms. With increased zooplankton biomass the grazing pressure on phytoplankton has intensified, and the phytoplankton face simultaneous, enhanced resource control due to lower P and N concentrations. Grazing control is strengthened by the shift to large-sized cladocerans *Daphnia hyalina* and *D. galeata* (Fig. 1), which have broader feeding capabilities than previously dominant *Bosmina* spp. and *Chydorus sphaericus*. Following the increase in zooplankton biomass and cladoceran size, and the zooplankton:phytoplankton ratio, water transparency has improved (Fig. 1), emphasizing the role of enhanced grazer control of phytoplankton.

Seasonal phytoplankton biomass reduction and Secchi depth increases are larger in spring, autumn and winter than in summer (Fig. 3). This also is true for the zooplankton:phytoplankton biomass ratio and cladoceran body mass, suggesting that changes in grazing pressure are important. The minor effect in summer coincides with fish larvae exploiting the pelagic in Danish lakes (Jeppesen et al., 2004). Moreover, during this period, nitrate is low (in all years) (Fig. 3), which likely may have dampened P loading reduction effects.

However, loading still remains too high to promote a clearwater state with macrophytes, which prevailed in the 1900's per paleolimnological analyses (Klein, 1989).

Accelerating the recovery of northern temperate lakes

Positive effects may not occur after nutrient input reduction. Several lakes have been resistant to loading reductions and shown slow recovery (Sas,

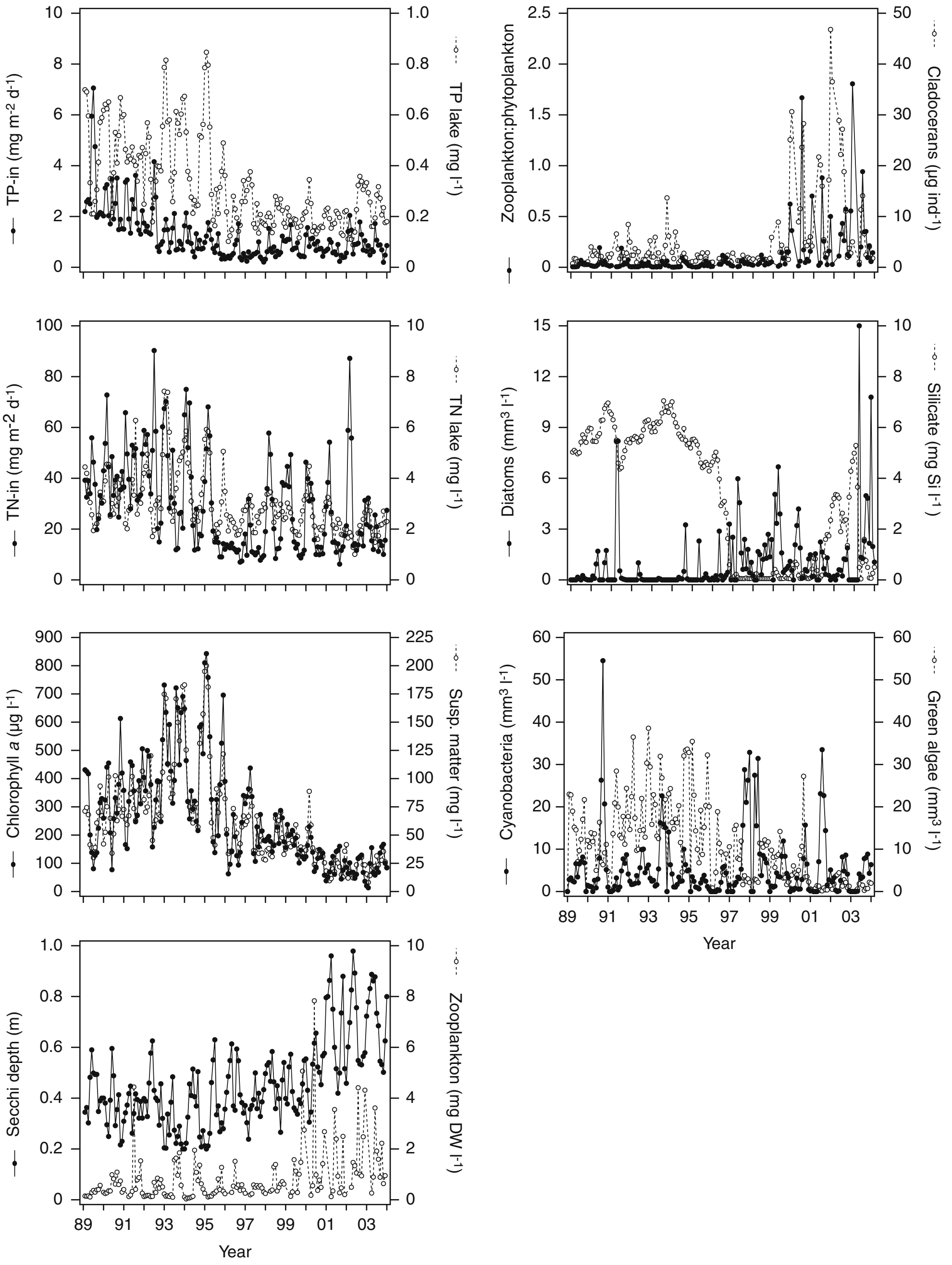

Fig. 1 Monthly mean data on various environmental variables in Arresø. TP_{in} and TN_{in} are the external loading of the lake. Zooplankton:phytoplankton is the biomass (mg DW) ratio

1989; Marsden, 1989). For some lakes, this reflects insufficient nutrient input reduction to promote a clearwater state. For example, significant and sustained changes in the biological community and water transparency of shallow, temperate, freshwater lakes may not appear unless TP is reduced below 0.05–0.1 mg P l^{-1} (Jeppesen et al., 2000) or, for deep lakes, 0.02–0.03 mg P l^{-1} (Sas, 1989). Even when P loading has been reduced sufficiently, resistance to improvement often is observed. This resistance may be ''chemical'', P concentrations remain high due to release from

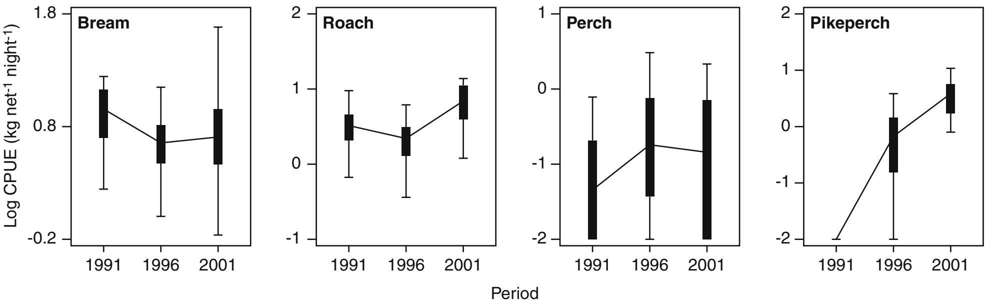

Fig. 2 Box plot (10, 25, 75, 90% percentiles) of log(base e) transformed catch per net per night in Arresø using 52 nets distributed in the lake according to Jeppesen et al. (2004)

the sediment pool accumulated when loading was high (Søndergaard et al., 2002a). Various methods have been used to reduce internal P loading (Cooke et al., 1993; Søndergaard et al., 2002a, b), including sediment removal and chemical treatment with aluminum or iron salts. In stratified lakes, oxygen or nitrate injections to the bottom layer or destabilization of the thermocline have been used (Cooke, 1993). For large, shallow lakes, it is debatable whether sediment removal and chemical treatment are feasible methods. Sediment removal is expensive, particularly for large lakes due to transport and disposal. Moreover, sediment resuspension and redistribution may hamper removal of the upper, nutrient-rich sediment layers. Resuspension also is a problem with chemical methods. P bound to aluminum or iron may return to the water on windy days and loosely bound P made available to phytoplankton. Finally, the sediment P pool often is small in large lakes because resuspension leads to washout of particulate TP (unless hydraulic retention time is long) and organic net sedimentation is low, the latter due to high mineralization. Thus, the usefulness of sediment removal or treatment is more limited in large than small lakes. The fast response of Arresø was attained without sediment removal.

The resistance also may be ‘‘biological’’. Planktivorous and benthivorous fish contribute to biological resistance in shallow eutrophic lakes (Moss, 1990; Scheffer et al., 1993). High fish predation prevents the appearance of large herbivorous zooplankton, which would otherwise clear the water, and diminishes benthic invertebrates, which stabilize and oxidize the sediment. Moreover, nutrient excretion to overlaying waters by benthic-feeding fish or fish bioturbation of surface sediment may play a role (Breukelaar et al., 1994; Persson, 1997). To overcome biological resistance, various fish manipulation methods have been developed (Benndorf, 1995; Drenner & Hambright, 1999; Søndergaard et al., 2001). One method is enhancement of top-down control of phytoplankton by selective removal of planktivorous fish; a method employed extensively in the temperate zone, but only just beginning in the subtropics (Scasso et al., 2001) and other warmer climate zones, such as Mediterranean arid lakes (Beklioglu & Tan, personal communication). Removal of 75–80% of the planktivorous and benthivorous fish stock over 1–2 years is recommended to avoid regrowth and stimulate growth of potentially piscivorous perch (Perrow et al., 1997; Hansson et al., 1998; Meijer et al., 1999). An alternative or supplementary method to fish removal is stocking of 0^+ pike to control newly hatched plankti-benthivorous roach and bream (Prejs et al., 1994; Berg et al., 1997; Skov & Berg, 1999) though the results are ambiguous (C. Skov et al., unpublished data). Others have stocked pikeperch, walleye (*Stizostedion vitreum*) and largemouth bass (*Micropterus salmoides*) (Benndorf, 1995; Lathrop et al., 2002). In contrast to chemical engineering methods, fish manipulation often is cheap (Jeppesen & Sammalkorpi, 2002) and therefore attractive, though its long-term stability is uncertain as a return to a more turbid state has occurred in many of the lakes. The reasons for this remain to be elucidated, but

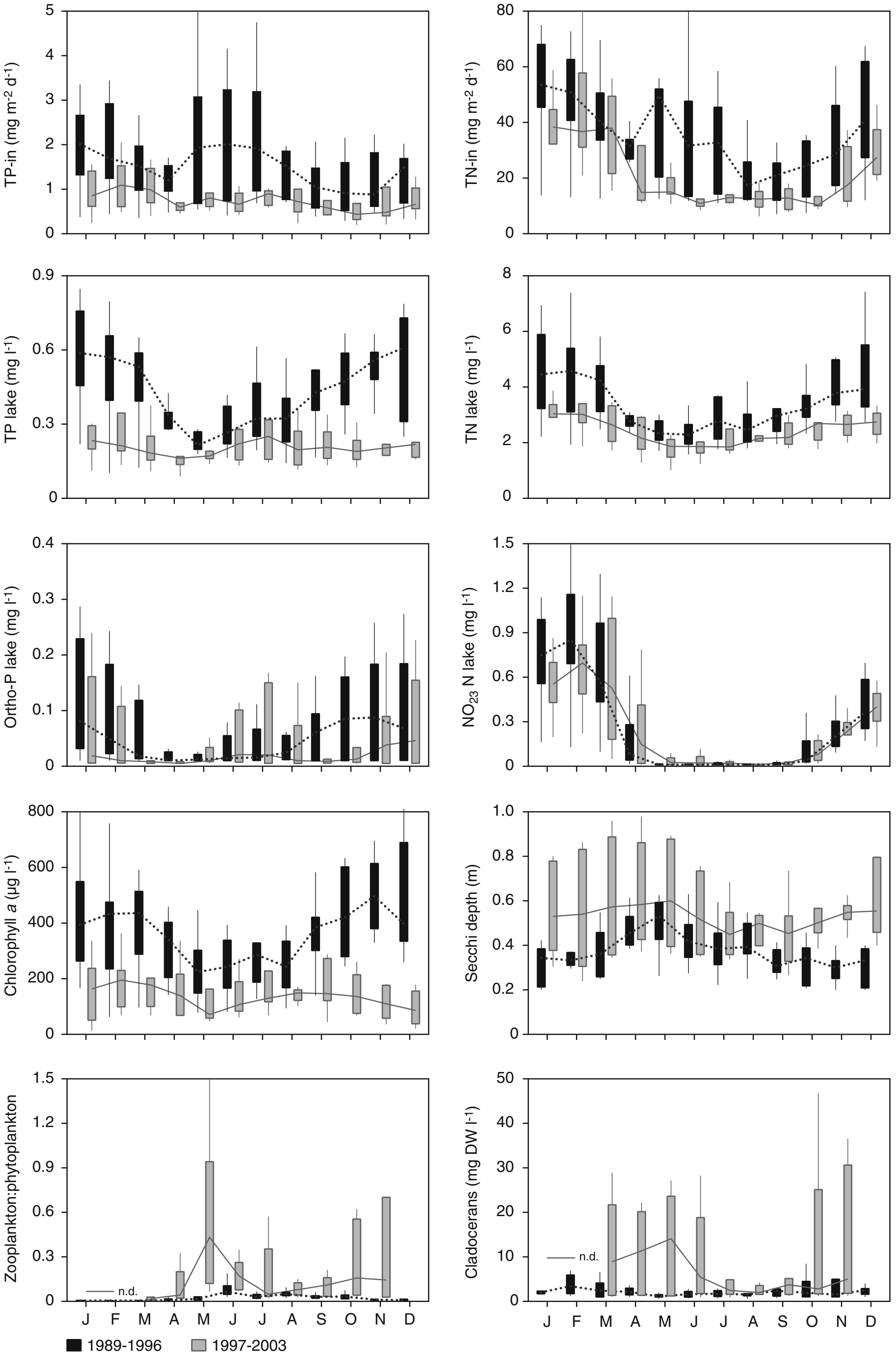

Fig. 3 Box plot (10, 25, 75, 90% percentiles) of selected environmental variables in Arresø during the first (1989–1996) and the last part of the study period (1997–2003). n.d. means no data in Jan–Feb for 1997–2003. See also legend of Fig. 1

factors such as reinforced internal loading of P, return of planktivorous dominance (particularly roach in Danish lakes) and large year-to-year variations in the coverage of the submerged macrophyte community may play a role. However, in Danish lakes suspended matter remains lower and Secchi depth higher likely reflecting an apparent permanent lower bream population (authors unpublished data).

It is unlikely that fish manipulation will be feasible for very large lakes (say >500 km^2). First, it is difficult to obtain a 'sledgehammer' effect on the target fish population in very large lakes. The fish cannot easily be removed fast enough to compensate for their annual reproductive rate. Changes in the fish stock may simply become difficult to discern unless the fishing effort is substantial. Second, recent studies indicate that the fish population responds quickly to a nutrient loading reduction (Jeppesen et al., 2005a, b, c). This may render fish stock intervention less attractive in very large lakes as the natural changes may occur at higher speed than those invoked by biomanipulation in such lakes. Third, fish stocking is expensive for large lakes. However, biomanipulation combined with nutrient loading reduction has yielded a fast response (higher transparency, fewer cyanobacteria and in some cases extensive growth of submerged macrophytes) in medium large lakes, examples being Lake Vesijärvi, Finland (109 km^2), Lake Wolderwijd, Holland (27 km^2), and Lake Christina, USA (16 km^2) (Hanson & Butler, 1990; Peltonen et al., 1999; Meijer et al., 1999).

Delay in recovery and re-establishment of submerged vegetation after nutrient loading reduction have often been noted (Sas, 1989; Cooke et al., 1993; Jeppesen & Sammalkorpi, 2002; Jeppesen et al., 2005c). The delay in plant appearance may be due to lack of seed banks, waterfowl grazing, limited grazing on periphyton or too high turbidity (Søndergaard et al., 1996; Mitchell & Perrow, 1997; Lauridsen et al., 2003). Construction of exclosures to protect macrophytes against waterfowl grazing to improve plant re-establishment has been used as an alternative or supplementary restoration tool to fish manipulation (Cooke, 1993; Jeppesen & Sammalkorpi, 2002). The exclosures enable macrophytes to grow in a grazer-free environment where they can spread seeds, turions or plant fragments and thereby augment colonization. Moreover, they serve as a daytime refuge for zooplankton. Plant refuges as a restoration tool is probably most useful in small lakes and in the littoral zone of other lakes where colonization is restricted to the near shore areas due to light limitation in the deeper main lake. Waterfowl aggregate in littoral emergent zones, which provide shelter and nest sites, and may impart higher grazing pressure on plants. Plants as a refuge have greater effect in nutrient-rich lakes where plant density often is highest and prey fish are confined to the pelagial (Jeppesen et al., 1997; Blindow et al., 2000; Burks et al., 2002). Transplantation or protection of plants (in sheltered beds) and seeds may be useful in large shallow lakes if pre-studies reveal that (re)-colonization is seed-limited (Weisner & Strand, 2002; Ke & Li, 2006). However, it is important to evaluate whether wind (wave) disturbance will prevent colonization. In large lakes effort should be concentrated on sheltered areas where plants can colonize gradually, as seen in large (27 km^2) Lake Veleuwe (Meijer et al., 1999).

Warm lakes

Few long-term lake recovery studies after reduced external loading exist for tropical and subtropical lakes: here we present an example from Brazil. Lake Paranoá (15°48′S, 47°47′W) is a shallow, urban, man-made lake (area 38 km^2, mean depth: 13 m, retention time: 0.9 years). It was created in 1959 for recreational purposes, hydroelectric power production, to increase the humidity of the region, as well as to receive wastewater and run-off from the city of Brasilia. The first plankton study recorded dominance of desmids and large-bodied cladocerans (*Daphnia* and *Ceriodaphnia*) (Oliveira & Krau, 1970). Later, phytoplankton biomass was dominated by *Cylindrospermospsis raciborskii*, which remained dominant in subsequent decades (Cronberg, 1976; Pinto-Coelho & Giani, 1985; Branco & Senna, 1991). *Microcystis aeruginosa* blooms occurred periodically during the end of the dry season

(Branco & Senna, 1994). Besides the permanent bloom of filamentous cyanobacteria (*C. raciborskii*), eutrophic conditions were also indicated by small-bodied zooplankton (mainly rotifers and small cladocerans, such as *Diaphanosoma birgei* and *Bosmina* spp.), low Secchi depth (<50 cm) and high levels of nutrients and chlorophyll *a* (Branco & Senna, 1996; Branco & Cavalcanti, 1999, Fig. 4). Aquatic macrophytes, such as free-floating *Eichhornia crassipes* and *Pistia stratiotes*, also spread in some areas. Eleven fish species colonized the lake from the catchment. In addition, the lake was stocked with exotic fish species, such as bluegill sunfish (*Lepomis macrochirus*), black-bass (*Micropterus salmoides*), carp (*Cyprinus carpio*), Congo (*Tilapia rendalli*) and Nile (*Oreochromis niloticus*) tilapias, and the piscivorous tucunaré (*Cichla ocellaris*) from the Amazon Basin (Ribeiro et al., 2001). In the late 1980s, tilapia dominated and accounted for 50% of total fish biomass. In subsequent years, the lake was stocked with tambaqui (*Colossoma macropomum*) and tamoatá (*Callychthys callychthys*), both from the Amazon Basin and with high commercial value.

In 1993–1994, two tertiary sewage treatment plants capable of processing 2,400 l s^{-1} were constructed in addition to a complementary sewage collecting system. Resultant decrease in external point-source of TP loading, from 6.3 g m^{-2} $year^{-1}$ in 1989 to 0.48 g m^{-2} $year^{-1}$ in 1998 (Pereira & Cavalcanti, 1997; Burnett et al., 2001), led to decreased mean TP, and also total Kjeldahl nitrogen (TKN) loading and concentration decreased (Fig. 4). Chlorophyll *a* values decreased (Fig. 4), and Secchi depth attained 2.4 m in 1999. Important planktonic community level changes were observed from 1996 to 1999: (1) decreased cyanobacteria dominance and replacement of *C. raciborskii* by green algae and diatoms by late 1998; (2) short-term dominance of colonial floating green algae (*Botryococcus braunii*), replacing *M. aeruginosa* in some hypertrophic areas in 1996; (3) re-appearance of *Ceriodaphnia cornuta*, *Daphnia gessneri*, other small cladocerans, such as *Moina micrura* and *Bosminopsis deitersi* (Elmoor-Loureiro et al., 2004), and *Notodiaptomus cearensis*, an oligotrophic calanoid copepod species (Padovesi-Fonseca et al., 2001). Other strategies, such as reducing the retention time of the lake and fish population management, were used to generate further improvements. An echo-sounding campaign in 1998 revealed a fish stock of 1,500 tons, with tilapia constituting up to 90% of fish biomass. Laboratory studies on fish feeding rates on lake plankton and P excretion rates, plus an assessment of planktivorous fish impacts in enclosures, indicated that tilapia overpopulation control would prevent accumulated P from being available to primary production, especially due to bottom feeding (Starling, 1993a, b; Starling & Rocha, 1990). Tilapia control was initiated in the most eutrophicated region by legalizing commercial cast-net fisheries. Continuous improvement of lake environmental conditions was confirmed in early 2000 by lower chlorophyll *a* values, enhanced water transparency, and decreased fish

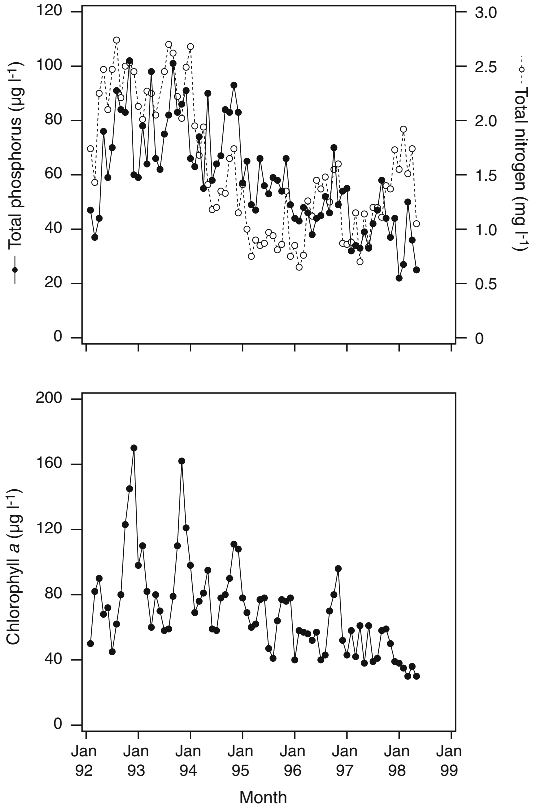

Fig. 4 Total phosphorus, total Kjeldahl nitrogen (TKN) and chlorophyll *a* in Lake Paranoá, Brazil, before and after (1993–1994) a major reduction of nutrient loading

biomass to 800 tons. Tilapia dominance declined, allowing recovery of a heterogeneous fish population, including native omnivores and piscivores, and some exotic species, all of which contributed to enhancement of large zooplankton populations.

Trophic dynamics and biomanipulation in warm lakes

While results from Lake Paranoá illustrate the importance of reducing external loading to restore subtropical and tropical lakes, it is difficult to evaluate effects of fish manipulations in the lake. It is debatable whether fish manipulation methods used in cold temperate lakes can be employed in warm temperate, subtropical and tropical lakes. Several factors indicate that fish stock manipulation may not have the same positive effects in warm lakes (Moss et al., 2004; Jeppesen et al., 2005d): (a) fish species richness often is higher and many fish show partial niche overlap, which should increase predator control of prey (Lazzaro, 1997; Aguiaro & Caramaschi, 1998); (b) fish stocks often are dominated by omnivores independent of trophic state (Lazzaro, 1997; Branco et al., 1997; Yafe et al., 2002; Blanco et al., 2003; Mazzeo et al., unpublished data) and generally few piscivores are present (Quirós, 1998); (c) fish density, but not necessarily biomass, is higher (1–2 orders of magnitude) (Scasso et al., 2001; Aguiaro et al., 2003; Mazzeo et al., 2003; Meerhoff et al., 2003); (d) fish reproduction occurs throughout the year (Fernando, 1994; Paugy & Lévêque, 1999) and many species are viviparous and/or show parental care (Lorier & Berois, 1995), assuring higher juvenile survival rates. Therefore, top-down control by piscivores probably is weaker in warm lakes. Since small fish are more zooplanktivorous and have higher energy demand per unit biomass (Kalff, 2002), small fish in high abundance leads to higher predation pressure on zooplankton.

Accordingly, zooplankton communities in tropical and subtropical lakes often are dominated by small cladocerans (i.e. *Diaphanosoma*, *Ceriodaphnia* and *Bosmina*), rotifers, and copepod juveniles and nauplii (Dumont, 1994; Lewis, 1996; Branco et al., 2002; Garcia et al., 2002; Lacerot et al., unpublished data). Large *Daphnia* spp. may appear in early spring and autumn in warm-temperate lakes (Romo et al., 2005) or, if fish are absent, for longer periods in subtropical lakes (Mazzeo et al., unpublished data). Omnivorous copepods usually dominate zooplankton biomass in oligo-mesotrophic systems, whereas microzooplankton prevail in eutrophic systems. Therefore, classic control of phytoplankton by large zooplankton usually is not found in warm lakes. However, the numerous microzooplankton in these systems may control nanophytoplankton, thus favouring larger cyanobacteria. Some works demonstrate that cyclopoid copepods can control diatoms, rotifers can graze small green algae, and particulate matter and associated bacteria is an important food resource for zooplankters in tropical lakes (Infante, 1978; González et al., 2005). The zooplanktivorous phantom midge *Chaoborus* also seems to be more abundant in tropical lakes (e.g. Aguilera & Goitia, 1999), perhaps because bottom water anoxia is more common, which may provide *Chaoborus* with a fish predation refuge (Lewis, 1996) and allow strong predation pressure on zooplankton (Arcifa et al., 1992). Finally, shrimps (e.g. *Palaemonetes argentinus* or *Macrobrachium borelli*) also can be important predators on zooplankton considering their high abundance, food preferences and several reproductive events from spring to summer (Boschi, 1981; Collins, 1999; Collins & Paggi, 1998).

Aquatic plants play an important structural role in most freshwater ecosystems (Moss, 1990; Scheffer et al., 1993), also in the tropics (Thomaz & Bini, 2003). In temperate nutrient-rich lakes, submerged plants act as daytime refuges for zooplankton against fish predators (Timms & Moss, 1984; Lauridsen et al., 1996; Burks et al., 2002). At night, large zooplankton move out to the open water to feed, thereby contributing to clearwater conditions in lakes with high macrophyte coverage (Jeppesen et al., 1997). However, in the tropics and subtropics, effects of macrophytes on trophic interactions are more complex, since all forms (i.e. emergent, submerged, floating-leaved and large free-floating species) can be prominent. Macrophytes are extremely important to fish in the tropics and subtropics. Removal of *Chara* spp. beds in an Itaipú reservoir resort

(Santa Helena, Brazil) with the purpose to decrease piranha (*Serrassalmus marginatus*) population led to decreased fish abundance and species richness from 25 to 10 species (Agostinho et al., 2003; Fig. 5). Studies comparing different habitats in tropical and subtropical lakes indicate that the smallest fish species and individuals aggregate in all vegetation forms (Conrow et al., 1990; Meschiatti et al., 2000; Meerhoff et al., 2003; Meerhoff et al. unpublished data). Densities above 140 ind m^{-2} of a single, small-sized species were found in submerged plant beds in a subtropical lake (Meerhoff et al., 2003). Therefore, submerged vegetation in warm lakes may be a poor refuge for large-bodied zooplankton, particularly cladocerans (Meerhoff et al., 2003, 2006). An inverse diel horizontal migration pattern (aggregating in the pelagial during day and among plants at night) was found for *Bosmina longirostris* and *Diaphanosoma birgei* during spring and autumn in a subtropical lake without piscivores (Lake Blanca, Uruguay; Iglesias et al., 2007). The preference of small omnivorous fish for emergent and submerged plant beds during day and the occurrence of *Chaoborus* in the pelagic at night determined the spatial distribution observed. In accordance with the suggestion of a poor refuge effect for zooplankton in warm lakes, no positive effect of plants on water clarity was found in nutrient-rich subtropical lakes in Florida, and nutrient rich lakes with high plant biomass often were turbid (Bachmann et al., 2002).

Considering the higher fish density in tropical systems and lack of refuges for zooplankton among macrophytes, fish biomass thresholds allowing major grazing pressure by zooplankton may be lower and fish reductions therefore have to be very large compared to temperate lakes to allow large-bodied grazers, like *Daphnia* spp, to dominate (Scasso et al., 2001; Mazzeo et al., unpublished data). The efficiency of decreasing planktivorous fish biomass by fish removal is further hampered by continuous and/or viviparous reproduction in many (sub)tropical species (Scasso et al., 2001 and Fig. 6). Therefore, it may be more difficult to provoke and maintain a trophic cascade effect in subtropical and tropical lakes than in temperate lakes. Accordingly, positive, but only short-term, cascading effects of a massive (>80%) fish kill (due to fungal infection) of the dominant planktivorous mosquito fish (*Gambusia affinis*) were found in Lake Naini Tal, India (Nagdali & Gupta, 2002). Zooplankton abundance increased, phytoplankton biomass and productivity declined, as did

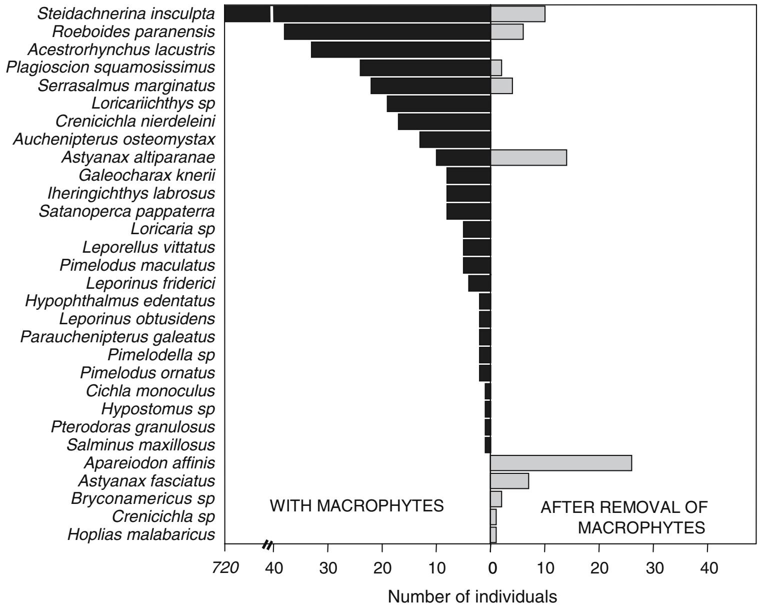

Fig. 5 Specific composition of fish assemblages in Santa Helena, Itaipú Reservoir (Paraná, Brazil) before (1987) and after (1988) a substantial removal of submerged macrophytes. Reproduced with kind permission from Agostinho et al. (2003)

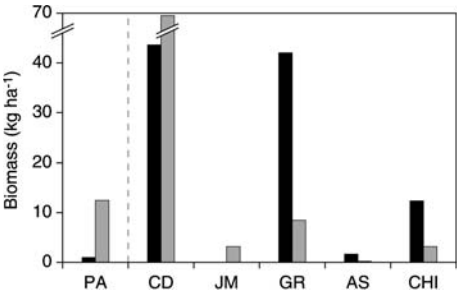

Fig. 6 Changes in the biomass of nekton at the beginning (black) and end (white) of summer 2003 in biomanipulated Lake Rodó (Uruguay) after an intensive programme of planktivorous fish removal. The biomanipulation had no effect on shrimps (*Paleomonetes argentinus*, PA) and viviparous fish, such as *Cnesterodon decemmaculatus* (CD) and *Jenynsia multidentata* (JM), while effective on the short-term for oviparous species: *Gymnogeophagus rhabdotus* (GR), *Astyanas* sp (AS) and *Cheirodon interruptus* (CHI). Moreover, no effect was observed on total fish biomass (from F. Quintans, unpublished data)

nutrient concentrations, resulting in higher water transparency. However, four months later, mosquito fish, plankton and nutrients had returned to previous levels.

In subtropical and tropical lakes, stocking of herbivorous silver carp (*Hypophthalmus molitrix*) has, with some success, been used to combat potentially toxic cyanobacteria (Starling et al., 1998; Datta & Jana, 1998). However, silver carp also consume zooplankton (Wu et al., 1997; Starling et al., 1998; Xu & Zie, 2004), which reduces grazing on small-sized phytoplankton. Therefore, it is unlikely that silver carp stocking, which is a symptom treatment rather than a restoration, will lead to a shift to a clear, macrophyte dominated stage (Matyas et al., 2003). Introduction of strictly piscivorous fish might be the only efficient biomanipulation strategy in (sub)tropical regions to control planktivorous fish. Ongoing mesocosm experiments using the sit-and-wait piscivore tararira (*Hoplias malabaricus*) support this hypothesis (Mazzeo et al., unpublished), but clearly more experiments are needed in this field before any firm conclusions can be drawn.

However, it is important to notice that trophic structure varies among warm lakes, depending on whether they are situated in wet or dry regions and temporal variations in temperature and salinity, and this may have implications on the restoration strategy as well. For example, tropical lakes are particularly sensitive to hydrological changes, which strongly affect their structure and functioning. In Cochabamba, Bolivia (17°S), switches from phytoplankton to macrophyte dominance in Lake Alalay have been associated to an increase in water level (Cadima, 1997). Higher densities and richness of zooplankton and fish were found during the low water season in several shallow lakes in Bolivia (Pouilly et al., 1999; Rejas & Maldonado, 2000). Water level changes also have strong effects on macrophyte abundance and water clarity in Turkish lakes (Beklioglu et al., 2003). These lakes, as well as northern Greek lakes, are, though warm in summer, subjected to cold winters, leading to a mixed fish community, often with low species richness compared to the subtropical and tropical lakes, and dominance of northern species (Beklioglu et al., 2003; Zalidis et al., 2002). These form an intermediate state between the north temperate lakes and winter warm temperate lakes and the subtropical/tropical lakes, which have to be taken into account when planning lake restoration (Beklioglu et al., 2003; Beklioglu & Tan, personal communication). Likewise, saline lakes are typically species poor (Williams, 1998) and, like in the subtropical lakes, submerged macrophytes appear to have little effect on water clarity in saline lakes (Moss, 1994a; Jeppesen et al., 1994) and form special cases.

In many experiments in temperate lakes, improvement in environmental state was observed without a trophic cascade after biomanipulation, i.e. without zooplankton species composition changes towards dominance of large-sized individuals and, consequently, higher phytoplankton grazing (Horppila et al., 1998). However, reductions in cyanobacteria and TP were observed, and water clarity increased. These phenomena may be due to reduced sediment P release and fish foraging following biomanipulation (Horppila et al., 1998). Biomanipulation also may reduce sediment nutrient release in tropical lakes, but the dominance of small fish species and better growth conditions for cyanobacteria suggest that effects may be temporary. Other methods, such as the combined use of aquatic plant harvests (mostly free-floating, if present) and hydraulic management, can be useful, though insufficient, for restoring small, shallow lakes in warm regions by decreasing internal nutrient loads (Rodríguez-Gallego et al., 2004). Sediment removal might be more attractive in such lakes, since P-content per unit volume of sediment exceeds that in the water column and plants (Søndergaard et al., 2003). However, drastic reduction of external nutrient loading seems to be the best method for restoring small or large subtropical and tropical lakes, but the scientific basis (e.g. nutrient threshold levels) to make decisions remains limited. Focus may well have to be on reducing external N loading as nitrogen has often been found to be the limiting nutrient for phytoplankton growth in tropical lakes (Lewis, 1996). Focus on nitrogen, in addition to phosphorus, is also relevant for temperate shallow lakes, as recent studies indicate that submerged macrophyte recovery after loading reduction is more likely to occur at moderately high TP when TN loading is low (Moss et al., 1994b; González Sagrario et al., 2005; James et al., 2005; Jeppesen et al., 2005b).

Conclusions

For small and large shallow lakes, the best strategy for improving the environmental state is external nutrient loading reduction. Like small lakes, large shallow lakes also may respond strongly and quickly to loading reduction. For smaller lakes resistant to nutrient loading reduction, physico-chemical and biological methods may enhance recovery. However, these methods are unlikely to be feasible in large shallow lakes. Sediment removal and chemical treatment, in particular, are less attractive because: (a) sediment transport and storage on land (if removed) will be expensive; (b) there is a large risk of sediment redistribution from resuspension; (c) the sediment P pool often is relatively small in large lakes. Fish manipulation also may be impractical because: (a) the large size makes it difficult to obtain a strong effect on the target fish population; and (b) fish population is among the first to respond to nutrient loading reduction, and natural changes in fish stock become difficult to discern in large lakes. If needed, transplantation/protection of aquatic plants (in sheltered beds) and seeds may be useful in large shallow lakes, the latter if pre-studies reveal that (re)-colonization is seed-limited. However, it is important first to evaluate whether wind (wave) disturbance will prevent colonization where seeds or plants are added.

Differences in biological interactions in cold temperate versus warm temperate-subtropical-tropical lakes make it difficult to apply biological restoration methods to warm lakes. Warm lakes often have prolonged growth seasons with a larger risk of long-lasting algal blooming and dense floating plant communities, higher dominance and abundance of small fish, higher fish aggregation in vegetation (loss of zooplankton refuge), more fish cohorts per year, and more omnivory by fish and less specialist piscivory. However, trophic structure varies among these lakes, depending on whether they are situated in wet or dry regions and temporal variations in temperature and salinity and this have implication for the restoration strategy.

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