Lake restoration and biomanipulation in temperate lakes: relevance for subtropical and tropical lakes

by

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Abstract

This introductory chapter to the book “Tropical eutrophic lakes: their restoration and management” gives a summary survey of the responses of temperate lakes to increased nutrient loading (the eutrophication process) and during remediation. Chemically and biologically conditioned resistance may cause a delayed response to the nutrient loading reduction and different methods of overcoming this resistance are briefly described. Biological restoration methods (termed “biomanipulation”) are promising new tools. However, a significant difference in biological interactions in temperate versus subtropical-tropical lakes renders it difficult directly to apply the biological restoration methods. These include often higher dominance and abundance of small fish, higher aggregation of fish in vegetation, higher number of fish cohorts per year, higher degree of omnivorous feeding by fish and less piscivory in subtropical and tropical lakes than in temperate lakes. Unfortunately, only little is known about the trophic dynamics and the role of fishes in warm lakes. Since many subtropical and tropical lakes are today heavily eutrophicated, there is a great need for gaining new knowledge of trophic interactions and possible lake restoration methods for these regions. This is amplified by the fact that the eutrophication problem is expected to increase in the near future due to both the economical development and global warming.

Eutrophication of lakes

During the past centuries, increased urbanization and sewage disposal, regulation of wetlands and streams and more intensive farming practices have increased the nutrient loading to many shallow lakes world-wide, not least in the industrialized part of the world. This has resulted in major changes in the biological structure and dynamics of the lakes and often in a shift from a clear to a turbid state.
A typical succession from temperate lakes in Northern Europe is as follows (Fig 1): At the top of the food web major changes have occurred in the fish community. At low nutrient concentrations, predatory perch (*Perca fluviatilis*) and pike (*Esox lucius*) dominate the fish community. When the nutrient loading increases, the biomass of fish increases as well. However, a shift occurs to dominance of cyprinids, especially roach (*Rutilus rutilus*) and bream (*Abramis brama*). Roach and bream are partly zooplanktivorous and the predation pressure on zooplankton therefore increases, which, in turn, results in a lower grazing pressure on phytoplankton. Changes in the size structure of zooplanktivorous fish towards dominance of small specimens further enhance the predation pressure on zooplankton. In addition, due to competition, perch more rarely reach the size of piscivory and therefore mainly predate on zooplankton and benthic invertebrates instead. Due mainly to the high fish predation pressure, the biomass ratio of zooplankton to phytoplankton decreases from 0.5-0.8 in mesotrophic lakes to less than 0.2 when phosphorus concentrations are above 0.1-0.15 mg P l\(^{-1}\), the latter figure being so low that zooplankton are not capable of controlling phytoplankton whose turnover time in eutrophic lakes may be 0.5-2 days. With a decreasing grazing pressure by zooplankton and an increased nutrient supply, the biomass of phytoplankton increases, resulting in reduced Secchi depth. In addition, the zooplankton become dominated by small forms, which are less efficient grazers on large phytoplankton. Large-sized phytoplankton forms, like filamentous cyanobacteria, therefore thrive in many nutrient-enriched lakes. An increase in fish predation may also reduce snail abundance and thus grazing of epiphytes on plants, which also impoverishes the growth conditions for submerged macrophytes. The plants disappear and with it the food source for a large number of herbivorous and macroinvertebrate-eating waterfowl. The result is a lake with a high roach and bream biomass, high abundance of phytoplankton, few or no submerged macrophytes and a greatly reduced density of birds dominated by fish-eating species (Fig 2).
Lessons to be learnt from restoration projects in temperate lakes

In recent decades large efforts have been devoted to combat eutrophication by reducing the external loading of phosphorus in many Western European countries and in North America and, in consequence, loading from sewage and industry sources has declined significantly since the 1970s.

Several lakes respond rapidly and positively to loading reductions; nuisance algal blooming and planktibenthivorous fish abundance decrease, while the percentage of piscivores increases as do water clarity and submerged macrophyte abundance. A study of 14 recovering lakes in Denmark (Jeppesen et al., 2002) showed that the phytoplankton and fish biomass generally declined, leading to an overall higher zooplankton:phytoplankton ratio, which suggests that enhanced grazing pressure on phytoplankton results in clearer water. Moreover, the biomass of planktivorous fish declined and the share of potential piscivores increased, most likely resulting in a stronger control by piscivores of planktivores. Accordingly, in most lakes the share of the large-bodied zooplankton *Daphnia* spp., which is particularly sensitive to predation by zooplanktivorous fish, and the body weight of *Daphnia* spp. and other cladocerans generally increased, further enhancing the grazer control of phytoplankton. The improvements in lake water clarity are therefore a result of higher resource control of phytoplankton (lower availability of nutrients) as well as of enhanced predator control of planktivorous fish, cascading to the phytoplankton level via increased grazer control by large-bodied zooplankton. Several other lakes have exhibited a fast response to nutrient loading reduction (Edmondson & Lehman, 1981; Bernhardt et al., 1985; Bäuerle & Gaedke, 1998).

However, positive effects cannot always be expected to occur, many lakes have proven to be highly resistant to loading reductions and have shown only little improvement (Sas, 1989, Marsden, 1989). For some lakes this reflects insufficient reduction of the nutrient input to trigger a shift to the clearwater state. For example, significant and sustaining changes in the biological community and water transparency of shallow temperate freshwater lakes cannot be expected to appear unless the TP concentration has been reduced to a level below 0.05-0.1 mg P l$^{-1}$ (Jeppesen et al., 2000), or for deep lakes below 0.02-0.03 mg P l$^{-1}$ (Sas, 1989). Even when the P loading has been sufficiently reduced, resistance to improvement is often observed. This resistance may be "chemical": P concentrations remain high because of P release from the sediment pool accumulated when loading was high (Søndergaard et al., 2002). Many years may pass before the surplus pool is released or permanently buried. The duration of this transitional period depends on, for instance, the duration of the
period with high TP loading, the residence time and the phosphorus binding sites (like iron) supplied from the surroundings. In some cases this transient phase towards a new equilibrium has spanned several decades (Søndergaard et al., 2001; Jeppesen et al., 2003). Various methods have been used to reduce the internal loading of phosphorus (Cooke et al., 1993; Søndergaard et al., 2002), including sediment removal and chemical treatment of the sediment with aluminum or iron salts. In stratified lakes also injections with oxygen or nitrate to the bottom layer or destabilization of the thermocline have been used.

The resistance may also be “biological”. In particular planktivorous and benthivorous fish contribute to biological resistance in shallow eutrophic lakes (Moss, 1990; Scheffer et al., 1993). A continuously high fish predation pressure prevents both the appearance of large herbivorous zooplankton that would otherwise clear the water as well as diminishes the number of benthic animals stabilizing and oxidizing the sediment. Moreover, excretion of nutrients to overlaying waters from benthic-feeding fish or fish bioturbation of surface sediment may also play a role (Breukelaar et al., 1994; Persson, 1997).

To overcome the biological resistance by fish, various fish manipulation methods have been developed (Benndorf, 1995; Drenner & Hambright, 1999; Søndergaard et al., 2001). One such method is the enhancement of top-down control of phytoplankton by selective removal of planktivorous fish; a method employed world-wide in the temperate zone. Removal of 75-80 % of the planktivorous and benthivorous fish stock during a 1-2 year period is recommended to avoid regrowth and to stimulate the 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 ample stocking of 0’ pike (>1000 ha⁻¹) to control newly hatched plankti-benthivorous roach and bream (Preijs et al., 1994; Berg et al., 1997). Others have used stocking of pikeperch (Sizostedion lucioperca), walleye (Sizostedion vitreum) and largemouth bass (Micropterus salmoides) (Benndorf, 1995; Lathrop et al., 2002). Opposite to the above-mentioned physico-chemical methods, fish manipulation is often cheap (Jeppesen & Sammalkorpi, 2002) and therefore attractive, though its long-term stability is uncertain. The findings to date indicate that fish manipulation may have a long-term effect in shallow temperate lakes provided that the nutrient loading is reduced to a TP level below 0.05-0.1 mg P l⁻¹ in the future state of equilibrium. However, if the nitrogen loading is low, fish manipulation may sometimes have a positive impact at higher TP concentrations (Moss et al., 1994; Jeppesen et al., 1999). The 0.05-0.1 mg P l⁻¹ threshold is in accordance with the empirical data appearing in this range (Fig. 1). However, temporary effects of fish manipulation can be obtained in lakes with high nutrient concentrations, but it seems unlikely that the effect will prevail in such lakes in the long term unless the abundance of planktivorous fish is repeatedly reduced. The TP threshold for positive effects to occur is most likely lower for deep lakes, but an accurate threshold has to be defined.

Can the knowledge of biomanipulation be transferred to subtropical and tropical lakes?

Fish community
Several factors indicate that fish stock manipulations would not have the same positive effect on the environmental state in tropical lakes as in temperate lakes. First, the fish species richness is often higher in tropical and subtropical lakes. South America and Africa have an extraordinarily rich freshwater fish fauna (Sunaga & Verani, 1997; Lévêque & Paugy, 1999). For example, 273 native fish species were found in aquatic environments in 44 x 10³ km² Rio de Janeiro State (Bizerril & Primo, 2001), and in Uruguay (171 x 10³ km²), for instance, 51 characid species are found (Reichert, 2002). Many of the fish species show partial niche overlap, which expectedly increases predator control of prey items (Lazzaro, 1997; Aguiaro & Caramaschi, 1998).

Second, the fish stock in tropical and subtropical lakes is often dominated by omnivorous species that feed on zooplankton but also consume phytoplankton, periphyton, benthic invertebrates, and detritus (species of clupeids, cyprinids, cichlids and poecilids) (Lazzaro, 1997; Branco et al., 1997; Yafe et al., 2002; Aguiaro et al., in press; Quintans et al., submitted). The subtropical and tropical fish stock that have the potential of
feeding on zooplankton may thus attain a higher carrying capacity than obligate zooplanktivores, which augments the potential control of the zooplankton. According to Blanco et al. (in press) the omnivorous structure of fish communities in Mediterranean lakes resembles that described for tropical lakes. Few piscivorous species are present and omnivorous fish generally dominate independently of trophic state. However, the latest research into temperate lakes has shown that many of the important zooplanktivorous fish also consume benthic prey, not least in shallow lakes (Vadeboncour et al., 2002; Jones & Waldron, 2003). Therefore, to a higher degree than hitherto anticipated, also temperate fish may sustain higher biomasses and thus exert a benthic-facilitated top-down control on zooplankton (Vander Zanden & Vadeboncœur, 2002).

Third, compared to North American and European freshwater fish communities, only few large strictly piscivores and small-sized carnivores occur and sit-and-wait predators are often more frequent (Quiró, 1998). In addition, some of the omnivorous-planktivorous species can neither be controlled by zooplankton availability (resources) nor by predation, since many are larger than their potential predators (Arcifa et al., 1995; Araújo Lima et al., 1995). Therefore, top-down control by piscivores is most likely weaker in subtropical/tropical lakes than in temperate lakes.

Fourth, recent studies suggest that fish density, but not necessarily biomass, is substantially higher (maybe 1-2 orders of magnitude) in subtropical and tropical lakes in South America than in comparable north temperate lakes (Scasso et al. 2001; Aguiaro et al., 2003; Meerhoff et al., 2003; Mazzeo et al., in press). Among those are Cnesterodon decemmaculatus and Jenynsia multitentata, both small omnivorous-planktivorous species that may be very abundant in eutrophic lakes in, for example, Uruguay and North Argentina (Bistoni 1999). Moreover, fish reproduction, which in temperate freshwater lakes takes place once a year, occurs throughout the year in many subtropical and tropical lakes (Fernando, 1994; Paugy & Lévêque, 1999) and many species such as C. decemmaculatus are viviparous. As small fishes are more zooplanktivorous and have a much higher energy demand per unit of biomass than large fish (Kalff, 2002), the dominance of small fish in such high abundances leads to a higher predation pressure on zooplankton than in temperate lakes, where the effect of juvenile fish is typically strong mainly in mid-late summer (Jeppesen et al., 1997a). Nutrient-rich temperate brackish lakes in Denmark provide an illustrative example of the impact of a prolonged spawning period and dominance of small fish. The fish stock of these lakes is dominated by the small three-spined stickleback (Gasterosteus aculeatus) having 2-3 cohorts per year. Accordingly, the predation pressure on zooplankton is substantially higher in brackish lakes than in comparable freshwater lakes dominated by fish with only one annual spawning (Jeppesen et al., 1994, 1997b).

**Zooplankton community structure**

Most likely due to high predation by fish, the zooplankton communities in tropical and subtropical lakes are frequently dominated by small cladocerans (like Diaphanosoma, Ceriodaphnia and Bosmina) and rotifers, and by juveniles and small copepodites among the copepods (Dumont, 1994; Lewis, 1996; Branco et al., 2002, Garcia et al., 2002). When fish are absent large Daphnia spp. may sometimes develop (Mazzeo et al., unpublished data). Omnivorous copepods usually dominate in terms of biomass in oligo-mesotrophic systems, whereas microzooplankton prevail in more eutrophic systems. The high temperatures, the daily fluctuations in physical and chemical conditions or sudden environmental changes due to heavy rains may add to the predominance of fast-recovering forms such as protozoans and rotifers in the zooplankton community. The classic control of phytoplankton by large zooplankton in temperate lakes is therefore not usually found in tropical lakes. Besides the zooplanktivorous phantom midge, Chaoborus, seems to be more abundant in tropical lakes, most likely because tropical lakes develop anoxia in the bottom water more quickly than do temperate lakes, which provides Chaoborus with a fish predation refuge for prolonged periods (Lewis, 1996). Invertebrate predation by Chaoborus and other invertebrates, such as freshwater shrimps (e.g. Palaemonetes spp.), could prevent large herbivorous zooplankton from developing and this explains the success of loricated rotifers, or species capable of rapid escape such as Hexarthra spp., as well as the high density of copepod nauplii (Branco et al., 2000), even in the absence of zooplanktivorous fishes (Roche et al., 1993). This predation pressure on zooplankton may represent a further limitation of the usefulness of biomanipulation in tropical and subtropical lakes.

**Fish-zooplankton-macrophyte interactions**

Aquatic plants play a very important structuring role in most freshwater ecosystems (Scheffer et al., 1993, Thomaz & Bini, 2003). In temperate nutrient-rich lakes, not least submerged plants often act as daytime
refuges for zooplankton against fish predators (Timms & Moss, 1984; Lauridsen et al., 1996; Burks et al., 2002). At night, when the risk of predation is lower zooplankton migrate to the open water for feeding and thereby contribute to maintaining clearwater conditions in lakes with high macrophyte coverage (Jeppesen et al., 1997a). However, in the tropics and subtropics, the effects of macrophytes on trophic interactions are more complex, as all life forms (emergent, submerged, floating-leaved and large free-floating species) can be extremely prominent. The few studies conducted so far in the subtropics and tropics indicate that fish, particularly the smallest species and individuals, aggregate in high numbers in the vegetation (Conrow et al., 1990; Meerhoff et al., 2003; Branco et al., submitted). Studies of the composition of tropical ichthyofauna associated to macrophytes have shown that the life cycle of some species is completely connected to this biotope, examples being small-sized tetragonopterins, characiforms and some cichlids (Sazima & Zamprogno, 1985; Delariva et al., 1994). Many fish species exhibit spatial distribution patterns often connected with zooplankton and predator densities, and also with different macrophyte life forms (Agostinho et al., 1994; Sunaga & Verani, 1997; Meerhoff et al., 2003). Besides, tropical aquatic vegetation can be intensively colonized by periphyton and provide microhabitats for many invertebrates, including chironomids, trichopterans and molluscs (Callisto et al., 1996; Masifwa et al., 2001).

One might therefore expect that the vegetation is a poor refuge for large-bodied zooplankton in warm lakes, which seems to be supported by the few field and experimental studies conducted so far (Meerhoff et al., 2003; Meerhoff, unpublished data). Fish aggregation in the vegetation and lack of zooplankton aggregated among plants have also been observed in brackish lakes dominated by small-sized sticklebacks in Denmark (Jeppesen et al., 1997b) and, accordingly, nutrient-rich brackish lakes are turbid, even when macrophyte coverage is high. Likewise, from subtropical freshwater lakes in Florida Bachmann et al. (2002) showed no positive effect of plants on water clarity and nutrient-rich lakes with high plant biomass were often turbid. These results may well be of general importance for subtropical and tropical lakes, although more research is needed within this field. Also, contrasting management approaches can alter the role of macrophytes in lake functioning and trophic interactions. While in temperate systems the introduction and development of aquatic plants are considered a key step in a restoration process (Moss et al., 1996), many aquatic plants in the tropics and subtropics are often considered nuisance and subject to severe eradication measures.

Limitations of biomanipulation in the subtropics and tropics

As can be deduced from the above, it seems more difficult to provoke and not least maintain a trophic cascade effect in subtropical and tropical lakes than in temperate lakes, for which the concept of biomanipulation as a restoration tool was developed. Supporting this view, Nagdali & Gupta (2002) found positive, but only short-term cascading effects of a massive (>80%) kill (due to fungal infection) of the most abundant planktivorous mosquito fish (Gambusia affinis) in Lake Naini Tal, India. Zooplankton abundance increased significantly, phytoplankton biomass and productivity declined as did nutrient concentrations, resulting in higher water transparency. However, only 4 months later the abundance of mosquito fish, plankton and nutrients had returned to the level recorded in the previous year (Fig 3). In a study performed by Scasso et al. (2001), a slowly increasing abundance of larger species was observed after two years of biomanipulation involving removal of small planktivorous fish, without, however, inducing cascading effects leading to clear-water conditions.
Yet, only few studies have investigated the applicability of the biomanipulation theory to tropical and subtropical freshwater ecosystems, and most of the existing ones have examined food interactions in eutrophic lakes and reservoirs with the aim to control cyanobacterial blooms via enhanced grazing by omnivorous fish such as silver carp (Arcifa et al., 1986; Northcote et al., 1990; Starling, 1993; Jones & Poplawski, 1998; Saha & Jana, 1998). The results obtained indicate that omnivory and strong shifts in fish diet and in the fish and zooplankton composition jeopardize successful biomanipulation (Boon et al., 1994; Arcifa et al., 1995; Starling & Lazarro, 1997; Starling et al., 1998; Boulton & Brock, 2001), but more information on phytoplankton-zooplankton interactions in the tropics is needed before its potential can be fully elucidated. Moreover, the absence of a native piscivorous fish culture in many tropical countries precludes the application of biomanipulation. There is a huge richness of fish species potentially useful for this purpose, but mass production for biomanipulation purposes has not yet been considered. Generally, aquaculture has so far focused on exotic species (i.e. common carp and grass carp) that have negative effects on water quality and biodiversity.

In many of the experiments undertaken in the temperate zone, an improvement in environmental state has, however, been recorded without the occurrence of a trophic cascade, i.e. without changes in the zooplankton species composition towards higher dominance of large-sized individuals and with it a higher grazing pressure on phytoplankton (Horppila et al., 1998). Even without such a trophic cascade, a significant reduction has been observed in the occurrence of cyanobacteria, total phosphorus has declined and water clarity increased. These phenomena have been ascribed to reduced release of phosphorus from the sediment, not least due to the lower rate of fish foraging in the sediment following biomanipulation (Horppila et al., 1998). Biomanipulation may therefore potentially also reduce the nutrient release from the sediment in
tropical lakes, but the dominance of small fish species and the improved growth conditions for cyanobacteria suggest that the effect will not be long-lasting. Therefore, a drastic reduction of the external nutrient loading seems to be the best way forward for restoring lakes also in the tropics, but clearly the scientific basis (e.g. nutrient threshold levels) on which to make decisions is yet too limited.

**Strong need for more research**

As it is today, many subtropical and tropical lakes are heavily eutrophied and biodiversity has declined, and in the years to come it is to be feared that many other lakes in these regions, especially in coastal areas, will follow the same negative developmental pattern both as a consequence of the future economical development and climate change. According to Vitousek et al. (1997), around 60% of the world’s population is concentrated in the outer 100 km coastal zone, and disordered urban expansion and agricultural activities have heavily impacted aquatic ecosystems in the developing countries located in tropical and subtropical regions. These already disturbed environments will expectedly face more stressful challenges as a result of increasing human activities and changing meteorological events associated to global warming.

One may hope that the developing countries will learn from the mistakes made in Europe and North America and adopt a farsighted policy and take actions to avoid the eutrophication of present-day high quality lakes and thus the need for initiating costly restoration projects in the future. However, whether they do so or not, more knowledge is needed to initiate suitable restoration projects of already eutrophied lakes in these regions. This book is an interesting step on the long road to the procurement of such knowledge.

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