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Do submerged macrophytes facilitate the development of large crustacean zooplankton in tropical shallow lakes?

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Abstract In temperate shallow lakes, submerged macrophytes facilitate zooplankton development by providing refuge against fish predation and, thereby, indirectly contribute to maintaining a clear-water state through enhanced zooplankton grazing. The role of macrophytes for zooplankton and their grazing potential is less clear for tropical lakes. We investigated crustacean zooplankton in a phytoplankton-dominated basin (algal basin) and two restored basins dominated by macrophytes (macrophyte basins) in the shallow Huizhou West Lake in tropical southern China. We found that copepods prevailed in all basins, but the dominant taxon differed, with omnivorous cyclopoids dominating in the algal basin and herbivorous calanoids in the macrophyte basins. Moreover, the biomass ratios of calanoid:copepod and zooplankton:phytoplankton were higher in the macrophyte basins than in the algal basin. Our results suggest that restoration measures involving macrophyte transplantation and fish removal lead to reduced fish predation on zooplankton, which help to maintain the clear-water state when macrophytes are established due to higher control on phytoplankton. However, unlike in temperate lakes, large-bodied *Daphnia* were generally absent and the zooplankton:phytoplankton ratio was overall low, indicating a weaker top-down control in tropical lakes, which is likely due to higher fish predation.

Keywords Zooplankton:phytoplankton ratio · Zooplankton size · Clear-water state

Introduction

Excess nutrient loading causes a shift from a clear-water state dominated by submerged macrophytes to

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a turbid state dominated by phytoplankton in shallow lakes (Moss, 1990; Scheffer et al., 1993). Such a shift is typically accompanied by a reduction in large-sized zooplankton, such as *Daphnia* spp., due to increased fish predation leading to a decreasing grazing pressure on phytoplankton (Jeppesen et al., 2002; 2005; Iglesias et al., 2011; Hilt et al., 2018). Submerged macrophytes not only provide shelters for zooplankton against predation by planktivorous fish (Jeppesen et al., 1998; Manatunge et al., 2004; Meerhoff et al., 2007), they also protect their resting eggs in the sediments from destruction by benthic fish (Gabaldón et al., 2018). Accordingly, studies have shown that biomanipulation (including fish removal and in some cases submerged macrophyte transplantation) resulted in recovery of large-sized zooplankton and a higher grazing pressure on phytoplankton (trophic cascade effect), promoting establishment of a clear-water state with macrophytes (Hansson et al., 1998; Søndergaard et al., 2007).

The refuge effects of submerged macrophytes are apparently not as strong in tropical and subtropical shallow lakes as in north temperate lakes as small planktivorous and omnivorous fish maintain high diversity and density almost all the year round (Ghadouani et al., 2003; González-Bergonzoni et al., 2012). Zooplankton, therefore, suffer from great fish predation (Iglesias et al., 2011), and studies have furthermore shown that small fish assemble around submerged macrophytes in warm lakes. Thus, areas with submerged macrophytes typically hold more fish than open water in warm lakes and may, therefore, no longer provide a safe shelter for large-sized zooplankton (Conrow et al., 1990; Meschiatti et al., 2000; Meerhoff et al., 2007; Yu et al., 2016a). Accordingly, lake restoration in warm lakes has often involved several simultaneously applied approaches (Yu et al., 2016b; Gao et al., 2017; Liu et al., 2018) as the use of only one method cannot be relied upon to obtain strong grazer control of clear-water condition. However, how the zooplankton community actually responds to lake restoration in the (sub)tropics is not well elucidated, which is unfortunate given that zooplankton grazing is known to be of key importance for maintaining the restored lakes in a clear state in the temperate zone.

Huizhou West Lake is a typical turbid eutrophic shallow lake in southern China (Li et al., 2004; Liu et al., 2018). Ecological restoration based on fish removal and submerged macrophyte transplantation was carried out in the two lake basins in 2004 and 2007, respectively, and clear-water states appeared in both lake basins afterwards (Jensen et al., 2017; Liu et al., 2018). In this study, we analysed crustacean zooplankton communities from 2015 to 2019 in an unrestored basin with a turbid-water state and in the two restored basins in a clear-water state. Thus, the sampling started 8–11 years after the restoration where we can assume that the lake has passed the initial transient phase occurring after the intervention. As fish are abundant in both the clear and the turbid basins (Gao et al., 2014), we hypothesised that small-sized crustacean zooplankton would dominate in all basins and that there would be no major differences between zooplankton communities and biomasses among the lake basins in this tropical shallow lake.

Material and methods

Study areas and sampling sites

Huizhou West Lake (23°04′43″-23°06′24″ N, 114°22′44″-114°24′03″ E) consists of five basins and is located in Huizhou city, Guangdong province of southern China. The monthly mean water temperature ranges from 12 °C to 35 °C. It is a typical eutrophic shallow lake with an area of 1.6 km^2 and a mean depth of 1.5 m. Two lake basins are isolated from the main Huizhou West Lake by dams, and fish removal and transplantation of submerged macrophytes were conducted in basin one in 2004 (MB1) and in basin two in 2007 (MB2) (Jensen et al., 2017; Liu et al., 2018) (Fig. 1). Pinghu basin (AB), dominated by algae, was used as a control and was monitored simultaneously with the restored basins (Fig. 1).

Sampling and sample analysis

One sampling station in each of the restored basins and two stations in the relatively larger unrestored basin were randomly chosen during each sampling event. Samplings were carried out four times per year in January (winter), April (spring), July (summer) and October (autumn) from 2015 to 2019. Water temperature (WT) was measured by a YSI probe (Yellow Spring Instruments 6600, USA), and transparency (Secchi depth, SD) was measured by a Secchi disc (25 cm in diameter) in situ. Water samples collected

Fig. 1 Location of Huizhou West Lake and the sampled lake basins: two restored basins Macrophyte basin 1 (MB1) and Macrophyte basin 2 (MB2) and one unrestored basin Algal basin (AB)
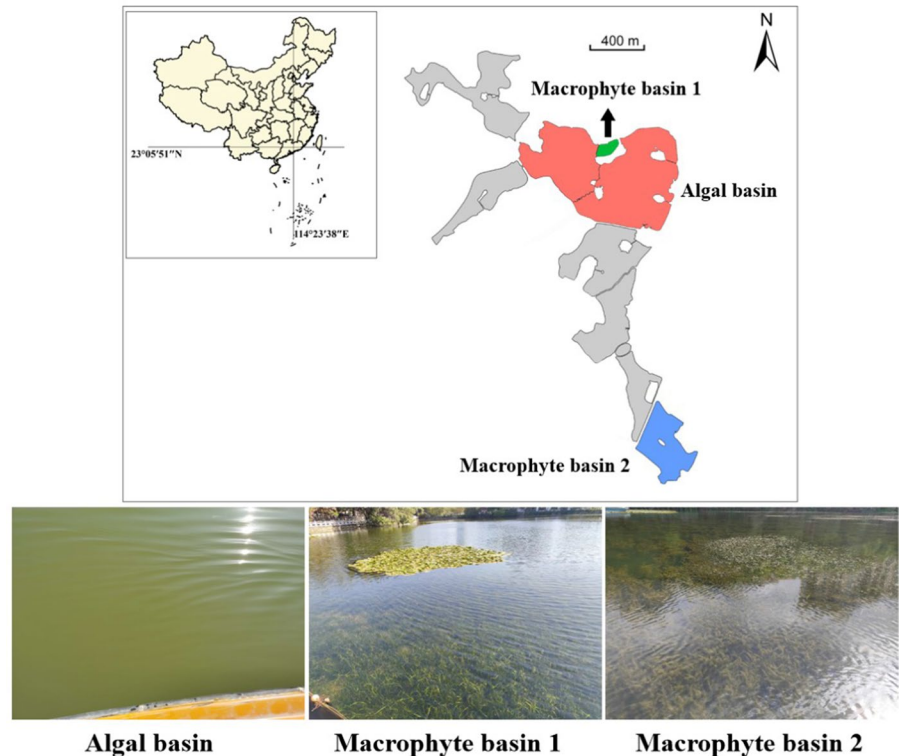
with a 5 L modified Van Dorn water sampler from the surface down to 0.5 m depth at each sampling site were mixed well and taken to the laboratory. The concentrations of total nitrogen (TN), total phosphorus (TP), chlorophyll *a* (Chl *a*) and total suspended solids (TSS) in the water were analysed in our study. TN and TP were determined by spectrophotometric analysis after persulfate digestion according to Chinese Standard Methods for Monitoring Lake Eutrophication (Jin, 1990). Chlorophyll *a* was determined by spectrophotometric analysis after acetone extraction (SEPA, 2002), and TSS was determined by filtering 1 L lake water through pre-weighted Whatman GF/C filters, after which the remains on the filters were calculated after drying at 105 °C for 24 h in the oven.

For crustacean zooplankton analysis, qualitative samples were collected by trawling horizontally and vertically with a conical plankton net (112 μm), while quantitative samples were collected from 50 L (except 10 L in AB and MB2 in summer 2015, 20 L in AB and MB1 in autumn 2015) integrated water at different depths, which was then filtered and concentrated with a 64 μm net. All zooplankton samples were preserved with 4% formaldehyde solution (final concentration) (Wetzel & Likens, 2000). Crustacean zooplankton were identified and counted at 40 × magnification under a microscope according to Shen (1979) and Chiang & Du (1979). When the number of zooplankton individuals in one sample was < 200, all the zooplankton were counted, when the number was > 200, three sub-samples (usually 5 mL or 1 mL each) were counted and then averaged. Zooplankton were separated into cladocerans, cyclopoids, calanoids and nauplii, while cladocerans and adult copepods were identified to species level. Simultaneously, we measured the body length of cladocerans and copepods and calculated their dry weight according to the length–weight regression (Dumont et al., 1975) to assess the biomass of crustacean zooplankton in each basin. When the number of adult crustacean zooplankton in the sample was < 50, all individuals were measured; otherwise, minimum 50 adults were measured.

Data analysis

To assess the strength of top-down control, we calculated five metrics. Zooplankton size, biomass ratios of nauplii to copepods (Nau/Cop) and

calanoid to copepods (Cala/Cop) were used to reflect the fish predation pressure on zooplankton, and crustacean zooplankton:phytoplankton (Zoo/Phyto) and Chl *a*:TP ratios to reflect the grazing effects of crustacean zooplankton. We calculated the biomass ratio of crustacean zooplankton to phytoplankton (in the following called zooplankton to phytoplankton) from their dry weight, the dry weight of phytoplankton being approximated as the concentration of chlorophyll *a* (Chl *a*) multiplied by 66 (Jeppesen et al., 2000).

To estimate changes in biodiversity, we estimated the annual averages of the diversity index over the survey period, the Shannon–Wiener index (H) (Shannon & Wiener, 1949) as well as the Margalef diversity index (D) (Margalef, 1978) of crustacean zooplankton, the latter two using the formulas:

$$H = -\sum(\frac{n_i}{N} * \log_2 \frac{n_i}{N})$$

$$D = \frac{(S-1)}{\ln N}$$

where n_i is the abundance of the *i*th species, *S* is the number of species, and *N* is total abundance (ind./L).

Boxplots were chosen to show ranges and averages of environmental and biotic variables in each basin on an annual basis (averages of the seasonal samples, $n = 4$). For the statistical analyses, the annual averages were regarded as replicates ($n = 5$). We compared environmental and biotic variables among the algal and the macrophyte basins to assess the differences between one unrestored basin and two restored basins by using non parametric Mann–Whitney *U* or Kruskal–Wallis tests. The values of TN, TP, Chl *a*, TSS, SD and Chl *a*:TP ratios were used in a principal components analysis (PCA) to ordinate water quality status for the basins from 2015 to 2019 using the function 'prcomp' with R 4.1.3. The difference in the body size distribution of crustaceans between the algal and the macrophyte basins was compared using the Kolmogorov–Smirnov test. Significance levels for independent variables were set at $P < 0.05$. All comparisons were performed using SPSS version 21.0. We examined the relationship of crustacean zooplankton taxonomic groups abundance and

biomass and environmental variables in the three basins using linear-based redundancy analyses (RDA) using the software Canoco5.0 for windows.

Results

Water quality

During the five years, the annual mean TN concentration in MB1 (range 0.71 – 1.15 mg/L) did not differ significantly (Mann–Whitney *U* test, $P = 0.056$) from AB (range 0.96 – 1.71 mg/L); however, annual mean TN in MB2 (range 0.39 – 0.50 mg/L) was significantly lower than in AB (Mann–Whitney *U* test, $P < 0.01$) (Fig. 2). The annual mean TP concentrations in both MB1 (range 31.9 – 54.9 µg/L) and MB2 (range 21.7 – 27.7 µg/L) were all significantly lower than that in the control, AB (range 78.9 – 161.0 µg/L) (Mann–Whitney *U* test, $P < 0.01$ for both MB1 vs. AB and MB2 vs. AB) (Fig. 2).

There were obvious differences between the two basin types in the variables related to water transparency. The annual averages of TSS in MB1 (range 1.58 – 3.00 mg/L) and MB2 (range 0.96 – 4.86 mg/L) were both significantly lower than in AB (16.9 – 29.4 mg/L) (Mann–Whitney *U* test, $P < 0.01$ for both MB1 vs. AB and MB2 vs. AB). The annual averages of Chl *a* (27.6 – 44.9 µg/L) in AB were much higher than in the two MBs, where the annual averages of Chl *a* varied from 1.84 to 8.89 µg/L in MB1 and from 3.39 to 6.37 µg/L in MB2 (Mann–Whitney *U* test, $P < 0.01$ for both MB1 vs. AB and MB2 vs. AB). For Secchi depth (SD), there was a major difference between the two basin types; thus, the annual averages ranged from 22.4 to 35.0 cm in AB and from 80.0 to 90.5 cm and from 90.0 to 110.0 cm, respectively, in the two MBs (Mann–Whitney *U* test, $P < 0.01$ for both MB1 vs. AB and MB2 vs. AB). The annual average ratios of Chl *a*:TP were significantly higher in AB than in MB1 and MB2 (Kruskal–Wallis test, $P < 0.01$) (Fig. 2).

The principal component analysis revealed that the first two PCs axes accounted for 97.57% of the overall variance. The first PC axe accounted for 91.41% of the total variance, was mainly determined by SD, the second PC axe accounted for 6.16% of the variance, was mostly determined by Chl *a*. In the plot of the first two PC axes (Fig. 3), the AB and MBs
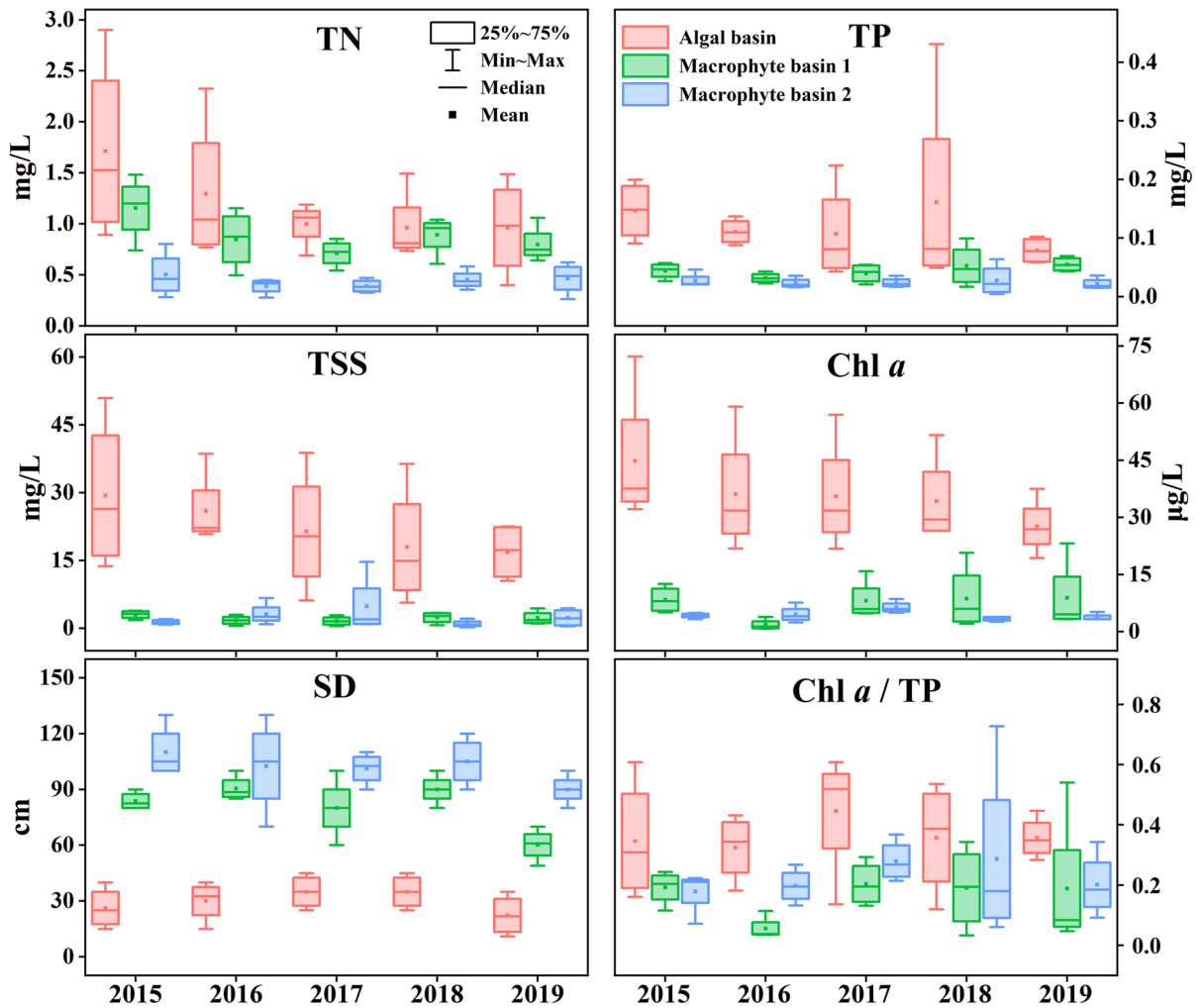
Fig. 2 Boxplot of intra-annual variations of the concentrations of total nitrogen (TN), total phosphorus (TP), chlorophyll *a* (Chl *a*), total suspended solids (TSS), Secchi depth (SD) and Chl *a* to TP ratio (Chl *a*/TP) in the two restored basins (MB1, MB2) and the unrestored basin (AB) from 2015 to 2019

distributed quite differently. The unrestored basin (AB) mainly distributed in the second and third quadrants and MB1 and MB2 primarily in the first and fourth quadrants.

Crustacean zooplankton

Community composition

During our survey period, 20 species of crustacean zooplankton were found in the three basins, all of which were observed in the macrophyte basins, including 6 species of copepods (belonging to 5 genera and 2 families) and 14 species of cladocerans (belonging to 14 genera and 7 families). Fourteen crustacean zooplankton species were detected in the algal basin, including 6 species of copepods as above and 8 species of cladocerans (belonging to 8 genera and 6 families) (Table 1). The common copepods in the macrophyte basins were calanoids *Allodiaptomus specillodactylus* Shen & Tai, 1964 and *Neodiaptomus schmackeri* Poppe & Richard, 1892, while the cyclopoids *Mesocyclops thermocyclopoides* Harada, 1931 and *Thermocyclops taihokuensis* Harada, 1931 were common in the algal basin. The large-sized zooplankton *Daphnia galeata* Sars, 1864 was only
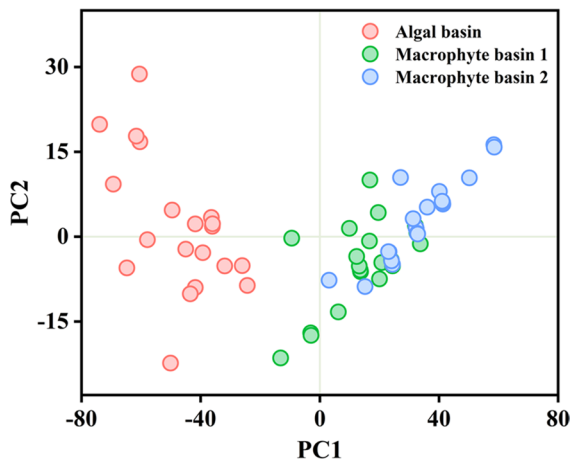
Fig. 3 Scatter plots of the first two principal components (PC1 and PC2) of water parameters in the two restored basins (MB1, MB2) and the unrestored basin (AB) from 2015 to 2019

recorded in winter 2018 and only in MB2. Chydoridae occurred frequently in basin MB1, and benthic-phytophilous species (*Ilyocryptus spinifer* Herrick, 1882*, Macrothrix spinosa* King, 1853) were only found in the macrophyte basins.

Based on our statistics result, the annual averages of the Shannon–Wiener and the Margalef index of crustacean zooplankton showed no significant differences among MB1, MB2 and AB (Kruskal–Wallis test, $P > 0.05$) (Table 1).

Abundance and biomass

The abundance and biomass of total crustaceans in the MBs varied significantly, while AB was more stable (Fig. 4). During the 5 years, the abundance and biomass averages of total crustacean zooplankton were significantly higher in MB2 than in AB (Mann–Whitney U test, $P < 0.05$), while there was no significant difference between MB1 and AB (Mann–Whitney U test, $P > 0.05$). Maximum abundance (266 ind./L) and biomass (2.78 mg/L) were observed in MB2 in 2018 (Fig. 4). The highest density of cladocerans after restoration was recorded in 2016 (59.2 ind./L) when *Bosmina longirostris* O. F. Müller, 1776 was the dominant species in MB1. There was no significant difference in the abundance

and biomass of cladocerans between MB1, MB2 and AB (Kruskal–Wallis test, $P > 0.05$).

Copepods accounted for the largest proportion of the abundance (range 53% – 100%) and biomass (range 28.7% – 100%) of total crustaceans in each basin. The composition of copepods in the MBs showed clear distinctions from AB; thus, calanoids dominated in both MBs, whereas AB was dominated by cyclopoids (Fig. 5). The average biomass ratios of calanoids to copepods (Cala/Cop) in the two restored basins (MB1, MB2) were, therefore, much larger than in the unrestored basin (AB) (Mann–Whitney U test, $P < 0.01$ for both MB1 vs. AB and MB2 vs. AB), while there were no significant differences in the average biomass ratios of nauplii to copepods (Nau/Cop) among the three basins (Kruskal–Wallis test, $P > 0.05$) (Fig. 6).

Body size

The body length of the crustacean zooplankton in AB typically varied between 0.2 to 0.6 mm (mainly cladocerans) and between 0.8 and 1.2 mm (mainly adult cyclopoids), the largest recorded length being 1.4 mm (*Allodiaptomus specillodactylus*). In the MBs, it was typically > 1.0 mm (mainly adult calanoids) (Fig. 7), the largest length measured being 1.85 mm (*Allodiaptomus specillodactylus*). There were significant differences in the distribution pattern of body size among AB and MBs (Kolmogorov–Smirnov test, $P < 0.001$ for both MB1 vs. AB and MB2 vs. AB). The proportion of large-sized zooplankton (with body length > 1.0 mm) was thus highest in MB1 and MB2, 57.3% and 44.6%, respectively, compared to 19.2% in AB (Fig. 7).

The mean size of adult copepods over the 5 years was larger in MB1 than in AB (Mann–Whitney U test, $P < 0.05$), while the difference was not significant between MB2 and AB (Mann–Whitney U test, $P > 0.05$) (Fig. 8). No distinct difference was found in the mean body size of cladocerans between AB and the MBs (Kruskal–Wallis test, $P > 0.05$), implying that small-sized species dominated in all three basins. The body length of the large-sized cladoceran *Daphnia galeata*, which appeared once in MB2 in 2018,

Table 1 The species and biodiversity (mean ± SD) of crustacean zooplankton in the three basins from 2015 to 2019

Species	Algal basin					Macrophyte basin 1					Macrophyte basin 2				
	2015	2016	2017	2018	2019	2015	2016	2017	2018	2019	2015	2016	2017	2018	2019
Copepoda															
Allodiaptomus specillodactylus Shen & Tai, (1964)			+	+		+	+	+	+	+	+	+	+	+	+
Neodiaptomus schmackeri Poppe & Richard, (1892)			+	+		+	+	+	+	+	+	+	+	+	+
Neodiaptomus yangtsekiangensis Mashiko, (1951)	+			+		+		+	+	+	+	+		+	
Mesocyclops thermocyclopoides Harada, (1931)	+	+	+	+	+					+			+		
Thermocyclops taihokuensis Harada, (1931)	+	+	+	+	+	+	+		+		+		+		
Limnoithona sinensis Burckhardt, (1913)				+			+		+			+		+	
Cladocera															
Diaphanosoma dubium Manujlova, (1964)	+		+	+	+	+	+	+	+	+	+	+	+	+	+
Daphnia galeata Sars, (1864)														+	
Simocephalus vetulus O.F.Müller, (1776)	+	+	+	+	+		+			+					
Moina micrura Kurz, (1875)	+	+	+	+	+					+	+	+	+		

Table 1 (continued)

Species	Algal basin					Macrophyte basin 1					Macrophyte basin 2				
	2015	2016	2017	2018	2019	2015	2016	2017	2018	2019	2015	2016	2017	2018	2019
Ceriodaphnia cornuta Sars, (1885)										+					
Alona rectangula G.O.Sars, (1862)	+		+	+		+	+	+	+	+	+	+	+	+	+
Chydorus ovalis Kurz, (1875)	+		+			+	+	+	+	+	+	+	+		
Pleuroxus laevis G.O.Sars, (1862)								+			+				
Bosmina longirostris O.F.Müller, (1776)	+	+		+		+	+	+	+		+		+	+	
Bosminopsis deitersi Richard, (1895)	+	+	+						+						
Scapholeberis mucronate O.F.Müller, (1785)			+				+								
Camptocercus rectirostris Schödler, (1862)						+									
Macrothrix spinosa King, (1853)									+	+					
Ilyocryptus spinifer Herrick, (1882)									+					+	
Shannon–Wiener (H)	1.462±0.359					1.599±0.605					1.644±0.566				
Margalef (D)	0.417±0.123					0.463±0.135					0.474±0.221				

+ appearance of species
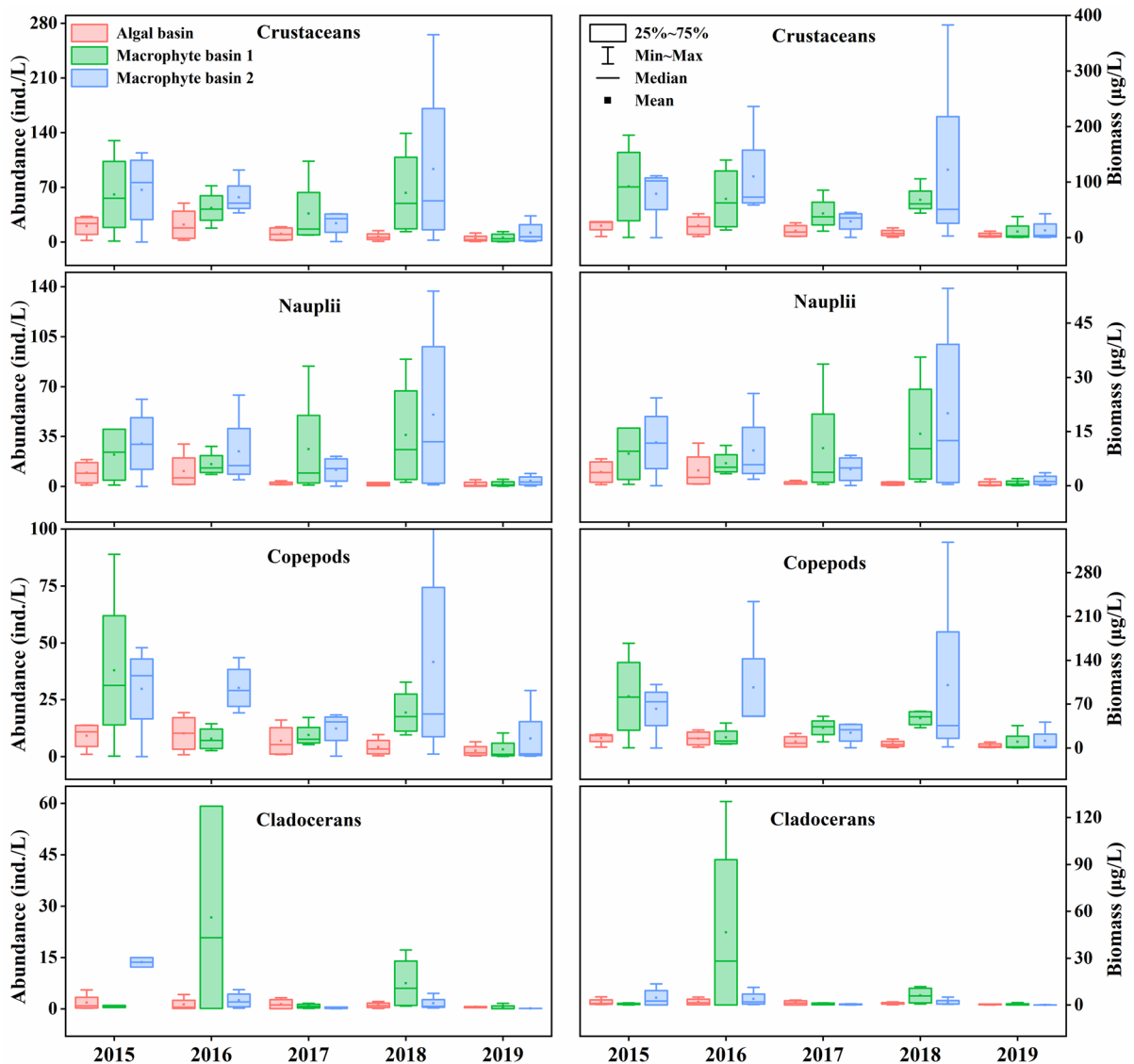
Fig. 4 Boxplot of intra-annual variations of the abundance and biomass of total crustacean zooplankton, nauplii, copepods (adults and copepodites) and cladocerans in the two restored basins (MB1, MB2) and the unrestored basin (AB) from 2015 to 2019

ranged from 0.65 to 1.47 mm, and the mean body length was 1.00 mm.

Zooplankton: phytoplankton ratio

The average zooplankton to phytoplankton ratios (Zoo/Phyto) were much lower in AB (0.003 – 0.009) than in the two MBs (0.03 – 0.77 in MB1 and 0.06 – 0.50 in MB2) (Mann–Whitney U test, $P < 0.01$ for

both MB1 vs. AB and MB2 vs. AB). The 5-year average of Zoo/Phyto was 0.006 in AB while and 0.25 in both MBs, i.e., 40-fold higher in the MBs than in AB (Fig. 9).

Environmental variables influencing the abundance and biomass of zooplankton

The crustacean zooplankton community structure of algal and macrophyte basins were further explored

Fig. 5 Relative abundance and biomass percentages of different zooplankton taxa in the two restored basins (MB1, MB2) and the unrestored basin (AB) from 2015 to 2019
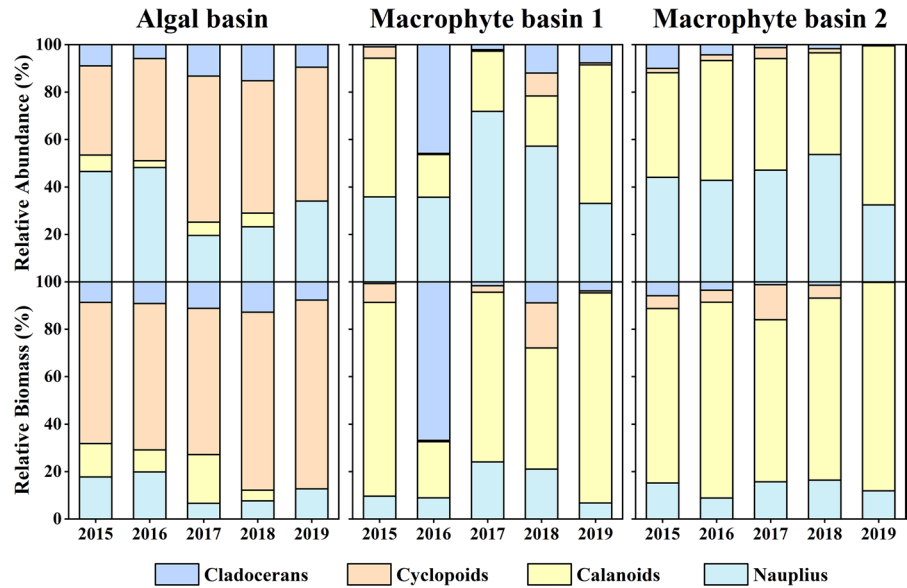
by RDA ordination. The results showed that two variables (SD and WT) collectively explained 48.2% of crustacean zooplankton abundance variation (SD 37.3% and WT 10.9%), and, the first two axes explained 38.9% and 9.2% respectively (Fig. 10). For

Fig. 6 The biomass ratio of nauplii to copepods (Nau/Cop) and of calanoids to copepods (Cala/Cop) in the two restored basins (MB1, MB2) and the unrestored basin (AB) from 2015 to 2019

biomass of crustacean zooplankton, three environmental variables SD, pH and WT explained 52.3% (SD 28.5%, 12.9% and 10.9%), and the first two axes 31.58% and 14.14% of the variation, respectively (Fig. 10). For both abundance and biomass, water transparency was positively correlated with advanced stages of calanoid copepods and nauplius, while negatively correlated with advanced stages of cyclopoids.

Discussion

The restored basins of Huizhou West Lake shifted from a turbid-water state dominated by phytoplankton to a clear-water state dominated by macrophytes after restoration by fish removal and macrophyte transplanting (Liu et al., 2018). The restored basins have remained in the clear-water state while the unrestored control basin remained in the turbid state during our study period. The abundance and biomass of crustacean zooplankton did not differ between restored and unrestored basins, and large-sized crustacean zooplankton (especially cladocerans) occurred in low density in all basins. However, the composition of the zooplankton assemblages differed, with calanoids dominating in the macrophyte basins and cyclopoids in the algal basin. The macrophyte basins also had higher calanoid:copepod and zooplankton:phytoplankton ratios compared with the algal basin.

Fig. 7 The cumulative frequency of crustacean zooplankton with different body sizes in the two restored basins (MB1, MB2) and the unrestored basin (AB) from 2015 to 2019
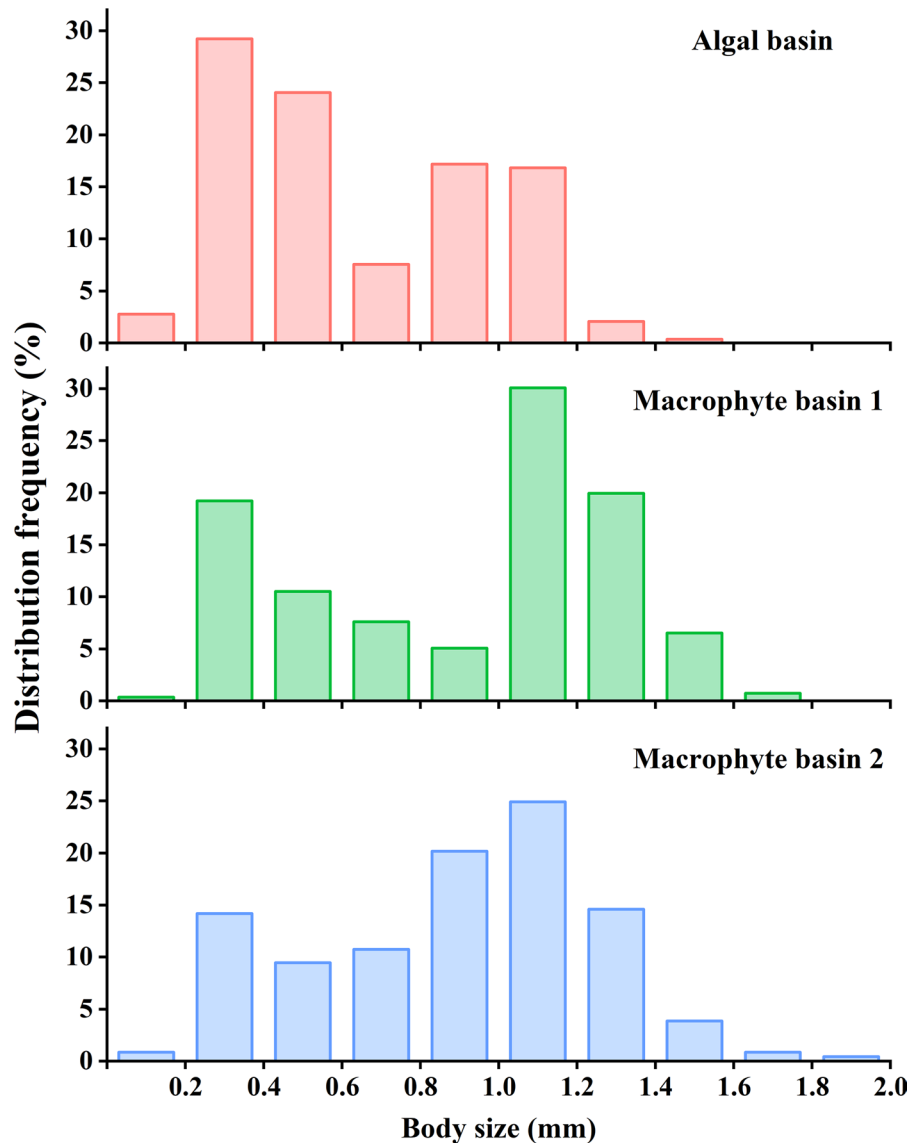
In temperate regions, large-sized zooplankton, especially large-sized cladocerans (e.g., *Daphnia* spp.), are of key importance for maintaining a clear-water state in shallow eutrophic lakes (Jeppesen et al., 1998, 2012). Biomanipulation and macrophyte development often leads to an increase in zooplankton body size and in the proportion of large-sized zooplankton such as the large cladoceran *Daphnia* (Hansson et al, 1998; Jeppesen et al., 2004). Several authors have argued that the low abundance of large-sized cladocerans (e.g., *Daphnia* spp.) in the tropics might be related to high temperatures (Gillooly & Dodson, 2000;

Havens et al., 2000). However, other researchers have observed dominance by large-sized cladocerans when small planktivorous fish were absent or controlled in warm lakes (Iglesias et al., 2008; Mazzeo et al., 2010). Likewise, Zeng et al. (2016) observed a relatively high density of large-sized cladocerans in a shallow tropical lake after biomanipulation, but they soon disappeared with the recovery of fish populations. In our study, the crustacean body size in both the macrophyte and algal basins was small, and large cladoceran *Daphnia galeata* occurred in only one sample in one of the macrophyte basins after biomanipulation, likely due

Fig. 8 Mean body sizes (mean ± SE) of adult copepods and cladocerans in the two restored basins (MB1, MB2) and the unrestored basin (AB) from 2015 to 2019
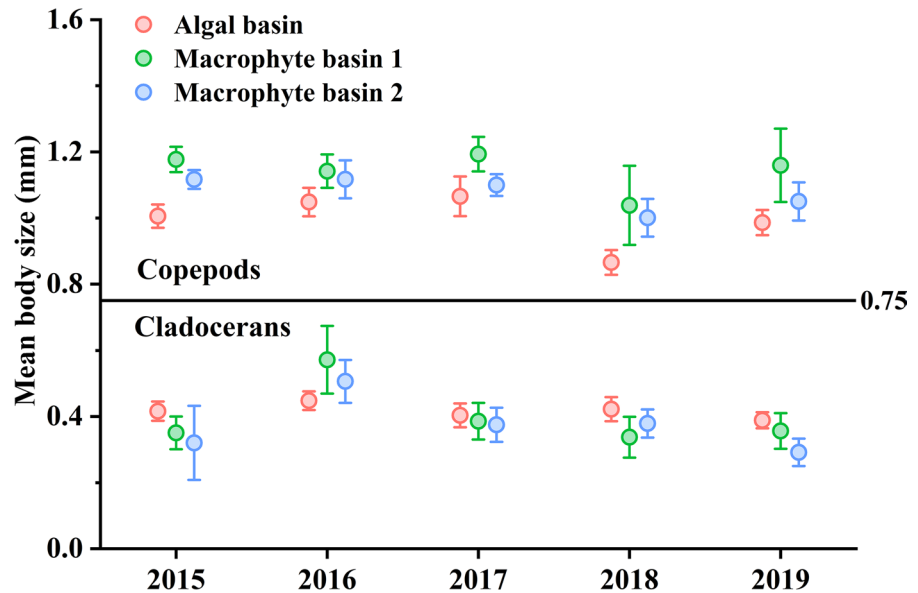
to high fish predation as judged from fish investigations conducted in the basins (Gao et al., 2014).

In general, species richness and zooplankton diversity show a decline with enhanced TP concentrations in freshwater lakes (Jeppesen et al., 2000). However, in the two restored basins with low phosphorus concentrations, the annual mean diversity indexes of zooplankton were not significantly different from the unrestored basin. Crustacean zooplankton usually have a lower diversity in tropical and subtropical lakes than in temperate lakes (Fernando et al, 1987; Pinto-Coelho et al., 2005), and a year-round high

Fig. 9 The biomass ratio of crustacean zooplankton to phytoplankton (Zoo/Phyto) (µg DW/L: µg DW/L) in the two restored basins (MB1, MB2) and the unrestored basin (AB) from 2015 to 2019

predation pressure by fish might be one of the main factors affecting zooplankton diversity in the tropics (Dumont, 1994; Fernando, 1994; Iglesias et al., 2011).

We found a higher proportion of large-sized crustacean zooplankton (with body length > 1.0 mm) in the macrophyte basins which indicate lower fish predation (Hall et al., 1976; Iglesias et al., 2008) than in the algal basin. Gao et al. (2014) demonstrated that planktivorous fish were less abundant in the macrophyte basins than in the algal basin in Huizhou West Lake. Moreover, macrophytes reduce the fish feeding efficiency on zooplankton (Winfield, 1986). In an experiment, Manatunge et al. (2004) demonstrated that the foraging efficiency of the planktivorous fish *Pseudorasbora parva* (Temminck & Schlegel, 1846) (Cyprinidae) decreased significantly with increasing complexity of the habitat consisting of artificial macrophytes and that the observed decline in feeding efficiency was related to the fact that submerged vegetation impeded the swimming and obstructed the sight while the fish were foraging. In our experiment, the lower fish predation on zooplankton in the macrophyte basins relative to algal basin was also evidenced by high ratios of calanoids to copepods in the MBs, while cyclopoids dominated in AB. Several researchers have pointed out that cyclopoids are less affected by fish predation than calanoids, and increased predation pressure of fish on zooplankton will therefore
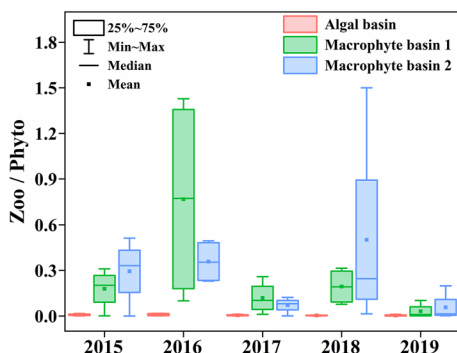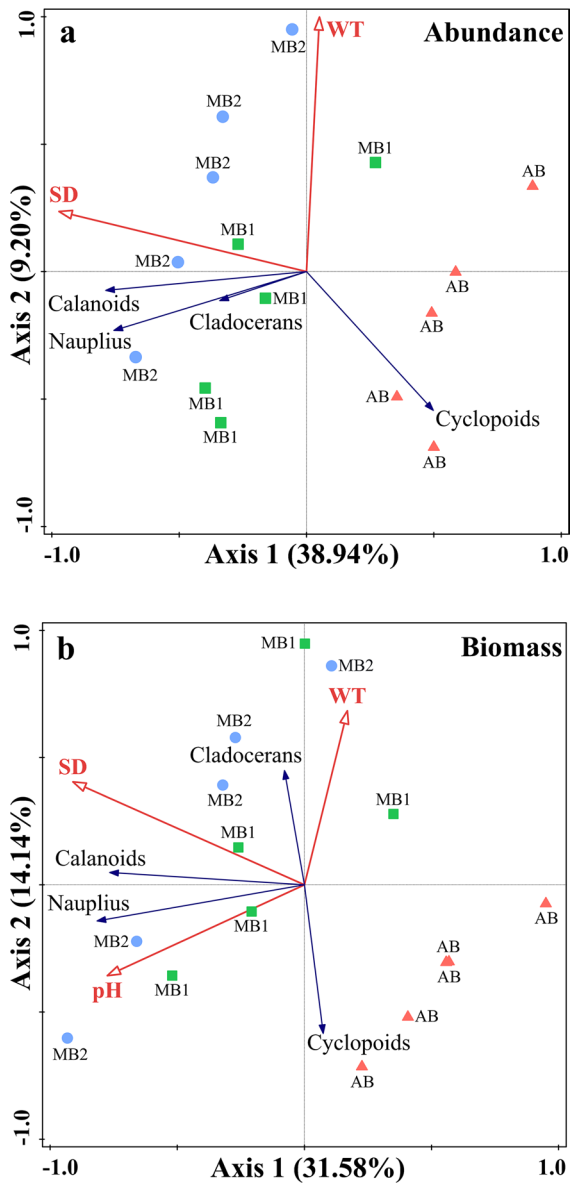
Fig. 10 Redundancy analysis triplot of abundance (**a**) and biomass (**b**) of zooplankton groups using the measured environmental factors, red arrows represent environmental variables and blue arrows represent zooplankton taxon

inevitably lead to a decrease of the calanoid:copepod ratio (Soto & Hurlbert, 1991; DeRobertis et al., 2000; Xie & Yang, 2000). In addition, calanoids are recognized as indicators of oligotrophic conditions at regional and global scale (Patoine et al., 2000; Pinto-Coelho et al., 2005), and the results of RDA showed a significant positive correlation between calanoids and

water transparency (SD), while cyclopoids were negatively related with water transparency in our study.

The filter-feeding effects of zooplankton have a great impact on water clarity (Scheffer et al., 1993). In our study, the average of the zooplankton:phytoplankton biomass ratio over 5 years was 0.25 in MBs and extremely low (0.006) in AB. Despite, that these ratios might be slightly underestimated as rotifers were not included in the zooplankton biomass, the lower Chl a:TP ratios and the higher zooplankton:phytoplankton ratios in the MBs indicate lower grazing pressure on phytoplankton in the algal basin than in macrophyte basins. According to Chen et al. (2010) and Min et al. (2011), the dominant phytoplankton were Cryptophyta and Pyrrophyta in MBs, while Cyanophyta dominated in AB, which may have contributed to the difference of grazing efficiency in AB and MBs as Cyanophyta are less palatable. However, the zooplankton:phytoplankton biomass ratio of all basins in our study were generally lower than the typical values recorded in temperate lakes (Jeppesen et al., 2012). In temperate lakes with the same total phosphorus content, the average value of the zooplankton:phytoplankton ratio was 0.35 (Jeppesen et al., 2003) or even 0.46 (Jeppesen et al., 2000). Similarly, in some eutrophic warm lakes in China (Zeng et al., 2016; Liu et al., 2022), the abundance of large-sized zooplankton such as *Daphnia* species increased after fish removals, but decreased due to fast recovery of fish populations. Therefore, macrophytes are even more important (thus higher coverage is needed) in sustaining a clear regime in tropical systems (Zeng et al., 2017; Gao et al., 2020) via various mechanisms such as reducing sediment resuspension and phosphorus release (Jensen et al., 2017; Zhang et al., 2017; Li et al., 2021) and inhibiting phytoplankton growth by nutrient competition and allopathic effects (Vanderstukken et al., 2011).

Conclusion

In tropical eutrophic shallow Huizhou West Lake, we found that calanoids dominated in the two clear macrophyte-dominated basins restored by biomanipulation, whereas cyclopoid dominated in one unrestored turbid phytoplankton-dominated basin. In addition, stronger grazing effects on phytoplankton in the macrophyte basins were also indicated by differences in

the Chl *a*:TP and zooplankton:phytoplankton ratios between the algal basin and the macrophyte basins. Our results suggest that submerged macrophytes enhance the grazing pressure by zooplankton on phytoplankton via reducing the foraging efficiency of fish due to a higher habitat structure in macrophyte beds. Therefore, macrophytes help to maintain the clearwater state by promoting trophic cascade effects in tropical shallow lake after restoration, although the top-down effects are lower than in restored temperate lakes.

Declarations

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