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PRIMARY RESEARCH PAPER

Restoration of a subtropical eutrophic shallow lake in China: effects on nutrient concentrations and biological communities

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Abstract While numerous reports exist on the results of lake restoration initiatives in temperate regions, only a few exist from subtropical lakes. We present results of the lake restoration of shallow, subtropical Lake Wuli, China, conducted between 1999 and 2010. After restoration, annual average concentrations of total nitrogen, total phosphorus (TP), and chlorophyll *a* and the chemical oxygen demand declined significantly, though summer TP remained high. Suspended solids increased significantly over the years, whereas transparency decreased, though not significantly so. The contribution of cryptophytes to total phytoplankton biomass decreased, while the proportion of cyanobacteria, especially potentially N_2-fixing species, increased. Rotifers were superseded by crustaceans as the dominant taxon of the zooplankton community. Enhanced abundance of *Daphnia* spp., appearance of *Leptodora kindti*, and increased biomass ratios of zooplankton to phytoplankton, calanoids to cyclopoids, and nauplii to copepods in the post-restoration period indicate reduced fish predation and stronger top-down control of phytoplankton. However, the increase in non-algal turbidity, probably caused by the higher biomass of benthivorous fish, apparently prevented the re-establishment of submerged macrophyte communities. We conclude that removal of fish, particularly benthivorous species, will further improve water quality in this and other subtropical shallow lakes.

Keywords Subtropical lake · Shallow lake · Restoration · Biomanipulation

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Introduction

During the past 40 years, much effort has been devoted to reduce the eutrophication of lakes in Europe and North America (Sas, 1989; Jeppesen et al., 2005b). In shallow lakes, increases in nutrient input have often been accompanied by reduced transparency, disappearance of submerged macrophytes, and repeated cyanobacterial blooms, leading to deterioration in water quality and ecological degradation. In temperate zones, such lakes have often been found to respond to reductions in nutrient loading, and they typically approach a new, low-nutrient equilibrium in <5 and <10–15 years for nitrogen (N) and phosphorus (P), respectively (Jeppesen et al., 2005b), but the recovery period may, in some cases, be much longer (Søndergaard et al., 2002). In hypereutrophic shallow lakes with high TN and TP, sometimes associated with high organic loading, phytoplankton are often dominated by green algae, cryptophytes, or euglenophytes (Leah et al., 1980; Jensen et al., 1994; Mataloni et al., 2000), and several of these lakes have shown a decline in such algae groups and an increase of cyanobacteria in the early phase of recovery from loading reduction (Krienitz et al., 1996; Jeppesen et al., 2005a, b, 2007). Numerous methods have been employed to reinforce recovery in shallow temperate lakes (Cooke et al., 2005; Jeppesen et al., 2007) after nutrient loading reduction, including sediment capping to reduce internal P loading, manipulation of the fish community and the food web, and restoration of submerged macrophyte communities (Gulati et al., 2008; Jeppesen et al., 2012).

A prerequisite for successful restoration of shallow lakes after a decrease of the external nutrient loadings is a reduction of the biomass of benthivorous and planktivorous fish, either naturally or, when needed, by targeted fish removal, as frequently undertaken in temperate lakes (Hansson et al., 1998; Jeppesen et al., 2005a, b, 2012; Søndergaard et al., 2008). A high fish biomass can negatively affect water quality in a variety of ways. Apart from directly influencing nutrient levels in the water and underlying sediments by excretion (Attayde & Hansson, 2001; Jeppesen et al., 2007; Bajer et al., 2009), fish may also influence the balance of biological communities by feeding selectively on large-bodied cladocerans. Heavy predation reduces the ratio of zooplankton to phytoplankton, thereby restricting the potential impact of zooplankton grazing and reducing the top-down control of phytoplankton. Meanwhile, disturbance and resuspension of sediments by benthivorous fishes in particular are likely to elevate levels of suspended solids (SS) and decrease the sedimentation rate (Jeppesen et al., 2007; Søndergaard et al., 2008). High concentrations of SS are an important cause of water quality deterioration, which may affect the composition of zooplankton communities and inhibit the rehabilitation of macrophytes (Bilotta & Brazier, 2008; Søndergaard et al., 2010).

Contrary to the relatively well-documented results of restoration attempts in temperate lakes, the responses of subtropical and tropical lakes to restoration measures are less well known (Jeppesen et al., 2007, 2012). In warm lakes, the greater abundance and frequent spawning of small fish tend to prevent large-bodied zooplankton from achieving dominance, which naturally limits the potential effect of enhanced grazing control on phytoplankton (Lazzaro, 1997; Havens & Beaver, 2011; Iglesias et al., 2011).

In China, the environmental state of many lakes has rapidly deteriorated to eutrophic conditions due to excessive external nutrient loading. A recent investigation concluded that 85.4% of 138 Chinese lakes with an area >10 km^2 were eutrophic, while 40.1% were hypereutrophic (Yang et al., 2010). In recent years, national and regional governments have made efforts to restore some of these lakes, including urban lakes, by adopting various management strategies (Li et al., 2005; Chen et al., 2006). However, the negative effects of high nutrient levels and high levels of fish disturbance and predation are often so strong that attempts to improve water quality by rehabilitating aquatic plants have often been unsuccessful (van de Bund & van Donk, 2002; Jeppesen et al., 2005a; Søndergaard et al., 2010).

Lake Wuli, a subtropical shallow lake located close to Wuxi City on the northern end of Lake Taihu, changed from a mesotrophic state with abundant macrophytes during the 1950–1970s to a eutrophic state with few macrophytes and frequent cyanobacterial blooms during the early 1980s. The increased productivity encouraged stocking of commercial fish, mainly bighead carp *Aristichthys nobilis*, silver carp *Hypophthalmichthys molitrix*, common carp *Cyprinus carpio*, Crucian carp *Carassius auratus*, and grass carp *Ctenopharyngodon idellus*. The annual fish yield increased to about 650–880 t in total, equivalent to 714–967 kg ha^{-1} (Chen, 2007). From 2002 to 2005, various restoration measures were introduced by the local government of Wuxi City in order to improve lake water quality. These included reduction of external nutrient loading and sediment dredging, but not fish removal. In the present study, we hypothesized that the reduction of nutrient loading would potentially result in a fast reduction in lake nutrient concentration, but that improvements in lake water transparency may be hampered by no control of benthivorous fish in subtropical shallow lakes. To test these hypotheses, we followed the effect of restoration on the water quality, zooplankton, and phytoplankton in Lake Wuli and compared the results with studies from temperate and other subtropical lakes. Possible methods for further improvements of the water quality of the lake and other subtropical hallow lakes were also discussed.

Methods and materials

Study site

Lake Wuli is located south of Wuxi City in Jiangsu, China (Fig. 1). Prior to sediment dredging and removal of in-lake ponds between 2002 and 2005, its area was 5.8 km^2 and its average depth 1.8 m. Following restoration, the lake area and average depth increased to 8.6 km^2 and 2.25 m (Zhu & Zhang, 2009), respectively. Annual average precipitation and air temperature in Wuxi City are about 1,100 mm and 15.4°C, respectively. Average wind speeds between 1961 and 2000 were 3.1 m s^{-1} in winter and 3.0 m s^{-1} in summer (Chen, 2007).

Since the 1950s, Lake Wuli has undergone significant changes in its ecological state (Table 1).

(1) In 1951, the annual averages of phosphate phosphorus (PO_4^{3-}-P), ammonium nitrogen (NH_4^+-N), and Secchi depth (SD) were 0.0097 mg l^{-1}, 0.12 mg l^{-1}, and 1.44 m, respectively. Macrophytes, including *Vallisneria natans*, *Potamogeton crispus*, *Trapa incise*, *Myriophyllum* sp., and *Phragmites communis* among others, were abundant (Wu, 1962). This state persisted until the beginning of the 1960s (NIGLAS, 1965)
(2) At the end of the 1960s, fish stocking in Lake Wuli and external nutrient loading from Wuxi City led to eutrophication (IEQLT, 1983; Sun & Huang, 1993). Macrophytes, especially submerged species, gradually disappeared. By 1980–1981, the average total nitrogen (TN), TP, and NH_4^+-N concentrations had increased to 0.85 mg l^{-1}, 0.016 mg l^{-1}, and 0.21 mg l^{-1}, respectively, and SD decreased to 0.45 m (IEQLT, 1983; Li et al., 1994).
(3) From the end of the 1980s to the beginning of the 1990s, cyanobacterial blooms occurred, mainly of *Chroococcus* spp. and *Microcystis* spp. (Li et al., 1994). Average TN, TP, NH_4^+-N, and SD during 1987–1988 were 3.1 mg l^{-1}, 0.076 mg l^{-1}, 0.61 mg l^{-1}, and 0.50 m, respectively (Sun & Huang,

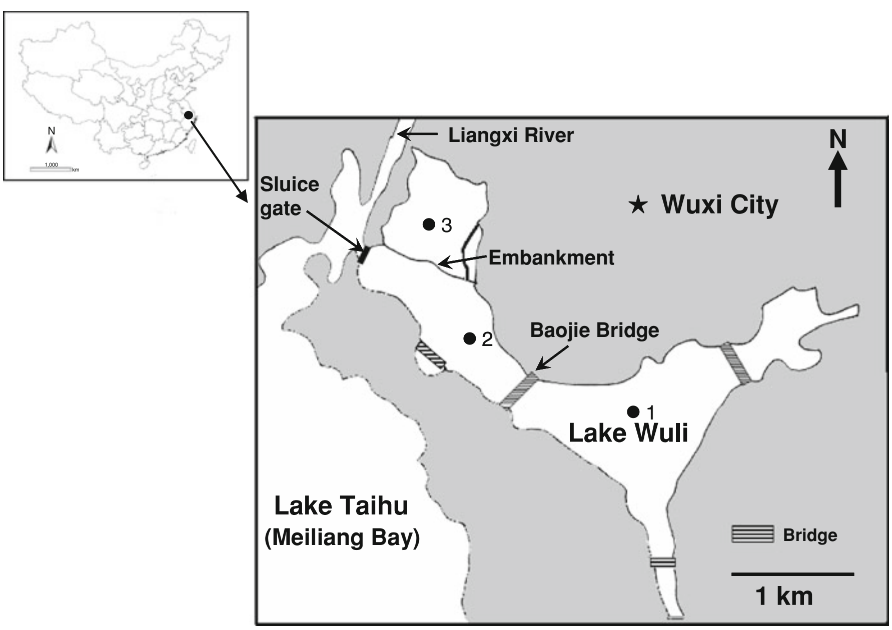

Fig. 1 Location of Lake Wuli. Sites 1 and 2 are sampling sites. Site 3 is not a sampling site. Baojie Bridge and an embankment divide Lake Wuli into three sections—East Lake Wuli (Site 1), West Lake Wuli (Site 2), and an area formerly occupied by fish ponds (Site 3). Two small bridges along the embankment permit water exchange between West Lake Wuli and Site 3. A sluice gate prevents exchange of water between Lake Wuli and Meiliang Bay in Lake Taihu

Table 1 TN, TP, NH_4^+-N, and SD from the 1950s to the 1990s in Lake Wuli

	TN (mg l^{-1})	TP (mg l^{-1})	NH_4^+-N (mg l^{-1})	SD (m)	Citation
1951	–	–	0.12	1.44	Wu (1962)
1980–1981	0.85	0.016	0.21	0.45	IEQLT (1983) and Li et al. (1994)
1987–1988	3.1	0.076	0.61	0.5	Sun & Huang (1993)
1990–1993	4.5	0.213	1.76	0.41	Li et al. (1994)
1994–1995	4.9	0.083	2.42	0.47	CNERN TLLER

– no data; CNERN TLLER: Taihu Laboratory for Lake Ecosystem Research

1993), and the situation continued to worsen into the early 1990s. Average TN, TP, NH_4^+-N, and SD during the period 1990–1993 were 4.5 mg l^{-1}, 0.213 mg l^{-1}, 1.76 mg l^{-1}, and 0.41 m, respectively (Li et al., 1994).

(4) From the mid-1990s, Lake Wuli was in a hypereutrophic state. Diatoms (*Cyclotella* spp. and *Melosira* spp.) and cryptophytes (*Chroomonas* sp. and *Cryptomonas* spp.), rather than cyanobacteria, dominated the phytoplankton community. Average TN, TP, NH_4^+-N, and SD during 1994–1995 were 4.9 mg l^{-1}, 0.0825 mg l^{-1}, 2.42 mg l^{-1}, and 0.47 m, respectively (data from CNERN, Taihu Laboratory for Lake Ecosystem Research).

In 1999, the government of Wuxi City closed hotels, restaurants, sanatoriums, and factories along the lake. Then, from 2002 to 2005, a series of active restoration measures were implemented including sediment dredging, reduction of external nutrient loading, removal of in-lake fish ponds, and reconstruction of the bank area. The latter involved the removal of concrete banks, planting with emergent macrophytes, and the construction of a small wetland. It was estimated that sediment dredging removed 41-t TN and 90-t TP from the lake and that the reduction in external loading and the removal of in-lake fish ponds accounted for further reductions of 93.1-t TN, 8.6-t TP, and 852-t COD_{Mn} per year (Gu & Lu, 2004).

Data source and analysis

The data were obtained from CNERN, the Taihu Laboratory for Lake Ecosystem Research. Samplings were conducted at Site 1 from 1999 to 2004 and at Sites 1 and 2 from 2005 to 2010 (Fig. 1). Average depth was 2.75 m at Site 1 and 2.40 m at Site 2. Samplings took place in winter (February), spring (May), summer (August), and autumn (November) each year. The variables analyzed included temperature, SD, COD_{Mn}, TN, TP, ammonia, soluble reactive phosphorus (SRP), dissolved inorganic nitrogen (DIN = nitrite + nitrate + ammonia), total SS, chlorophyll *a* (Chl *a*), and biological community compositions.

Water temperature and SD were measured using a thermometer and a Secchi disk. TN and TP concentrations were analyzed by colorimetry after digestion (Ebina et al., 1983). Samples were filtered through pre-dried Whatman GF/C filters, dried (105°C for 4 h) and weighed to measure the concentration of SS. Chl *a* was extracted with 90% acetone for 24 h, and its concentration was subsequently determined by colorimetry and calculated according to the equation of Jin & Tu (1990).

For biological community analyses, microcrustaceans were collected by filtering 7.5 l of mixed water collected at three depths through a 64-μm net and preserved in 4% formaldehyde. For phytoplankton and rotifer microscopic counting, 1-l water samples mixed from the three depths were treated with 10 ml Lugol's iodine and sedimented for 48 h. The supernatant was removed and the residue was collected. Crustacean zooplankton (cladocerans and copepods) and rotifers were counted at 40× magnification. Species identification was made according to Wang (1961), Chiang & Du (1979), and Shen & Du (1979). Zooplankton biomass (dry weight) was estimated using equations from Huang (1999). Phytoplankton biomass was estimated from algal counts using the nearest geometric volume of each taxon, assuming a mean density of phytoplankton of 1, i.e., 1-g wet weight of phytoplankton has a volume of 1 × 10^3 mm^3.

In order to evaluate the effectiveness of restoration, the time series was divided into three periods: pre-restoration (1999–2001), during restoration (2002–2005), and post-restoration (2006–2010). Annual averages of the biotic and abiotic parameters were calculated from data on Site 1 from 1999 to 2004 and on Sites 1 and 2 from 2005 to 2010. *T* tests for annual data on Sites 1 and 2 showed no significant difference ($P > 0.05$). We therefore averaged the Sites 1 and 2 data before analyses. To evaluate the effect of zooplankton grazing on phytoplankton, the ratios of zooplankton biomass to phytoplankton biomass (ZB:PB) and of Chl *a*:TP concentrations were calculated. ZB:PB was calculated as zooplankton biomass/Chl *a* concentration/66 (Jeppesen et al., 2005a). To assess changes over time, Spearman's correlations were conducted between the various environmental variables and years after log transformation of the data. *T* tests were used to compare the environmental variables and ratios between the pre- and the post-restoration period.

Results

Changes in physico-chemical variables

Average water temperatures from 1999 to 2010 were 8.1 ± 1.7, 22.2 ± 1.8, 29.6 ± 1.8, and 13.5 ± 2.4°C in February, May, August, and November, respectively. Annual water temperatures calculated using four-month averages fluctuated between 17.3 and 19.7°C, but no obvious trend was discernible during the study period.

Annual mean concentrations of TN, TP, and COD_{Mn} decreased significantly over the years (Fig. 2; Table 3). Winter TN decreased more dramatically than summer values. Summer TP tended to decrease, though not significantly. However, winter TP declined pronouncedly during the study period. COD_{Mn} changes followed the pattern of TP. There were statistically significant changes in annual average concentrations of TN, TP, and COD_{Mn}. Summer TN was significantly lower in the post-restoration period than in the pre-restoration period, whereas summer TP and COD_{Mn} showed no statistically significant changes between the two periods (Table 2). There was a dramatic drop in TN, with post-restoration concentrations being less than half of those observed prior to restoration. Since 2007, summer TN remained below 2 mg l^{-1}, while summer and annual TP remained above 0.10 mg l^{-1} after restoration. COD_{Mn} decreased gradually to <5 mg l^{-1} after 2007 (Fig. 2).

Annual average Chl *a* decreased significantly after restoration. Annual SD showed no significant change, while SS increased significantly (Fig. 2; Table 3). There were no statistically significant changes in the ratios of summer SRP:TP and DIN:TN, but the Chl *a*:TP and Chl *a*:SS ratios decreased significantly (Table 2).

Changes in phytoplankton and zooplankton

Marked changes were also observed in the phytoplankton community (Fig. 3). Annual phytoplankton biomass averages decreased by 90.7%. Cryptophytes (*Cryptomonas ovata*, *C. erosa*, *Chroomonas acuta*) and diatoms (*Cyclotella* sp., *Melosira granulata*) generally dominated the phytoplankton community prior to restoration. Cryptophyte biomass decreased from 81.7 to 17.1% of the total biomass between 1999 and 2010, whereas the proportion of cyanobacteria of the annual total phytoplankton biomass increased from 0.3 to 29.9%. The cyanobacterial community was mainly represented by *Anabaena* sp. and *Aphanizonmenon* sp. without heterocysts.

Distinct trends were observed in the abundance of crustaceans and rotifers during the study period (Fig. 3). After 2005, cladoceran biomass increased markedly during the warm seasons, in particular, the large-sized cladoceran *Daphnia* spp., occurring in abundance only in spring (May) (Fig. 4a). In summer (August), the cladoceran communities became dominated by small-sized species (*Bosmina longirostris*, *Ceriodaphnia cornuta*, *Moina micrura*, *Diaphanosoma dubium*). At the same time, the predatory cladoceran *Leptodora kindti* appeared, with a peak density of 1.4 ind. l^{-1} in summer 2006 (Fig. 4b). The average body lengths of summer cladocerans and copepods varied markedly between 2004 and 2010, but with an overall tendency of showing increased length by the end of the study (Fig. 4c). The ratios of calanoid:cyclopoid and nauplii:copepod increased significantly ($P = 0.040$ and 0.027, respectively) from 2004 to 2010 (Fig. 4d). Prior to restoration, the rotifer community was dominated by the genera *Brachionus*, *Polyarthra*, *Filinia*, and *Trichocerca*.

The crustacean proportion of total summer zooplankton biomass increased from 0.04 before restoration to 0.30 afterward. However, total copepod and

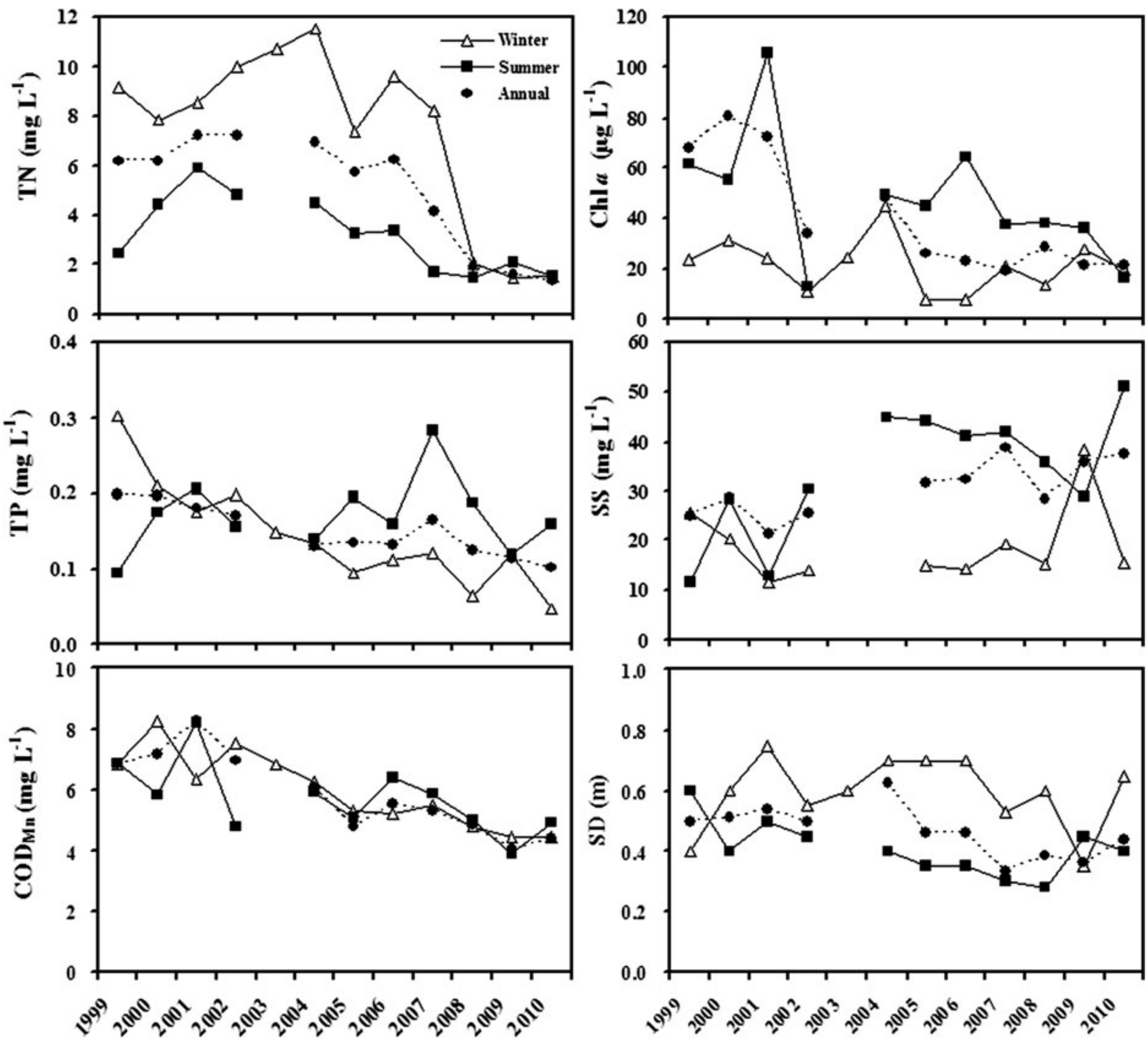

Fig. 2 Annual average, summer (August), and winter (February) concentrations of TN, TP, COD_{Mn}, SD, Chl *a*, SS in Lake Wuli from 1999 to 2010

cladoceran biomass declined dramatically after 2007; thus, total summer zooplankton biomass declined from 2342 μg l^{-1} before restoration to 507 μg l^{-1} in the post-restoration period.

Spearman's correlation analysis indicated that the total phytoplankton biomass for a given year exhibited a significant positive correlation with COD_{Mn} ($r = 0.72$, $P = 0.009$). The ratio of cyanobacteria biomass to total phytoplankton biomass correlated negatively with TN ($r = -0.85, P < 0.001$), TP ($r = -0.69, P = 0.014$), TN:TP (molar ratio, $r = -0.75$, $P = 0.005$), and COD_{Mn} ($r = -0.83, P = 0.001$). Conversely, the ratio of cryptophyte biomass to total phytoplankton biomass was positively correlated with TN ($r = 0.60, P = 0.04$), TP ($r = 0.72$, $P = 0.008$), and COD_{Mn} ($r = 0.60$, $P = 0.04$). The summer ratio of zooplankton to phytoplankton biomass increased significantly ($r = 0.74$, $P = 0.009$) over the years (Fig. 3).

Discussion

The physico-chemical and biological variables of Lake Wuli responded dramatically to the reduction of external nutrient loading and the removal of sediment from the lake basin. Significant winter decreases in TN

Table 2 Average values (±SE) of parameters and ratios before (1999–2001) and after (2006–2010) restoration in Lake Wuli

Response variables	Pre-restoration	Post-restoration	*P* value
TN annual (mg l^{-1})	6.56 ± 0.33	3.05 ± 0.95	<0.0001
TN summer (mg l^{-1})	4.24 ± 0.99	2.03 ± 0.34	0.038
TP annual (mg l^{-1})	0.19 ± 0.006	0.126 ± 0.011	0.002
TP summer (mg l^{-1})	0.16 ± 0.033	0.18 ± 0.028	0.639
COD_{Mn} annual (mg l^{-1})	7.43 ± 0.43	4.84 ± 0.27	<0.0001
COD_{Mn} summer (mg l^{-1})	6.98 ± 0.69	5.23 ± 0.43	0.062
Chl *a* annual (μg l^{-1})	73.8 ± 3.63	22.8 ± 1.60	0.001
Chl *a* summer (μg l^{-1})	74.2 ± 16.0	38.6 ± 7.68	0.062
SS annual (mg l^{-1})	25.0 ± 2.01	34.6 ± 1.92	0.031
SS summer (mg l^{-1})	17.6 ± 5.34	39.9 ± 3.67	0.012
SD annual (m)	0.52 ± 0.011	0.40 ± 0.024	0.019
SD summer (m)	0.50 ± 0.058	0.36 ± 0.031	0.052
SRP summer (mg l^{-1})	0.035 ± 0.015	0.062 ± 0.030	0.532
DIN summer (mg l^{-1})	2.83 ± 0.42	1.29 ± 0.44	0.058
SRP:TP summer	0.287 ± 0.157	0.289 ± 0.099	0.993
DIN:TN summer	0.70 ± 0.07	0.59 ± 0.09	0.408
Chl *a*:TP summer	0.50 ± 0.10	0.23 ± 0.06	0.047
Chl *a*:SS summer	0.34 ± 0.11	0.07 ± 0.01	0.022
Cladoceran biomass summer (μg l^{-1})	9.44 ± 1.75	182.8 ± 34.40	0.003
Copepod biomass summer (μg l^{-1})	10.5 ± 5.52	80.4 ± 19.28	0.014
Rotifer biomass summer (μg l^{-1})	691.9 ± 385.10	125.3 ± 44.60	0.094
Zooplankton biomass summer (μg l^{-1})	712.9 ± 383.2	388.4 ± 35.5	0.298
Phytoplankton biomass summer (mg l^{-1})	39.0 ± 27.28	1.76 ± 0.47	0.111
Zooplankton:phytoplankton biomass ratio summer	0.004 ± 0.002	0.12 ± 0.035	0.044

TN total nitrogen, *TP* total phosphorus, *SS* suspended solids, *Chl a* chlorophyll *a*, *SD* Secchi depth, *SRP* soluble reactive phosphorus, *DIN* dissolved inorganic nitrogen

P values were used for comparisons of average values during two periods using *t* test

Table 3 Spearman's correlations between years (1999–2010) and various parameters (log) for winter, summer, and annual averages in Lake Wuli

	TN	TP	SS	Chl *a*	COD_{Mn}	SD
Winter	−0.74*	−0.89**	0.13	−0.20	−0.92**	−0.04
Summer	−0.72*	0.23	0.70*	−0.43	−0.63	−0.60
Annual	−0.82**	−0.90**	0.79**	−0.89**	−0.91**	−0.67

TN total nitrogen, *TP* total phosphorus, *SS* suspended solids, *Chl a* chlorophyll *a*, *SD* Secchi depth

* $P < 0.05$; ** $P < 0.01$

and much lower summer values indicate a rapid response to external N loading, though lack of input data hinders a firm conclusion. However, a cross comparison of a number of European and North American case studies also suggests a general fast response of TN to external load reduction in mainly temperate lakes, where a new equilibrium is reached typically in less than 5 years (Jeppesen et al., 2005a, Table 4), perhaps even faster in warm regions due to higher denitrification rates (Lewis, 2000). TP decreased in winter and on an annual basis as expected from other studies (Table 4), but remained high in summer, likely reflecting a continuing high rate of P release from the sediments as seen in other studies (Köhler et al., 2005; Søndergaard et al., 2005, 2013). Contrary to most other studies of temperate lakes (Jeppesen et al., 2005b), TN:TP and DIN:SRP ratios decreased in summer, whereas summer SRP:TP

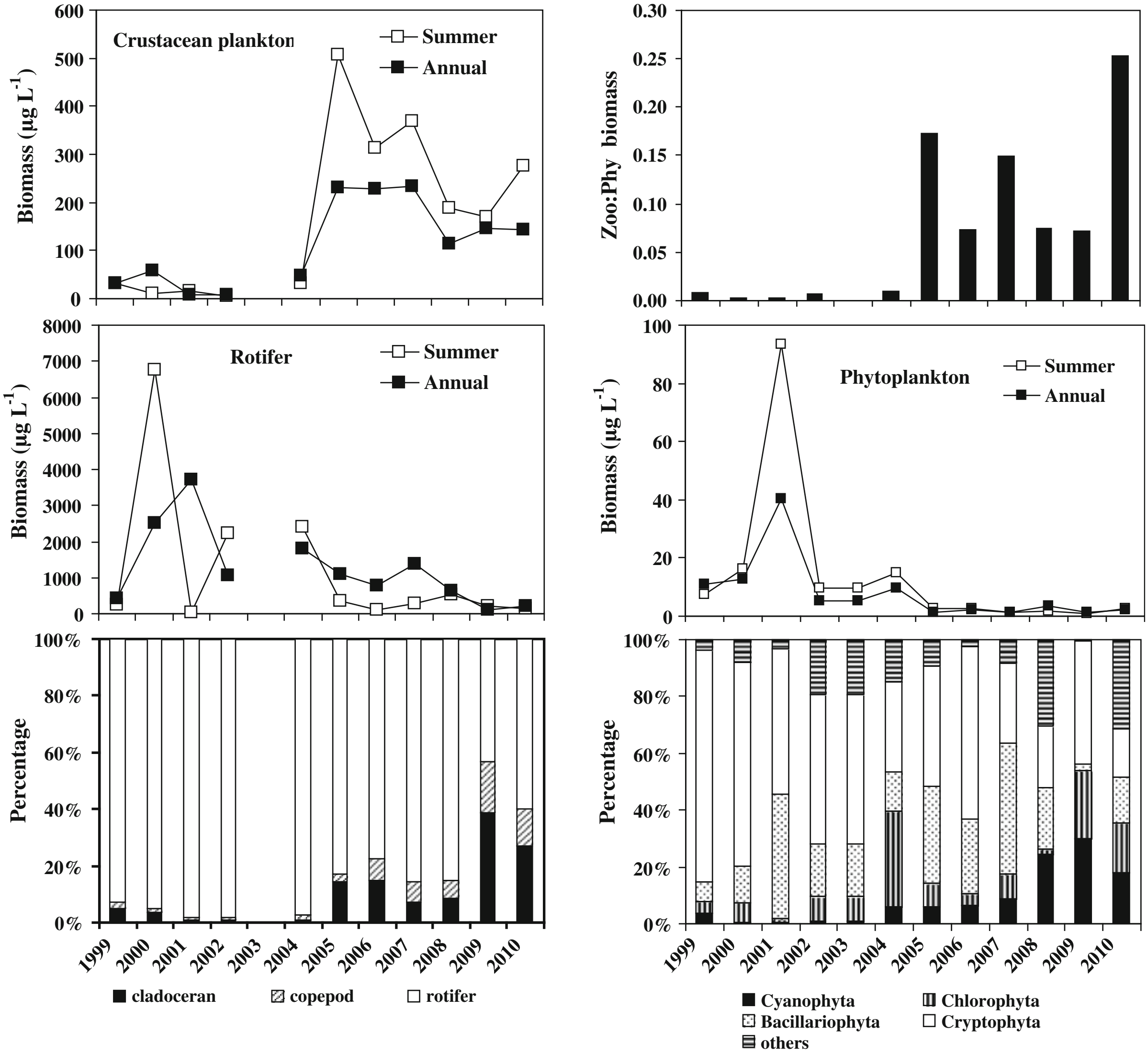

Fig. 3 Lake Wuli plankton dynamics from 1999 to 2010. (1) Annual average, summer (August) biomass of crustacean plankton (cladocerans + copepods), rotifers (dry weight, μg l^{-1}), and phytoplankton (wet weight, mg l^{-1}); (2) percentage biomass of different zooplankton and phytoplankton taxa; (3) zooplankton (Zoo):phytoplankton (Phy) biomass ratio in summer

exhibited no change after restoration (Table 4). These differences are attributed to the particularly strong decrease of TN and DIN summer in Lake Wuli and high level of TP and SRP summer.

SS increased despite a clear decline in summer Chl *a* suggesting that the turbidity is largely due to inorganic suspended matter and detritus, most likely in consequence of sediment resuspension. Lakes with a dynamic ratio (square root of lake surface area in square kilometers divided by mean depth in meters) >0.8 are prone to wave disturbance (Håkanson, 1982; Bachmann et al., 2000). The dynamic ratio of Lake Wuli, however, only decreased from 1.34 in the pre-restoration years to 1.25 after restoration due to the increase in lake area, a change that is too low to explain the increase in SS. The similar water contents observed in the surface sediment before (55.0%) and after (57.6%) restoration (Fan & Zhang, 2010) also suggest no important change in the risk of wind-induced resuspension. Moreover, the wind speed was

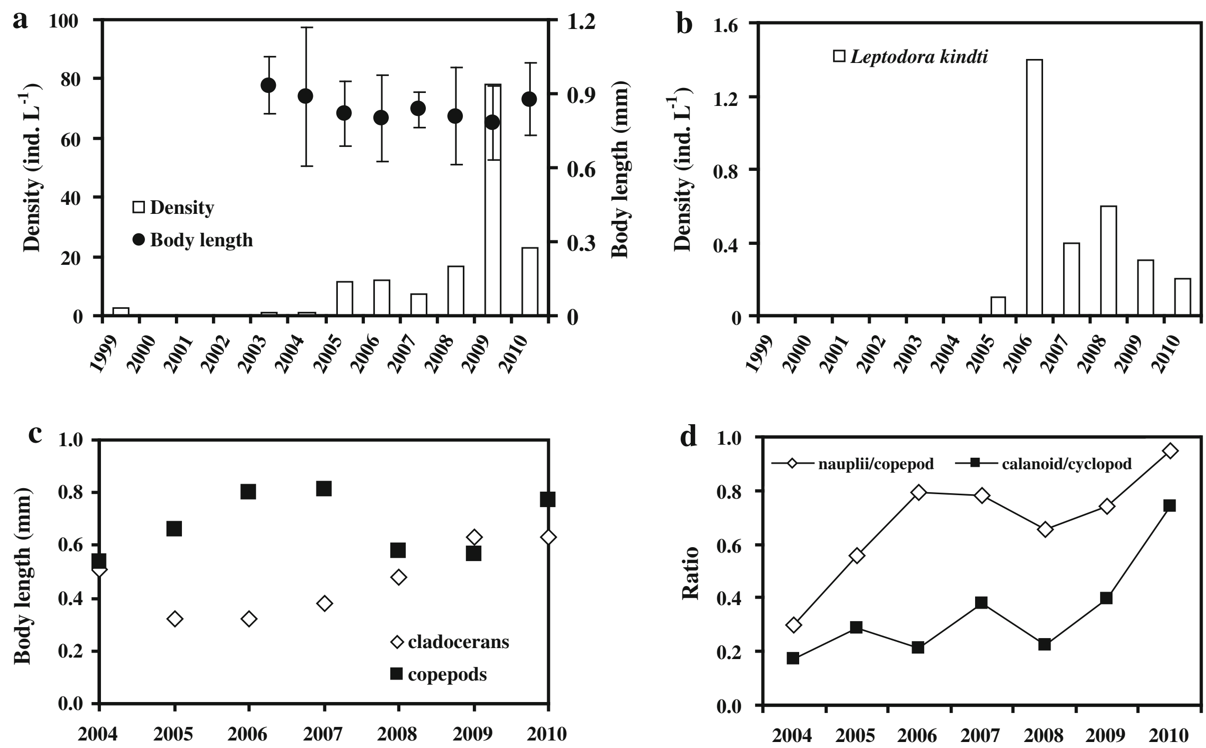

Fig. 4 Variations of zooplankton in Lake Wuli from 1999 to 2010. **a** density and body length (±SD) of *Daphnia* spp. in May (spring); **b** density of *Leptodora kindti* in August (summer); **c** average body length of cladocerans and copepods in summer; **d** density ratios of calanoids to cyclopoids and nauplii to copepods in summer

similar in winter (3.1 m s^{-1}) and summer (3.0 m s^{-1}), and there were no significant changes in water levels between summer and winter (Zhu & Zhang, 2009), but still SS varied markedly, being much higher in summer. Benthivorous fish, on the other hand, can substantially enhance sediment resuspension in shallow lakes (Breukelaar et al., 1994). In Lake Wuli, prior to restoration, the annual fish yield reached 650–880 t, equivalent to 714–967 kg ha^{-1} (Chen, 2007). The dominance of planktivorous and benthivorous species, such as *Aristichthys nobilis, Hypophthalmichthys molitrix, Cyprinus carpio*, and *Carassius auratus*, of the fish community (Duan et al., 2009; Zhang et al., 2010) provides a likely explanation for the observed increase in SS. Fish-induced sediment resuspension may also explain the higher concentrations of SS in summer, as fish become more active in warm water (Hernandez et al., 2002). Nothing has so far been done to reduce the abundance of fish in the lake, and fish fry continues to be stocked periodically (Q. J. Luo pers. communication). Higher fish disturbance may also explain that TP in summer actually increased after restoration and that SRP:TP, contrary to observations from many other studies (Table 4), did not decline.

Major changes occurred in the zooplankton community structure, shifting from rotifer to crustacean dominance. High rotifer abundance is typical of eutrophic lakes with high levels of fish predation (Shao et al., 2001; May & O'Hare, 2005). The increased abundance of *Daphnia* spp., the appearance of the predatory *Leptodora kindti*, and the increased ratios of zooplankton:phytoplankton and calanoid:cyclopoid after the restoration process suggest a reduced fish predation pressure on large-bodied crustacean zooplankton (Adrian, 1997; Liu, 2001; Jeppesen et al., 2005b). The observed increase in SS after restoration might have contributed to the reduction in fish predation pressure as turbidity may offer refuge from visual predators (Jeppesen et al., 1999; Horppila et al., 2009; Nurminen et al., 2010). In an enclosure experiment, increasing SS reduced the predation efficiency of a visually oriented hunter, perch (*Perca fluviatilis*), on two large-sized cladoceran species (Nurminen et al., 2010).

Table 4 Response comparisons of different variables to shallow lake restoration in mainly temperate lakes (reviewed by Jeppesen et al., 2005b) and subtropical lake Wuli

Response variable	Temperate lakes	Subtropical lake (Lake Wuli)
P response time to TP loading reduction	Typically 10–15 years	Differ with season
N response time to TN loading reduction	Typically <5 years	<5 years
TP summer and annual	Decreased in most lakes	No change in summer/decreased annually
TN summer	Decreased in most lakes	Decreased
TN:TP summer	Increased in most lakes even in some lakes with lower TN:TP in the inlet	Decreased
SRP summer	Decreased in all lakes when TP decreased	Increased
SRP:TP summer	Decreased in all lakes when TP decreased	No change
DIN:SRP summer	Increased in most lakes	Decreased
Secchi depth summer	Increased in most lakes	Decreased
Chl *a* summer	Decreased in most lakes	Decreased
Chl *a*:TP summer	Increased or no change	Decreased
Phytoplankton biovolume	Decreased in most lakes	Decreased
Phytoplankton community changes	Higher importance of diatoms, cryptophytes and chrysophytes	Cryptophytes, cyanobacteria
Fish biomass	Decreased in most lakes	Unclear
Zooplankton biomass	Decreased	Decreased, however an increase for crustaceans
Zooplankton:phytoplankton biomass ratio	Increased in many lakes, probably reflecting release from fish predation	Increased
Indications of enhanced bottom-up control of phytoplankton	Nearly all lakes	Yes
Indications of enhanced top-down control of phytoplankton	Many lakes	Yes

Despite the elevated summer levels of TP, the phytoplankton biomass and Chl *a* in summer declined over time. This may in part be attributed to increased zooplankton grazing as indicated by an increase in the biomass ratio of zooplankton:phytoplankton and a reduction of summer Chl *a*:TP ratios, as seen in other studies of lakes in recovery (Jeppesen et al., 2005a, b, Table 4), but the higher concentration of inorganic SS may also have contributed by shading the phytoplankton (Kang et al., 2013). We also found marked changes in the phytoplankton community. Cryptophytes declined from 68% of phytoplankton biomass prior to restoration to 27% in recent years, while the proportion of cyanobacteria increased from 0.3% to 29.9% during the same period. While a decline of cryptophytes following nutrient loading reduction may be appear counterintuitive as eutrophic lakes are often considered as cyanobacteria dominated, there is substantial evidence now that hypereutrophic shallow lakes with high TN and TP, sometimes associated with high organic loading, are often dominated by green algae, cryptophytes, or euglenophytes (Leah et al., 1980; Jensen et al., 1994; Mataloni et al., 2000), and several have shown a decline in such algae groups and an increase of cyanobacteria in the early phase of recovery from loading reduction (Krienitz et al., 1996; Jeppesen et al., 2005a, b, 2007). Low TN:TP (molar ratio) (Smith, 1983) and low light levels (Scheffer et al., 1997) due to increased turbidity may further have favored cyanobacteria in Lake Wuli in recent years, although the role of the TN:TP ratio for phytoplankton dominance is ambiguous, not least for the shallow lakes (Jensen et al., 1994).

Contrary to findings from temperate Danish lakes (Jeppesen et al., 2005a, b), we did not observe an intermediate state with dominance of *Microcystis* (despite dominating in Lake Taihu) during recovery before the shift to dominance by *Anabaena* sp. and *Aphanizonmenon* sp. This may reflect the fast reduction in nutrients (notable TN) in Lake Wuli as a consequence of the multiple restoration measures initiated. Also, higher grazing may favor filamentous cyanobacteria over *Microcystis* as seen in lakes and ponds with high abundance of *Daphnia magna* (Fott et al., 1980; Lynch, 1980).

The present environmental state of Lake Wuli is unfavorable for the rehabilitation of a submerged macrophyte community. The high biomass of benthivorous fish is detrimental to submerged macrophytes in several ways: The macrophytes suffer directly by consumption by fish and indirectly through the effects of reduced light levels caused by sediment resuspension and the proliferation of phytoplankton in water enriched with excreted nutrients (Haas et al., 2007; Gulati et al., 2008; Bajer et al., 2009). In lakes with a mean depth <3 m, submerged macrophyte growth is adversely affected when SS exceeds 15 mg dw l^{-1} (Søndergaard et al., 2010). In Lake Wuli, having a mean depth of only 2.25 m, SS reached as much as 40 mg dw l^{-1} after restoration. Fish removal is likely to increase the light available to submerged macrophytes, and rehabilitation efforts might be further improved by a reduction of the water level. A demonstration project in a branch of Lake Wuli involving fish removal and lowering of the water level has resulted in clear water and extensive growth of macrophytes (Zhang et al., 2012).

To improve water clarity and thus enhance the rehabilitation of submerged macrophytes in Lake Wuli, removal of benthivorous fish should be considered as a restoration measure. Biomanipulation has been extensively used in the restoration of temperate waterbodies (Søndergaard et al., 2008), but its effect in subtropical and tropical lakes is less well studied (Jeppesen et al., 2007, 2012). It is to be expected that the top-down effect might be less dramatic in warm lakes due to the greater abundance of small fish (Meerhoff et al., 2007; Jeppesen et al., 2010, 2012). However, recent studies suggest that this may not be a barrier to success, at least in the short term, as removal of large benthivorous fish may reduce a resuspension-induced increase in turbidity. Beklioglu & Tan (2008) reported successful short-term restoration of a subtropical lake using biomanipulation, and successful restoration via biomanipulation was also achieved in the Huizhou West Lake, a tropical shallow eutrophic lake in south China (Chen et al., 2010; Jeppesen et al., 2012; Z. Liu et al., unpublished results). We therefore recommend removal of fish, particularly benthivores, in order to re-enforce ecological restoration and further improvement of the water quality of Lake Wuli, and we further argue that fish removal may also be a relevant restoration measure in many other Asian lakes used for fish production in either the past or the present.

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