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Successful restoration of a tropical shallow eutrophic lake: Strong bottom-up but weak top-down effects recorded

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ABSTRACT

Fish manipulation has been used to restore lakes in the temperate zone. Often strong short-term cascading effects have been obtained, but the long term-perspectives are less clear. Fish manipulation methods are far less advanced for warm lakes, and it is debatable whether it is, in fact, possible to create a trophic cascade in warm lakes due to the dominance and high densities of fast-reproducing omnivorous fish. However, removal of benthic feeding fish also reduce disturbance of the sediment, which not only affects the nutrient level but also the concentration of suspended organic and inorganic matter with enhanced water clarity and potentially better growth conditions for submerged macrophytes. We conducted a biomanipulation experiment in one of the basins in Chinese Huizhou West Lake that have remained highly turbid after extensive nutrient loading reduction. Another basin was used as control (control-treatment pairing design). Removal of a substantial amount of plankti-benthivorous fish was followed by planting of submerged macrophytes and stocking of piscivorous fish. We found strong and relatively long-lasting effects of the restoration initiative in the form of substantial improvements in water clarity and major reductions in nutrient concentrations, particularly total phosphorus, phytoplankton and turbidity, while only minor effects were detected for crustacean zooplankton grazers occurring in low densities before as well as after the restoration. Our results add importantly to the existing knowledge of restoration of warm lakes and are strongly relevant, not least in Asia where natural lakes frequently are used extensively for fish production, often involving massive stocking of benthivorous fish. With a growing economy and development of more efficient fish production systems, the interest in restoring lakes is increasing world-wide. We found convincing evidence that fish removal and piscivores stocking combined with transplantation of submerged macrophytes may have significant effects on water clarity in warm shallow lakes even if the zooplankton grazing potential remains low, the latter most likely as a result of high predation on the zooplankton.

1. Introduction

For 50–100 years eutrophication has posed a serious threat to lakes world-wide. High nutrient loading has resulted in turbid water, excessive blooms of nuisance algae, dominance of planktivorous and benthivorous fish and loss of biodiversity. While countries in the developing world face an alarming increase in eutrophication of lakes as a result of the rapid economic development, large efforts have been devoted to combat eutrophication by reducing the external loading of especially phosphorus (P), not least in Western Europe and North America (Sas, 1989; Jeppesen et al., 2005a; Schindler, 2009). In consequence, the P loading from sewage and industrial sources has declined significantly since the 1970s (overviews in Sas, 1989; Jeppesen et al., 2005b). This has led to a reduced phytoplankton abundance, lower cyanobacteria dominance and often a shift in fish community structure towards

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lower abundance and proportions of planktivorous and benthivorous fish with a resulting reduced predation on zooplankton. However, many lakes have responded slowly to nutrient loading reduction (Marsden, 1989; Sas, 1989; Jeppesen et al., 2005a,b), partly due to internal P loading (release from the stored P pool in the sediment) (Søndergaard et al., 2013) and to biological resistance (Jeppesen and Sammalkorpi, 2002). The latter reflects that fish after an external nutrient loading reduction may exert a continuous predation pressure on large-bodied grazers (e.g. *Daphnia*) and thereby maintain the grazing pressure on phytoplankton at a low level, diminishing also the number of benthic animals that stabilize and oxidize the sediment. Furthermore, persistence of benthivores (e.g. carp, *Cyprinus carpio*, bream, *Abramis brama*) that stir up the sediment while feeding and translocate nutrients from the sediment to the water (Meijer et al., 1994; Breukelaar et al., 1994) contributes to maintain high internal P loading and high inorganic turbidity. Moreover, grazing by herbivorous waterfowl such as coot (*Fulica atra*) and mute swan (*Cygnus olor*) may hamper recovery by delaying the recolonization of submerged plants (Perrow et al., 1997; Mitchell and Perrow, 1998).

To re-enforce recovery, several physico-chemical and biological methods have been used (for an overview see Cooke et al., 2005). The typical measure applied to overcome biological resistance is removal of plankti-benthivorous fish. This method has been extensively used in north temperate lakes, particularly in Europe. Removal of approx. 75%of the plankti-benthivorous fish stock over a 1–2 year period has been recommended to avoid regrowth and to stimulate the growth of potentially piscivorous fish (Hansson et al., 1998; Jeppesen and Sammalkorpi, 2002; Mehner et al., 2002; Gulati et al., 2008). An alternative or supplementary method to fish removal is stocking of piscivores (for a review see Drenner and Hambright, 1999). To reinforce recovery of submerged macrophytes active planting (entire plants, turions, plant fragments or seeds) has been used (Jeppesen et al., 2012), in some cases also by constructing plant exclosures to protect the macrophytes against grazing by waterfowl and fish (Søndergaard et al., 1996). In the exclosures the macrophytes can grow in a grazing-free environment from where they may spread seeds, turions or plant fragments to the entire lake, thereby augmenting the chances of successful colonization (Søndergaard et al., 1996; Mitchell and Perrow, 1998; Lauridsen et al., 2003).

In north temperate lakes efficient fish reduction in eutrophic lakes has generally often led to major cascading effects in the form of reduced phytoplankton biomass, dominance by large-sized zooplankton and improved transparency (Carpenter and Kitchell, 1993; Hansson et al., 1998; Søndergaard et al., 2008; Bernes et al., 2015), although there are also examples of little or no cascading effects for various reasons (Horppila et al., 1998; Jeppesen and Sammelkorpi, 2002; Søndergaard et al., 2008). The effects of fish manipulation may cascade to the nutrient level as well. A reduction ranging from 30 to 50% in lake concentrations of TP has been recorded in the relatively successful fish manipulation experiments conducted in shallow and stratified eutrophic lakes (Søndergaard et al., 2008). A significant contributory factor is increased growth of microbenthic algae owing to improved light conditions at the sediment surface (Hansson, 1990; Genkai-Kato et al., 2012). More benthic algae and less sedimentation of phytoplankton due to intensified grazing, and more benthic animals due to reduced fish predation, may all result in a higher redox potential in the surface sediment, potentially reducing the P release (Søndergaard et al., 2005; Zhang et al., 2013, 2017). So far, the long-term perspectives of fish removal are less promising. A gradual return to the turbid state and higher abundance of zooplanktivorous fish after 5–10 years have been reported in many case studies (Søndergaard et al., 2008). Moreover, stocking of piscivorous fish has often been less successful than fish removal (Drenner and Hambright, 1999).

Experience with lake recovery is far less advanced for warm than for temperate lakes (Jeppesen et al., 2005b, 2012). Studies conducted in (sub)tropical and Mediterranean lakes have shown that nutrient loading reduction may improve the ecological state via a declining algal biomass and increased water transparency (Jeppesen et al., 2005a; Coveney et al., 2005; Romo et al., 2005; Beklioğlu and Tan, 2008). However, it is debatable whether the fish manipulation approach used in cold temperate lakes to re-enforce recovery can be used with success in warm lakes as well (Jeppesen et al., 2005b, 2012). The high species richness and high densities of plankti-benthivorous fish, with dominance of omnivores, a few efficient predators and several cohorts lead to higher predation on zooplankton in warm lakes than in temperate lakes (Lazzaro, 1997; Meerhoff et al., 2003, 2007; Teixeira-de Mello et al., 2009). It is therefore likely that a removal-induced reduction of the biomass of planktivorous fish will be compensated by fast adjustment of the remaining population, and the impact will consequently be of short duration (Jeppesen et al., 2012). Hence, it may be more difficult to provoke and maintain a pelagic trophic cascade effect in subtropical and tropical lakes than in temperate lakes. However, an important effect of removal of benthic feeding fish, such as carp and bream, is reduced stirring of the sediment, which not only affects lake nutrient levels but also the concentration of suspended organic and inorganic matter (Breukelaar et al., 1994; Horppila et al., 1998). Not least in systems with high dominance of carp, either naturally or stocked, as is the case for many Chinese lakes (Jia et al., 2013), carp removal may potentially lead to substantial improvement of lake water quality due to a reduced disturbance.

In the present study we conducted a biomanipulation experiment in a basin of Chinese Huizhou West Lake that has remained highly turbid after an extensive nutrient loading reduction (Li et al., 2007). Removal of plankti-benthivorous fish was followed by planting of submerged macrophytes and stocking of piscivorous fish. Our working hypothesis was that albeit a major trophic cascade mediated by enhanced zooplankton grazing (due to the high density of small fish in warm freshwaters) could not be expected, plankti-benthivorous fish reduction (through direct removal, and stocking of piscivorous fish) would lead to clear-water conditions and low nutrient levels due to reduced disturbance of the sediment, and water clarity would be maintained via introduction of submerged macrophytes.

2. Material and methods

2.1. Study site

Huizhou West Lake is a tropical shallow lake located in the city of Huizhou (23° 06′ 24” - 23° 04′ 43” N, 114° 22′ 44” - 114° 24′ 03” E) in the Guangdong province (southern China) (Fig. 1), which is characterized by a subtropical and tropical monsoon climate. The multiannual mean air temperature is 21.7 °C, the lowest monthly mean is 13.1 °C in January and the highest monthly mean 28.3 °C in July. The multi annual mean precipitation is 1649 mm of which about 80% falls during April to August. The lake has a total surface area of about 1.5 km^2 and a mean depth of 1.6 m. The lake is divided into several basins connected through waterways under bridges. The water temperature ranges from 12 to 35 °C. The hydraulic retention time is about three months (Li et al., 2007).

Due to its city location the lake has long been a valuable part of are creational garden that is extensively used by the local population. However, the lake has become eutrophic due to input of wastewater from Huizhou city. To restore the lake, several measures have been implemented since the 1990s, including wastewater treatment, effluent diversion and sediment removal (Li et al.,

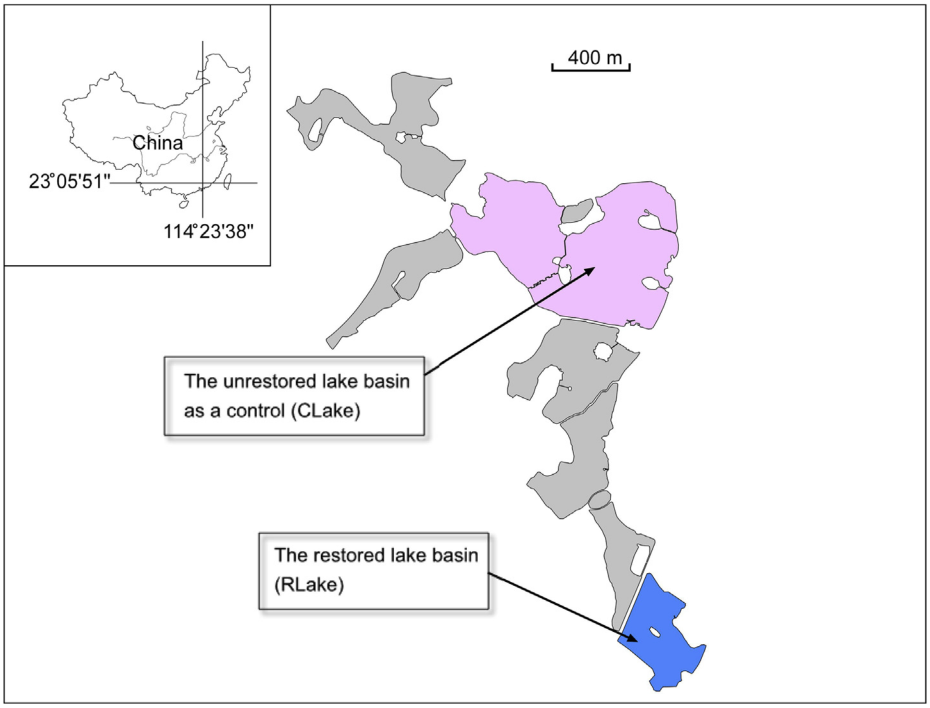

Fig. 1. Location of Huizhou West Lake and the restored lake basin (RLake) and one unrestored basin (CLake) sampled in this study.

2007), but with no substantial effect – the lake has remained eutrophic and turbid. Total phosphorus typically ranges between 100 and 200 $\mu g\,L^{-1}$, total nitrogen between 1.0 and 2.5 $mg\,L^{-1}$, chlorophyll a between 30 and 70 $\mu g/L$ and total suspended solids between 20 and 90 mgL^{-1}; Secchi depth is as low as 30–40 cm. The fish communities are dominated by omnivorous and plankti-benthivorous fish, including tilapia (*Oreochromis niloticus*), common carp (*Cyprinus carpio*), crucian carp (*Carassius carassiu*), mud carp (*Cirrhina molitorella*), silver carp *(Hypophthalmichthys molitrix),* bighead carp (*Aristichthys nobilis*) and long-tailed anchovy (*Coilia grayii*) (Gao et al., 2014). Common zooplankton include small-sized cladocerans such as *Chydorus* sp., *Alona* spp., *Bosmina* spp., *Diaphanosoma* spp. and *Moina micrura*, and the dominant copepods are *Mesocyclops thermocyclopoides*, *Allodiaptomus specillodactylus*, *Neodiaptomus schmackeri* and *Phyllodiaptomu stunguidus*. There are no submerged macrophytes, and the phytoplankton is dominated by *Gleobacterviolaceus*, *Pseudoanabaena*, *Merismopedia* and *Dactylococcopsis*.

2.2. Biomanipulation

To improve water quality and especially the clarity of the lake, large-scale ecological restoration (biomanipulation) experiments were conducted in a basins with a surface water area of 12 ha (RLake) in 2007 (Fig. 1). RLake was connected with the rest of the lake by waterways under bridges before restorations.

In RLake the biomanipulation included removal of plankti-benthivorous fish, stocking of piscivorous fish and transplantation of submerged macrophytes. The lake basin was isolated from the rest of the lake by building a small soil dam under the bridge in May 2007. After lowering the water level by 50 cm, a total of 29.7t (2.5 $t\,ha^{-1}$) fish were removed by seine fishing, encompassing 65% tilapia, 16% silver carp and bighead carp, 12% common carp and 1.6% anchovy. After fish removal, transplantation of the submerged macrophytes *Hydrilla verticillata* and *Vallisneria denseserrulata* was conducted. *Vallisneria* ramets were planted in the sediment at a density of about 10–15 plants per m^{-2}, and apical sections of young *H. verticillata* shoots were planted at a density of 20–30 plants m^{-2}. Juveniles of piscivorous fish (18,000 snakehead *Channa argus* and 16,000 mandarin fish *Siniperca chuatsi*, 1500 and 1333 ha^{-1}, respectively) were stocked.

In RLake maintenance fishing was conducted after restoration to minimize the effects of fish recruitment using fish traps. Fish removed were mainly benthivorous tilapia and crucian carp (ca. 450 $kg\,ha^{-1}\,year^{-1}$). Meanwhile, commercial fishing in the control lake basin CLake was also conducted, and the catches were about 500 $kg\,ha^{-1}\,year^{-1}$, consisting mainly silver carp (Gao et al., 2014). Fish investigations conducted bimonthly from May 2010–March 2011 (6 and 3 years after the first and second biomanipulation) using multi-mesh sized gill-nets revealed that crucian carp, common carp and snakehead dominated the catches in terms of biomass in the restored basin, while planktivores (silver carp, long tailed anchovy, white semiknife-carp *Hemiculter leucisculus*) and crucian carp dominated in the unrestored basin. No among-site difference was recorded in total fish catches in terms of biomass (Gao et al., 2014).

2.3. Sampling and analyses

Another basin, Pinghu (CLake), which has an area of 57 ha and mean depth of 2.1 m (Fig. 1), was used as a non-restored reference lake and have been sampled monthly since 2005 excepting two samplings in August and October 2004, respectively. In RLake, sampling was undertaken 3–4 times per year before May 2007 when restoration was initiated. Weekly sampling was carried out during the early period of restoration, but since August 2007 only monthly samplings had been conducted.

Water temperature and Secchi depth (SD) were recorded at each sampling event. Integrated water samples by mixing 5 l water samples collected from surface and at the depth of 0.5 m using a modified Van Dorn water sampler were used for under taking analyses of chemical variables including total nitrogen (TN), ammonium nitrogen (NH_4-N), nitrate nitrogen (NO_3-N), nitrite nitrogen (NO_2-N), total phosphorus (TP), total dissolved phosphorus (TDP), soluble reactive phosphorus (SRP), total suspended solids (TSS) and inorganic suspended solids (ISS). SRP was determined spectrophotometrically according to the molybdenum blue method (APHA 1998). NH_4-Nconcentrationswere measured by the indophenol blue method, and NO_3-N and NO_2-N concentrations were analysed by the cadmium reduction method (APHA, 1998). TP, TDP, TN and TDN concentrations were determined after thawing of the frozen samples using persulfate digestion (Ebina et al., 1983) followed by spectrophotometric analysis similar to the analyses for SRP and nitrate. TSS were determined as matter retained on GF/C filters after drying at 105 °C for 24 h and ISS at 550 °C for 2 h. Chlorophyll a (Chl a) concentrations were determined spectrophotometrically after extraction in 90% hot ethanol (Pápista et al., 2002).

Zooplankton were concentrated by filtering 20 l integrated lake water samples collected from the surface and at the depth of 0.5 musing a modified Van Dorn water sampler through a 20 μm mesh size and fixed in 5% formalin. Cladocerans and copepods were identified according to Shen (1979), Chiang and Du (1979) and Guo (1999) and counted under a dissection microscope. Dry weight of zooplankton was estimated according to length-weight relationships (Huang, 1999). Zooplankton to phytoplankton ratio was calculated as zooplankton biomass/Chl a concentration/66 (Jeppesen et al., 2005a).

During May 2010 to November 2011, submerged macrophytes were collected from 12 randomly selected locations in RLake using a quantitative iron clamp with an area of 0.06 m^2, The collected submerged macrophytes were subsequently sorted, dried at 105 °C for 24 h, and weighed to determine biomass (dry weight).

2.4. Data analysis

The boxplots were used to show the magnitude and direction of changes in different variables on an annual basis. In order to statistically assess the changes occurring in two basins (one restored and another one unrestored) we compared time series data before and after restoration (by particularly submerged macrophyte transplantation and piscivorous fish stocking), and to account for problems connected with natural seasonal change we paired measurements from the restored basin with those from the unrestored basin (control), using the control-treatment pairing design or BACIP as described by Stewart-Oaten et al. (1986).

The statistical model can be expressed as

$$D_{ik} = X_{iC_j} - X_{iR_k} = \mu + \eta_i + \varepsilon_{ik}$$

where X stands for the parameter measured, i denotes before or after, C_j denotes control site, R_k denotes restored site, k denotes sampling time, μ is the mean difference between control and restored, η_i is the change in difference from before to after, and ε_{ik} is the error associated with the difference. Measurements made for the period during the restoration in RLake (from June 7 to September 6, 2007) were excluded from the statistical analyses due to initial manipulation-induced disturbances.

Differences, D_{ik}, between the before and after periods were compared using a two-sample test. If no impact from the restoration was registered, the differences in the before period were assumed to be similar to those in the after period. Testing for a significant change in the restored basins was performed as a standard T-test (Snedecor and Cochran, 1989). Homogeneity of variances was tested by the Folded F (Steel and Torrie, 1980) method. To estimate unequal variances in the two groups of data, Welch-Satterthwaite approximation was used in the *t*-test (Welch, 1947). When testing for differences in abundance between different groups of zooplankton, square root transformation was conducted before calculating differences. The statistical software SAS® was applied for formal testing (SAS Institute Inc. 2002). The difference was set to be significant when $p < 0.05$.

3. Results

3.1. The water quality

In RLake TP varied from 48 to 228 $\mu g\, L^{-1}$ and averaged 126 $\mu g\, L^{-1}$ before restoration. After restoration TP dropped markedly in the restored site, frequently reaching values lower than 50 $\mu g\, L^{-1}$, while the concentrations in CLake remained within the range of 52–340 $\mu g\, L^{-1}$. Accordingly, the BACIP analysis revealed a significant drop in TP in the restored site ($t = -4.24$, $df = 51$, $p < 0.0001$). SRP was generally low and no significant change in SRP was observed in CLake ($t = -0.83$, $df = 8.9$, $p > 0.42$) (Fig. 3).

After restoration the mean value of TN was 0.83 mg $L^{-1}$and significantly lower in RLake than in CLake with a mean value of 1.29 mg L^{-1} (BACIP, $t = -4.20$, $df = 52$, $p = 0.0001$). Before restoration and immediately after restoration values varied widely, but were relatively stable after February 2009. NO_x-N concentrations in RLake (mean concentration of 0.095 mg L^{-1}) were significantly lower than in CLake (mean concentration of 0.337 mg L^{-1}) (BACIP, $t = -4.60$, $df = 72.7$, $p < 0.0001$), while NH_4-N did not differ significantly ($t = -2.01$, $df = 8.7$, $p > 0.07$) (Fig. 3).

A major reduction in TSS was observed upon restoration (Fig. 3). Thus, annual mean values were constantly lower than 5 mg L^{-1}, which is much lower than both before restoration (annual mean values > 21 mg L^{-1}) and in the reference lake (annual mean values > 30 mg L^{-1}) (BACIP, $t = -7.99$, $df = 23.2$, $p < 0.0001$). ISS in the restored site followed the TSS pattern observed in the reference lake, and compared to CLake the differences in ISS were significant (BACIP, $t = -2.65$, $df = 45$, $p < 0.012$) (Fig. 3). The percentage of ISS to TSS also decreased significantly (BACIP, $t = -2.4$, $df = 45$, $p < 0.021$).

Before restoration Chl a in RLake ranged from about 20 to 80 $\mu g\, L^{-1}$ and decreased markedly after restoration, with a value range of 0.6–30 $\mu g\, L^{-1}$. Relative to CLake, Chl a in RLake decreased significantly ($t = -6.37$, $df = 9.3$, $p < 0.0001$), and Secchi depth increased ($t = 19.82$, $df = 28.1$, $p < 0.0001$) (see Figs. 2 and 4).

3.2. Zooplankton

The two lake basins lack large zooplankton grazers such as *Daphnia* spp., and the dominant cladocerans are *Chydorus* sp., *Alona* spp., *Diaphanosoma* spp. and *M. micrura*, albeit in low densities. The highest number of cladocerans was recorded in August 2007 in the restoration period in RLake due to the occurrence of high numbers of *Moina micrura* (120 ind. L^{-1}). After restoration the densities of cladocerans remained low, most often <1 ind. L^{-1}. The dominant copepods were *M. thermocyclopoides*, *T. taihokuensis*, *N. schmackeri* and *P. tunguidu*. The BACIP analysis revealed no significant differences in total biomass between the restored cite and CLake ($p = 0.26$) and for size of copepods ($p = 0.41$) (Fig. 4). For the zooplankton:phytoplankton biomass the ratio was higher in RLake than in CLake ($t = 3.62$, $df = 22.1$, $p < 0.002$). After restoration average size of both cladocerans and copepods in RLake and CLake was the same, 0.45 mm for cladocerans and 0.65 mm for copepods. After restoration zooplankton biomass averaged 22 $\mu g\, l^{-1}$ in RLake (51 $\mu g\, l^{-1}$ in CRLake) and the same figures for the zooplankton:-phytoplankton biomass ratio were 0.09 and 0.02, respectively (Fig. 4).

Fig. 2. Photo showing the contrast of the lake basin before and after restoration.

3.3. Chl a:TP, Chla:TN and TN:TP ratios and submerged macrophytes

No significant change was registered in the Chl a:TP ratio (annual mean values ranged from 0.24 to 0.42) in RLake and it was not significant from that in CLake (ranged from 0.21 to 0.41) (BACIP, $t = -1.70$, $df = 51$, $P > 0.09$). Chl a:TN (BACIP, $t = -4.39$, $df = 52$, $p < 0.001$) was significantly lower and TN:TP significantly higher in the restored site (BACIP, $t = 7.9$, $df = 50.34$, $p < 0.001$) (Fig. 5).

In RLake the total biomass of submerged macrophytes averaged 254.7 (SD: 69) g dw m^{-2} and ranged between 134.4 and 385.3 g dw m^{-2}. No submerged macrophytes were observed in CLake.

4. Discussion

We found strong effects of the biomanipulation initiative encompassing removal of plankti-benthivorous fish, macrophyte transplantation and stocking of piscivorous fish. This include substantial improvements in water clarity and major reductions in the concentrations of nutrients, particularly TP, phytoplankton (Chl a) and turbidity (TSS), while only minor changes were detected for the crustacean zooplankton grazers occurring in low biomasses and having small sizes before as well as after biomanipulation. Moreover apart from some few peaks in the zooplankton:phytoplankton ratio the ratio was generally low indicating overall low grazing pressure by zooplankton on phytoplankton. Thus, we found evidence for strong bottom-up effects, while top-down effects apparently played a minor role in the improvement of the ecological status of the lake.

We observed a particularly strong decline in TSS and ISS, which may reflect both a reduction in fish disturbance of the sediment due to the removal of benthivorous fish during and after restoration and, more importantly, a reduced risk of resuspension following the development of submerged macrophytes. The dominant benthivorous fish were common carp and crucian carp that feed mainly on benthos (Richardson et al., 1995; García-Berthou, 2001) by sucking up sediments from where they pick up edible items and release the sediment to the water (Scott and Crossman, 1973). Such feeding behaviour can cause high sediment resuspension. Both common carp (Breukelaar et al., 1994; Zambrano et al., 2001; Wahl et al., 2011) and crucian carp (Richardson et al., 1995) have been shown to cause high sediment resuspension in temperate lakes, and resuspension may be even higher in warm lakes where the fish forage more actively due to the higher temperatures (Lankford and Targett, 1994; He et al., 2017). Tilapia can also suspend sediment and increase turbidity in shallow systems (Jiménez-Montealegre et al., 2002). Furthermore, fish biomass values were high (nearly 2500 kg ha^{-1}) compared to most temperate lakes (Jeppesen and Sammalkorpi, 2002). Re-establishment of submerged macrophytes may further stabilize the sediment and it reduces sediment resuspension (Hamilton and Mitchell, 1996). Several biomanipulation studies conducted world-wide have observed effects on TSS after removal of benthivorous fish (Meijer et al., 1994, 1999; Jeppesen et al., 2007; Ibelings et al., 2007; Yu et al., 2016a).

Fish removal in temperate lakes has also resulted in major reductions in TN and TP (Jeppesen et al., 2007; Ibelings et al., 2007; Søndergaard et al., 2008). In our study, the most clear response emerged for TP, which, on average, declined by >70% compared to both the level before restoration and the level in the reference lake. Fish feed on benthos and excrete nutrients in the water column and thus fish removal may reduce the translocation of nutrients from benthic habitats to water column (Glaholt and Vanni, 2005; Vanni et al., 2013). Submerged macrophytes oxidize the sediment and increase its capacity of binding inorganic P, there by reducing P release to the water column (Carpenter and Lodge, 1986). In our study, the dominant species after plant introduction (*Vallisnaria*) has relatively well developed root systems (Xie et al., 2005; Zhang et al., 2010) and thus a high potential of oxidizing the sediment, thereby reducing the P release (Jessen et al., 2017; Zhang et al., 2017). Moreover, high water clarity and improved light conditions may allow development of benthic algae and consequently cause a reduction in the sediment P release (Hansson, 1990; Genkai-Kato et al., 2012; Zhang et al., 2013) in shallow lakes, such as Huizhou West Lake.

In north temperate lakes appearance of large-sized zooplankton has been shown to be of key importance for enhancing water clarity after biomanipulation. The large-sized zooplankton increase the grazing pressure on phytoplankton, as has been evidenced in several studies by a major increase in the zooplankton:phytoplankton biomass ratio and a larger body size of cladocerans (Hansson et al., 1998; Jeppesen et al., 2004, 2012; Søndergaard et al., 2008). Higher water clarity, in turn, promotes growth of submerged macrophytes, further stabilizing the lake ecosystem through a number of positive feedback mechanisms (Moss, 1990; Scheffer et al., 1993; Jeppesen et al., 1998). In our study the phytoplankton biomass (Chl a) also decreased substantially after biomanipulation. However, top-down effects appeared to be of minor importance, the evidence being that we found 1) no clear change in the zooplankton community –the abundance of cladocerans remained low and small species such as *Chydorus* sp., *Alona* spp. and *M. micrura* continued to dominate, 2) no change in size of cladocerans or copepods and sizes was small and 3) the zooplankton:phytoplankton ratio, although increasing after restoration, was low compared similar studied from north temperate lakes (Jeppesen et al., 2007). This lack of response by the zooplankton may be attributed to continuously high fish predation although fishing continued even after restoration. Gao et al. (2014) showed that fish biomass and densities remained unchanged in RLake comparing with that in unrestored control CLake. Many of

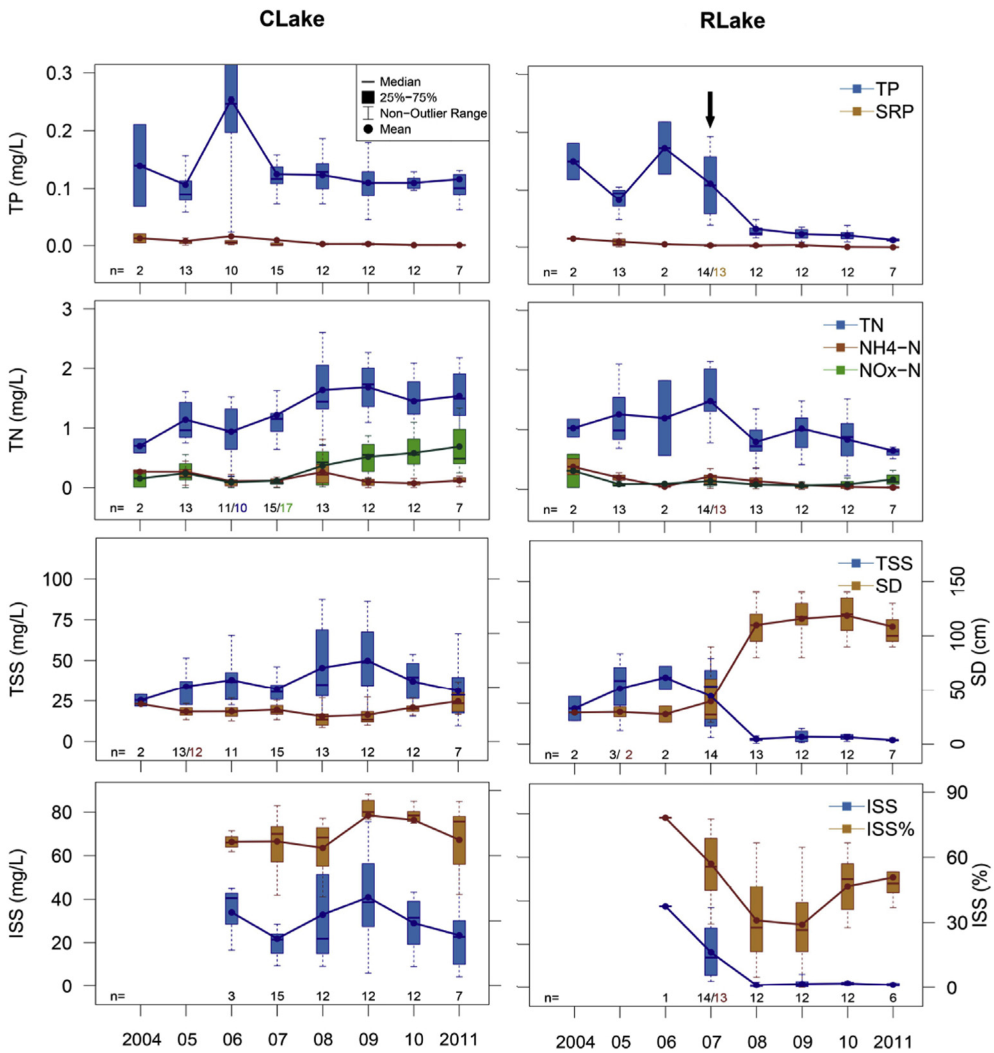

Fig. 3. Boxplot of intra-annual variation in the concentrations of total phosphorus (TP), total nitrogen (TN), ammonium nitrogen (NH_4-N), nitrate-nitrite nitrogen (NOx-N), total suspended solids (TSS), Secchi depth (SD), inorganic suspended solids (ISS) and percentages of ISS to TSS (ISS%). The vertical arrows indicate the start year of restoration. Numbers of samples (n) are shown above the X-axis and are coloured according to the variables they represent in the graph.

the fish species present in the study lakes spawn several times per year, including crucian carp and tilapia (Pan et al., 1991; Gao et al., 2014), and young-of-the-year fish are thus abundant all year around to prey on the large-bodied zooplankton, as seen in other warm lakes (Havens and Beaver, 2011; Meerhoff et al., 2007, 2012; Gao et al., 2014). It has been suggested that dominance of small-bodied zooplankton maybe attributed to the higher temperatures which may render small-sized forms superior competitors for physiological reasons (Moore et al., 1996), but a recent study clearly indicates that large-bodied zooplankton may become dominant even in warm lakes if fish predation is absent (Iglesias et al., 2011; Zeng et al., 2016). Consequently, we attribute the low abundance and dominance of small-sized zooplankton to continuously high fish predation after restoration.

Submerged macrophytes can reduce phytoplankton through bottom-up effects and consequently promote clear water due to both direct and indirect suppression (Jeppesen et al., 1998; Yu et al., 2016a). As the fish biomass and densities remained unchanged in RLake and similar to those in unrestored control CLake (Gao et al., 2014), submerged macrophytes likely played a key role in maintaining the clear water state in RLake after restoration. Macrophytes and associated periphyton may compete with phytoplankton for nutrients (Sand-Jensen and Borum, 1991), reduce phosphorus availability for phytoplankton through diminished nutrient release from the sediment or produce allelopathic substances against phytoplankton (Gross et al., 2007). The unchanged Chl a to TP ratio indicates, however, that allelopathic effects did not play an important role in controlling phytoplankton biomass in our restored basin. Following the restoration the TN:TP ratio rose in both basins relative to the unrestored site (significantly in only one of the basins), which might indicate less limitation of phytoplankton by nitrogen. Nitrate nitrogen was also lower, not least in the winter season. However, as no change occurred in Chl a:TP with decreasing Chl a:TN and as the TN:TP ratio increased after restoration, we suggest that bottom-up effects through reduced phosphorus availability are the likely main mechanisms behind the phytoplankton reduction after restoration in Huizhou West Lake.

Due to lack of efficient grazers, improved light conditions mediated by a reduction in the concentrations of suspended solids, due to the reduction in benthivorous fish stock, may potentially favour phytoplankton growth if natural colonization of macrophytes is delayed. Speeding up the re-establishment of submerged macrophytes via transplantation may therefore be a useful tool in restoring and maintaining the clear state in warm lakes. The re-

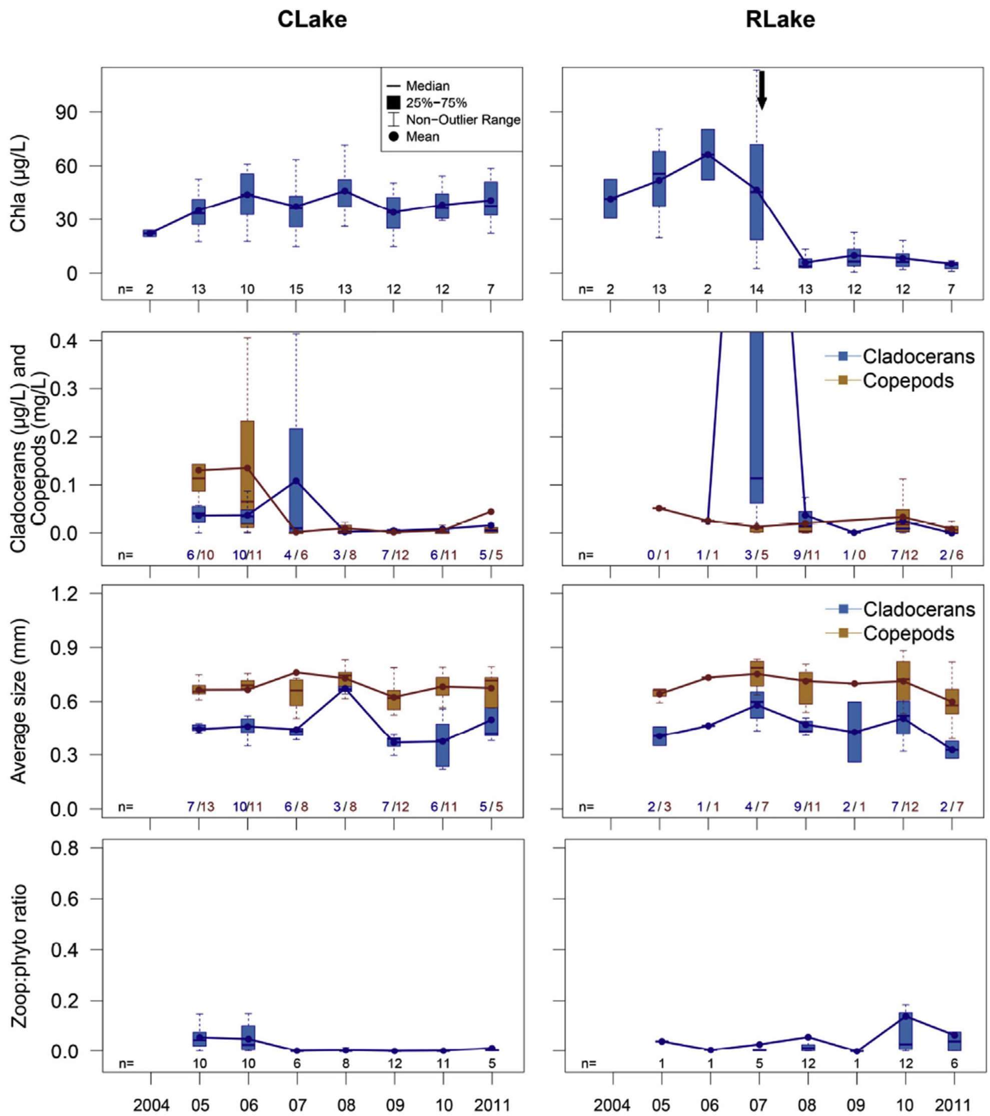

Fig. 4. Boxplot of intra-annual variation in the concentrations of chlorophyll *a* (Chl *a*), biomass (Zoop. biom.) and average size of zooplankton (cladocerans and copepods) and zooplankton to phytoplankton ratio (zoop/phyto ratio) in restored lake basin RLake and unrestored lake basin (CLake). The vertical arrows indicate the start year of restoration. Numbers of samples (n) are shown above the X-axis and are coloured according to the variables they represent in the graph.

establishment of the restored clear state in Huizhou West Lake may in part be due to the high coverage and dominance of *Vallisneria. Vallisneria* is well-rooted and is a meadow-forming species with a high capacity of reducing sediment resuspension from fish. Tilapia and common carp graze submerged macrophytes to a certain degree (Petr, 2000; Miller and Provenza, 2007; Rao et al., 2015; Yu et al., 2016b), but *Vallisneria* is less vulnerable to grazing than *Hydrilla* (Van et al., 1998). Another factor may be the maintenance fishing of mainly tilapia and crucian carp (ca. 450 kg ha.$^{-1}$ year^{-1}) in the restored sites following the restoration (Gao et al., 2014).

Our results have important implications for lake restoration, not least in Asia where natural lakes so far have been used extensively for fish production with often massive stocking of benthivorous fish. With a growing economy and the development of more efficient fish production systems, the interest in restoring lakes is increasing. Scientists, not least in China, have argued for massive stocking of silver carp and bighead carp to control phytoplankton growth and not least nuisance cyanobacteria. This suggestion is supported by analyses using minimal models with all their limitations (Attayde et al., 2010), whereas the results of field experiments are ambiguous and mostly negative (Wang et al., 2008). Our results together with those of later biomanipulation experiments in Chinese lakes and mesocosm studies (Yu et al., 2016a; He et al., 2018) provide strong evidence that fish removal combined with transplantation of submerged macrophytes may have strong effects on the water clarity in warm shallow lakes despite a low zooplankton grazing potential, which is probably due to high fish predation on the zooplankton.

5. Conclusions

Biomanipulation via removal of a substantial amount of plankti-benthivorous fish followed by planting of submerged macrophytes and stocking of piscivorous fish was conducted to restore a shallow eutrophic lake in tropical China. We found strong effects of the restoration initiative in the form of substantial improvements in water clarity and major reductions in nutrient concentrations, particularly total phosphorus, phytoplankton and turbidity. No effects were detected for crustacean zooplankton grazers occurring in low densities before as well as after the restoration. Our results

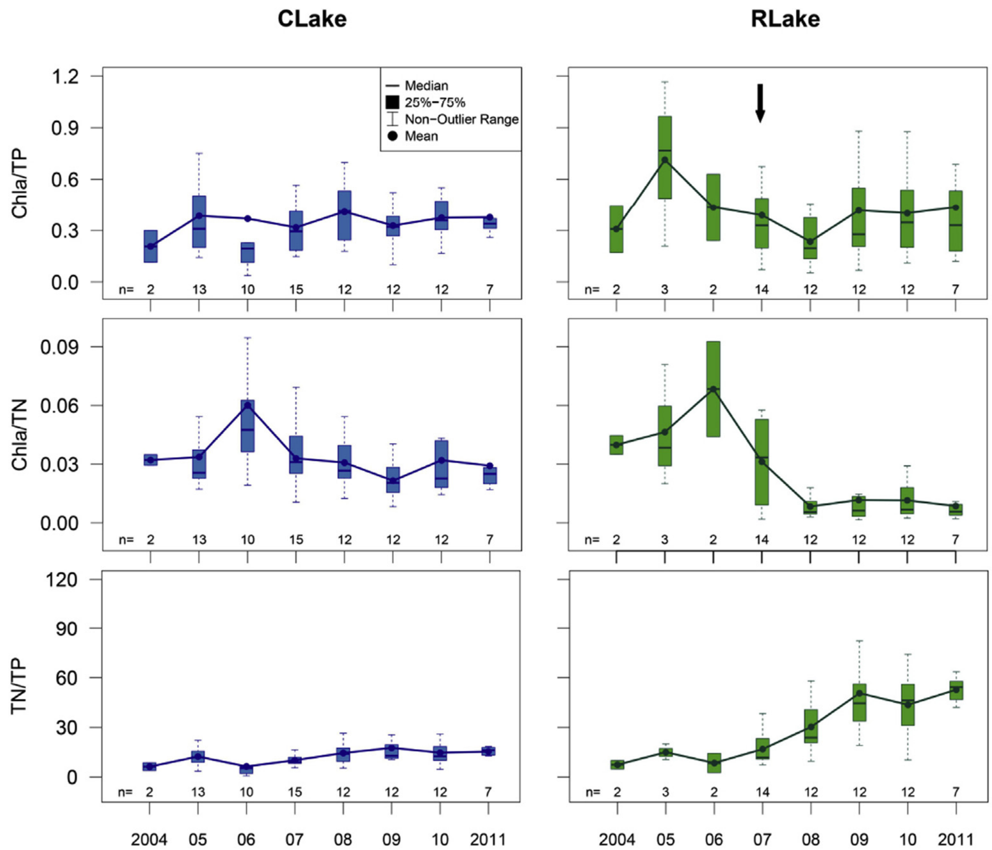

Fig. 5. Boxplot of intra-annual variation in chlorophyll a to total phosphorus ratio (Chl a/TP), chlorophyll *a* to total nitrogen ratio (Chl *a*/TN), total nitrogen to total phosphorus ratio (TN/TP) in restored lake basin (RLake) and unrestored lake basin (CLake). The vertical arrows indicate the start year of restoration. Numbers of samples (n) are shown above the X-axis and are coloured according to the variables they represent in the graph.

suggest that the success of the restoration resulted from the increased bottom-up effects through reduced sediment resuspension and nutrient release, rather than increased top-down effects observed in temperate lakes. Our results add to the existing knowledge of restoration of warm lakes and are strongly relevant, not least in Asia where natural lakes frequently are used extensively for fish production, often involving massive stocking of benthivorous fish.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.watres.2018.09.007.

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