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Size-dependent responses of zooplankton to submerged macrophyte restoration in a subtropical shallow lake*

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Abstract To explore the size-dependent responses of zooplankton to submerged macrophyte restoration, we collected macrophyte, zooplankton and water quality samples seasonally from a subtropical shallow lake from 2010 to 2012. Special attention was given to changes in rotifers and crustaceans (cladocerans and copepods). The rotifers were grouped into three size classes (<200 μm, 200 μm–400 μm, >400 μm) to explore their size-related responses to macrophyte restoration. The results showed that during the restoration, the annual mean biomass and macrophyte coverage increased significantly from 0 to 637 g/m^2 and 0 to 27%, respectively. In response, the density and biomass of crustaceans and the crustacean-to-rotifer ratio increased significantly, while the rotifer density decreased significantly. Moreover, rotifers showed significant size-dependent responses to macrophyte restoration. Specially, rotifers <400 μm were significantly suppressed, while those ≥400 μm were significantly encouraged. Overall, the population of large-sized zooplankton tended to boom, while that of small rotifers was inhibited during macrophyte restoration. Redundancy analysis (RDA) revealed positive correlations between macrophytes and crustaceans, rotifers and COD or Chl-*a*, but negative correlations between macrophytes and COD or Chl-*a*, and between crustaceans and Chl-*a*. Moreover, the results indicate that increased predation on phytoplankton by large-sized zooplankton might be an important mechanism for macrophyte restoration during development of aquatic ecosystems, and that this mechanism played a very important role in promoting the formation of a clear-water state in subtropical shallow lakes.

Keyword: crustacean; rotifer; large-sized zooplankton; subtropical shallow lakes

1 INTRODUCTION

Shallow lakes, which generally have water columns less than 3 m in depth, are characterized by strong material exchange between the water column and sediment, slow deposition, unstable thermal stratification and increased sensitivity to pollution compared with deep lakes (Jeppesen et al., 1997; Sachse et al., 2014). Most shallow lakes are confined to low-lying areas and are vulnerable to nutrient enrichment from domestic sewage, intensive agricultural activities and industry (Kõiv et al., 2011). During the past 50 years, eutrophication has become a serious threat to shallow lakes around the world, causing deterioration of aquatic ecosystem quality and toxic algal blooms, which has resulted in water shortages for residential supplies and decreased lake recreational values. Eutrophication and the changes associated with it are especially problematic in developing countries, where they constantly endanger human health and the quality of aquatic products.

In recent decades, many efforts have been made to solve the problems associated with eutrophication, particularly in Europe and North America (Jeppesen et al., 2005a, b; Søndergaard et al., 2005). Although substantial reduction in external nutrient loading is

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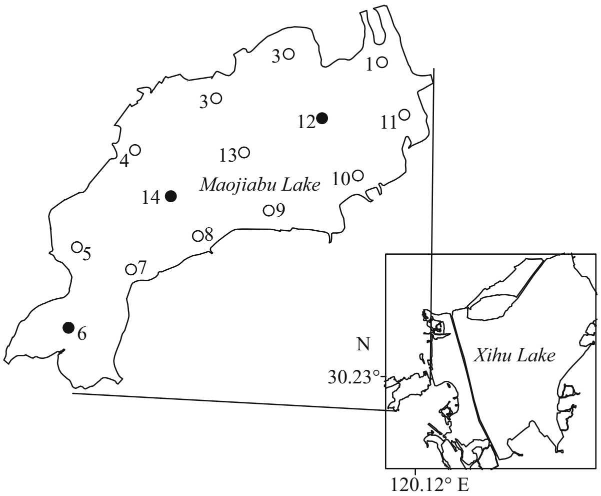

Fig.1 Location and enlarged view of Maojiabu Lake in the Xihu Lake in Hangzhou, China

The 14 sites and three black filled circles were designed to collect samples of submerged macrophyte and water quality from 2010 to 2012, respectively.

widely regarded as a prerequisite for restoring lake ecosystems (Jeppesen et al., 2007a; Xu et al., 2010), this alone is not sufficient because of the delayed effects of internal nutrient release from sediments and biological resistance (Søndergaard et al., 2002; Gulati et al., 2008; Jeppesen et al., 2009). Accordingly, various physico-chemical and biological methods have been used and developed to overcome these problems, such as sediment removal (Zhang et al., 2010a), chemical treatment of sediment (Reitzel et al., 2005), fish manipulation (Beklioglu et al., 2008) and protection and restoration of submerged macrophytes (Lauridsen et al., 2003; Zhang et al., 2010b).

The restoration and protection of macrophytes has received increasing attention from lake managers and ecologists. Moreover, lake managers have adopted the option of increasing macrophyte abundance to restore eutrophic waters in temperate and subtropical/tropical regions. The extensive use of macrophyte restoration to reconstruct aquatic ecosystems mainly results from its positive impacts on the formation and stabilization of a clear-water state in shallow lakes, and various mechanisms have been proposed for these impacts. One suggested mechanism is that the allelopathic substances released by macrophytes significantly suppress phytoplankton, decreasing the risk of algal blooms (Mulderij et al., 2003). Another mechanism is that macrophytes can develop water transparency by reducing wind- and fish-induced sediment resuspension (Gulati and van Donk, 2002). In addition, the direct absorption of nutrients by macrophytes can effectively decrease nutrition loading in the water column, thereby acting as a major nutrient sink. Finally, macrophytes can provide refuge for large-sized zooplankton from fish predation, resulting in increased phytoplankton grazing (Peretyatko et al., 2009).

Among the aforementioned mechanisms, the increased predation pressure of large-sized zooplankton on phytoplankton has been widely studied in many shallow lakes around the world (Brönmark and Weisner, 1992; Romo et al., 2005; Beklioglu et al., 2007), especially in European temperate lakes (Jeppesen et al., 2007b). In these lakes, zooplankton can enhance survival by migrating to habitats in which predation risk is low, such as littoral areas that are covered with submerged macrophytes (Estlander et al., 2009; Sagrario et al., 2009), after which they exert strong grazing pressure on phytoplankton (Agasild et al., 2007). However, while studies of the effects of macrophyte restoration on zooplankton in temperate, shallow lakes has provided relatively comprehensive information, the size-dependent responses of zooplankton to macrophyte restoration are less known in subtropical (Meerhoff et al., 2007) and tropical lakes (Jeppesen et al., 2007b, 2012).

Therefore, we conducted a three year investigation to explore the size-dependent responses of rotifers and crustaceans to macrophyte restoration in a subtropical shallow lake. Moreover, macrophytes and water quality were also investigated to explore the potential relevant factors responsible for the size-dependent responses of zooplankton.

2 MATERIAL AND METHOD

2.1 Study site

The Xihu Lake (30°15′N, 120°09′E) is a typical shallow lake located in Hangzhou City, Zhejiang Province, eastern China that attracts a great number of tourists from all over the world. The lake was officially added to the World Heritage List in 2011. The lake occupies an area of 6.5 km^2 and has a mean depth of 2.27 m, giving a water volume of 1.49×107 m^3.

This study investigated Maojiabu Lake (30°13′N, 120°07′E), which has an area of 0.27 km^2 and a mean depth of 1.3 m and is located in the western portion of the Xihu Lake (Fig.1). Before macrophyte restoration, this lake was in a turbid state with a high chlorophyll a (Chl-*a*) concentration (mean: 25±6 μg/L) and low transparency (Secchi depth: 0.6±0.12 m). Additionally, the lake was characterized by high total nitrogen (TN) (2.6±0.29 mg/L) and chemical oxygen demand

(COD) (2.2±0.34 mg/L) and low total phosphorus (TP) (0.03±0.01 mg/L) levels. At this time, almost no submerged macrophytes were present in the lake (Zeng, unpublished data).

2.2 Submerged macrophyte restoration

To restore the aquatic ecosystem in Maojiabu Lake, an attempt was first made to reconstruct the submerged macrophyte community in autumn 2010 to spring 2011. In November 2010, macrophyte restoration started and turions of *Potamogeton crispus* were planted in most parts of the lake (*ca*. 80% of the overall area). In February 2011, seeds of *Vallisneria spiralis* were planted in zones less than 0.5 m deep. One month later, adult *V. spiralis*, *Ceratophyllum demersum* and *Myriophyllum verticillatum* were planted, mostly in zones that were greater than 0.5 m in depth. The *V. spiralis* seedlings in the shallow zones grew poorly from March to October in 2011, but adult macrophytes exhibited exuberant growth in the zones deeper than 0.5 m.

In November 2011, a second attempt at macrophyte restoration was made, mainly in zones less than 0.5 m. This time, adult *V. spiralis* instead of their seeds were planted in the shallow zones, and successful macrophyte restoration was achieved in 2012.

2.3 Sampling and treatment

During the restoration, continuous tracking surveys of the macrophyte community were conducted in spring (April), summer (July) and autumn (October) from 2010 to 2012. Fourteen sampling sites were selected across the lake to measure the biomass and percentage coverage of macrophytes (Fig.1). At each sampling site, we used a grass sickle to collect triplicate macrophyte samples, with each sample being collected from an area of about 0.18 m^2. In addition, species and coverage were recorded simultaneously during field sampling. The fresh weight was obtained after washing the plants with tap water and weighing them in a PuChun electronic scale (6 kg/0.2 g) in the laboratory.

Water quality was also monitored seasonally at the same frequency as the macrophytes, but only three sampling sites (6, 12 and 14) were selected to collect the water samples (Fig.1). COD, TN, nitrate nitrogen (NN), ammonium nitrogen (AN), TP and Chl-*a* were analyzed according to the standard methods (Editorial Board of Monitoring and Determination Methods for Water and Wastewater, State Environmental Protection Administration of China, 2002).

Triplicate zooplankton samples were also collected seasonally in the same frequency from the same sampling sites used to evaluate water quality (Fig.1). Crustaceans (cladoceran and copepod) were collected by filtering 10 L of water through a 64-μm plankton net into a 30-mL plastic bottle, after which they were preserved by adding 3 mL 5% formalin. Rotifer samples were obtained by injecting 1 L of water into a 1.5-L plastic bottle, then fixed with 9 mL Lugol's solution. In the laboratory, crustacean samples were identified directly in a dissecting stereoscope at 40× magnification. Rotifer samples were first concentrated to 30 mL sub-samples, after which 1 mL sub-samples were absorbed with a graduated pipette into a count-frame and counted using an inverted microscope at 160× magnification. Zooplankton species were identified to the genus/species level with reference to Wang (1961), Tai and Chen (1979) and Chiang and Du (1979).

2.4 Statistical analysis

The Shapiro-Wilks test and Levene's test were used to assess the normality and equality of variance, respectively. To analyze the size-dependent responses of zooplankton to macrophyte restoration, zooplankton was divided into two subgroups (crustacean and rotifer), and rotifers were divided into three groups based on their sizes (G1: <200 μm; G2: 200 μm–400 μm; G3: >400 μm) (Wang et al., 1961). Moreover, one-way ANOVA and Duncan's test were conducted to identify significant differences in the density and biomass of rotifers, crustaceans and zooplankton, as well as the crustacean-to-rotifer ratio with changes in macrophyte cover. Significant changes in rotifers with different sizes were also evaluated to analyze the effects of reconstructed macrophytes on rotifers. All analyses were completed using the statistical program SPSS 21.0 for windows.

Multivariate analysis using redundancy analysis (RDA) was conducted with the CANOCO 4.5 software to study the correlations between environmental factors and zooplankton during macrophytes restoration. The Monte Carlo permutation test was conducted to test the significance of eigenvalues of the first and all ordination axes. Eight environmental variables were included in this analysis: macrophyte biomass and coverage, COD, TN, TP, AN, NN and Chl-*a*. The six zooplankton parameters included in this analysis were the densities of total zooplankton, total rotifer, crustaceans and rotifers at size categories G1, G2 and G3.

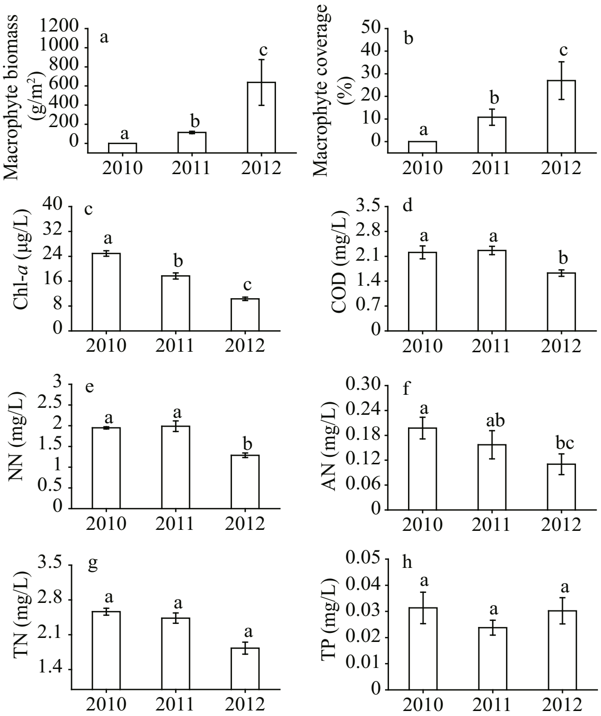

Fig.2 Interannual mean variations (±SE) in submerged macrophyte (MB (a) and MC (b)) (*n*=126) and water quality parameters (Chl-*a* (c), COD (d), NN (e), AN (f), TN (g), and TP (h)) (*n*=27) from 2010 to 2012

The abbreviations of the environmental variables are defined in Table 2. Bars with identical lowercase letters indicate no significant differences ($P>0.05$), while bars with different letters indicate significant differences ($P<0.05$).

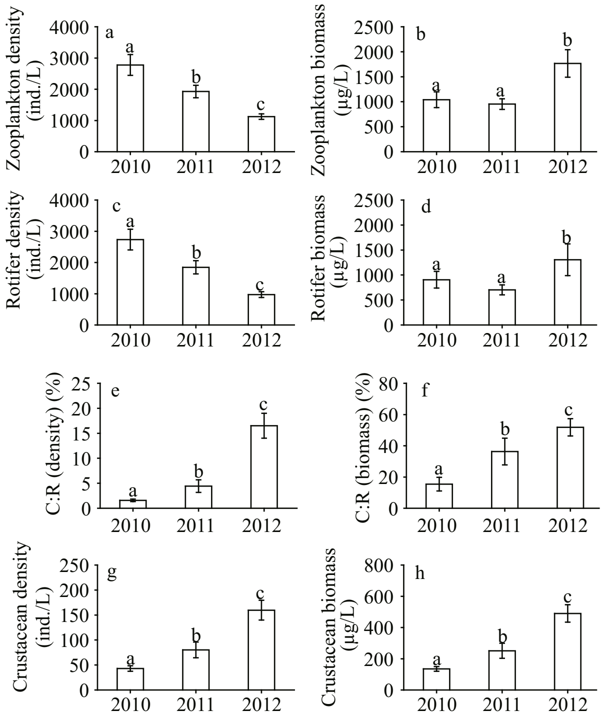

Fig.3 Interannual mean variations (±SE) in zooplankton density (a) and biomass (b), rotifer density (c) and biomass (d), the density (e) and biomass (f) ratio of crustaceans to rotifers (C:R), and crustacean density (g) and biomass (h) from 2010 to 2012 (*n*=27)

Bars with identical lowercase letters indicate no significant differences ($P>0.05$), while bars with different letters indicate significant differences ($P<0.05$).

3 RESULT

3.1 Interannual variations in macrophyte and water quality

The three surveys conducted in 2010 prior to the restoration showed that almost no submerged macrophytes were present in the lake. After the first restoration trial in winter of 2010 and February of 2011, the annual mean biomass and coverage of macrophytes in 2011 had increased significantly from 0 to 113±12 g/m^2 and 0 to 11%±4% compared to those in 2010, respectively ($P<0.05$, Fig.2a–b). The dominant species (*V. spiralis*, *P. crispus*, *C. demersum* and *M. verticillatum*) were mainly distributed in the deep zone. However, the germination rate of *V. spiralis* seeds in shallow areas was very low, and the seedlings showed poor growth.

Surveys conducted in 2012 showed that the annual mean biomass and coverage of macrophytes increased significantly compared to those in 2011 ($P<0.05$), and were 637±239 g/m^2 and 27%±8%, respectively. The dominant species were *V. spiralis*, *Najas marina* and *M. verticillatum*. The *N. marina* was likely brought into the lake with other macrophytes during two restoration attempts.

All water quality parameters except for TP presented significant differences during the restoration ($P<0.05$, Fig.2c–g). Specifically, the concentrations of TN, NN and COD did not differ significantly between 2010 and 2011, but decreased in 2012 ($P<0.05$). The Chl-*a* concentration also gradually decreased significantly every year ($P<0.05$), while significant differences in AN only occurred between 2010 and 2012. The TP concentration was in a stable state throughout the restoration (Fig.2h).

3.2 Interannual variations in zooplankton related to body size

During the restoration, similar changes in the density and biomass of zooplankton and rotifers were observed (Fig.3a–d). Specifically, their density decreased significantly every year ($P<0.05$), but their biomass increased significantly in 2012 ($P<0.05$) after undergoing a stable period from 2010 to 2011. Moreover, the change trends in the crustacean-to-

Table 1 Representative rotifers of particular body sizes in Maojiabu Lake

<200 μm	200 μm–400 μm	>400 μm
Polyarthra trigla (Ehrenberg, 1834)	*Synchaeta stylata* (Wierzejski, 1893)	*Synchaeta pectinata* (Ehrenberg, 1832)
Keratella cochlearis (Gosse, 1851)	*Synchaeta bologna* (Ehrenberg, 1832)	*Eosphora najas* (Ehrenberg, 1830)
Anuraeopsis fissa (Goose, 1851)	*Diurella tenuior* (Grose, 1886)	*Enteroplea lacustris* (Ehrenberg, 1830)
Lepadella quinquecostata (Lucks, 1912)	*Trichocerca gracilis* (Tessin, 1886)	*Epiphanes brachionus* (Ehrenberg, 1837)
Testudinella patina (Hermann, 1783)	*Gastropus hyptopus* (Ehrenberg, 1838)	*Asplanchna brightwelli* (Gosse, 1830)
Trichocerca pusilla (Lauterborn, 1898)		*Asplanchna priodonta* (Gosse, 1850)

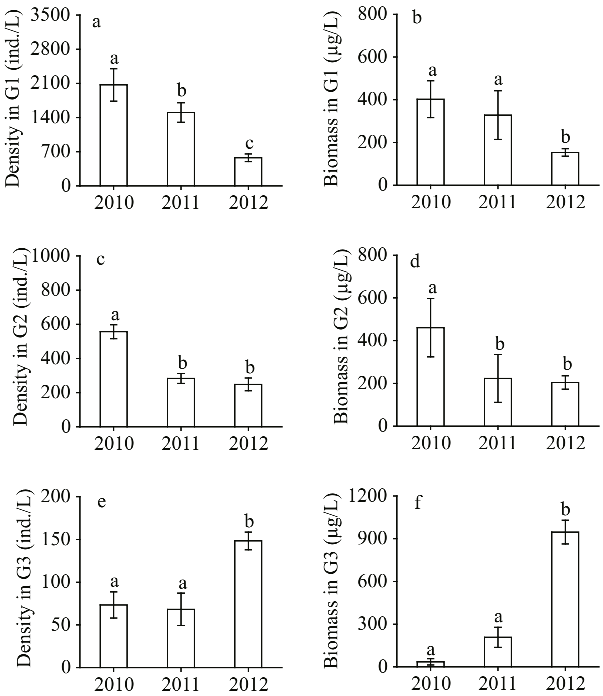

Fig.4 Interannual mean variations (±SE) in rotifer density and biomass in G1 (a–b), G2 (c–d) and G3 (e–f) from 2010 to 2012 (*n*=27)

RD: rotifer density; RB: rotifer biomass. Bars with identical lowercase letters indicate no significant differences ($P>0.05$), while bars with different letters indicate significant differences ($P<0.05$).

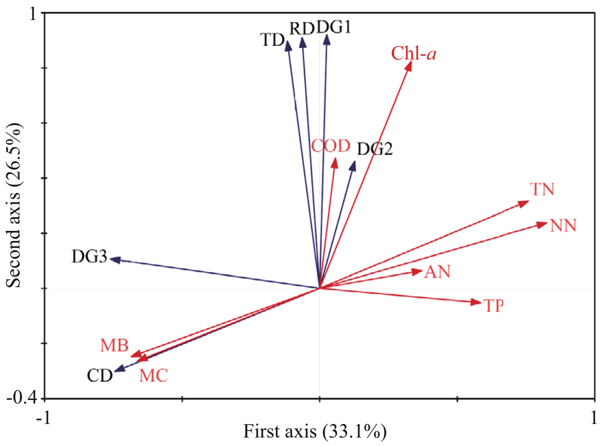

Fig.5 The RDA ordination plots with zooplankton and environment variables and samples

The red arrows represent environment variables (water quality and macrophytes), and the blue arrows represent zooplankton variables. Abbreviations of environmental variables are presented in Table 1. TD, CD and RD represent densities of total zooplankton, crustaceans and rotifers, respectively. DG1, DG2 and DG3 represent rotifer density in G1, G2 and G3, respectively.

rotifer ratios and in crustaceans were similar (Fig.3e–h), with both gradually increasing significantly every year ($P<0.05$).

Rotifers of different sizes also exhibited different responses to macrophyte restoration (Fig.4). Specially, the rotifer density in G1 (representative species: *Polyarthra trigla*, *Keratella cochlearis*, *Anuraeopsis fissa*) (Table 1) decreased significantly every year ($P<0.05$, Fig.4a), as did the biomass in 2012 compared to 2010 and 2011 ($P<0.05$, Fig.4b). The density of rotifers in G2 (representative species: *Synchaeta stylata*, *S. bologna*.) showed a similar change trend as biomass, with significant decreases occurring in 2011 and 2012 compared to 2010 ($P<0.05$, Fig.4c–d). However, the density of rotifers in G3 (representative species: *S. pectinata*, *Eosphora najas*, *Enteroplea lacustris*, *Asplanchna priodonta*) increased significantly in 2012 compared to 2010 and 2011, and the biomass increased significantly every year ($P<0.05$, Fig.4e–f).

3.3 Redundancy analysis of zooplankton and environmental variables

In the ordination diagram, strong correlations existed between zooplankton and environmental factors (water quality and macrophyte), with zooplankton-environment correlations of 0.81 on the first axis and 0.927 on the second axis. The cumulative percentage variance of the zooplankton-environment relationship on the first axis was 53.2%, whereas that on the second axis was 42.5%. The cumulative percentage variance of the zooplankton data explained by the first four axes of the RDA was 62.2%, with 33.1% on first axis and 26.5% on the second axis (Fig.5). The Monte Carlo permutation test was

Table 2 Correlation analysis matrix of influence factors in the RDA

Influence factor	MB	MC	COD	TP	AN	NN	Chl-*a*
MB	1						
MC	0.93**	1					
COD	-0.69**	-0.59**	1				
TP	-0.32	-0.42*	0.06	1			
TN	-0.74**	-0.72**	0.43*	0.44*			
AN	-0.35	-0.29	0.16	0.27	1		
NN	-0.62**	-0.53*	0.28	0.34	0.38	1	
Chl-*a*	-0.68**	-0.74**	0.64**	0.26	0.2	0.38	1

Abbreviations of macrophyte and water quality parameters: MB: macrophyte biomass; MC: macrophyte coverage; COD: chemical oxygen demand; TP: total phosphorus; TN: total nitrogen; AN: ammonia nitrogen; NN: nitrate nitrogen. The abbreviated environment variables were used in subsequent RDA analysis. * Significant difference at the 0.05 level; ** significant difference at the 0.01 level. Environment abbreviations were used in subsequent Pearson's correlation and RDA analysis.

significant on the first axis (*F*-ratio=8.903, *P*-value=0.01) and on all axes (*F*-ratio=3.707, *P*-value=0.002). According to the permutation test of all environmental factors, six variables (macrophyte biomass and coverage, TN, NN Chl-*a* and TP) were the best explanatory variables for zooplankton variations, explaining 0.503 of total zooplankton variations (0.622).

According to the centroid principle and distance rule implied in RDA, the crustacean density was positively correlated with macrophyte biomass and coverage, but negatively correlated with Chl-*a*, COD, TN and NN. Significant positive correlations also existed between total zooplankton, total rotifer, rotifer in G1 and G2, COD and Chl-*a*. In addition, rotifer in G3 was only negatively correlated with TN and NN (Fig.5).

The correlations between macrophytes and water quality obtained through RDA (Table 2) showed that macrophyte biomass and coverage were negatively correlated with COD, TN, NN and Chl-*a*. However, COD showed significantly positive correlations with TN and Chl-*a*, and significantly positive correlations also existed between TP and TN, TN and NN or Chl-*a*.

4 DISCUSSION

4.1 Responses of crustaceans

The results of this study revealed that a successful macrophyte restoration in 2012 led to significant increases in the density and biomass of crustaceans compared to 2010 and 2011. When combined with the positive correlations between macrophytes and crustaceans, these findings suggest that macrophytes enhanced the survival of crustaceans by providing refuge effects against fish predation. This conclusion is consistent with the findings of studies conducted in temperate lakes (Špoljar et al., 2011, 2016). For example, Cazzanelli et al. (2008) and Špoljar et al. (2012) stated that dense macrophytes in the littoral zone with a low predation risk might enhance crustacean survival. Burks et al. (2002) also suggested that crustaceans could take full advantage of the barrier function of macrophytes in the littoral zone to escape predator predations when a high risk of predation existed in the open water during the daytime.

However, some studies in tropical and subtropical lakes have suggested that the areas of refuge provided for large-sized zooplankton by submerged macrophytes were very limited (Jeppesen et al., 2005b; Castro et al., 2007; Meerhoff et al., 2007). This conclusion is primarily based on the fact that the number and diversity of fish in macrophytes in subtropical/tropical lakes is greater than in temperate lakes, thus producing greater predation pressures on large zooplankton (Teixeira-de Mello et al., 2009). Indeed, fish communities in warm tropical/subtropical lakes are characterized by short lifespan, early maturity, vigorous growth and frequent reproduction (Blanck and Lamouroux, 2007; van Leeuwen et al., 2007), and can exhibit stronger predation pressures on large-sized zooplankton than temperate lakes. However, the fact that the predation efficiency of fish can also be significantly influenced by the complex structure of macrophytes should not be ignored. Theoretically, fish predation of large zooplankton will be weakened if macrophyte coverage or biomass is sufficient. Whether large-sized zooplankton select macrophytes or not largely depends on the trade-off analysis of refuge and predation among macrophytes.

In this study, when macrophyte mean coverage and biomass in 2011 reached 11% and 113 g/m^2, respectively, the crustaceans increased significantly compared with those in 2010, suggesting that the protection of crustaceans by macrophytes already existed in 2011. Moreover, the protection of crustaceans from fish predation was enhanced by the increasing vegetation coverage and biomass in 2012. These results were consistent with those of enclosure experiments conducted by Schriver et al. (1995), who found that some crustaceans could be effectively protected against fish predation when macrophyte coverage exceed 15%–20%, but that the protection would disappear when macrophyte coverage was lower than 10%.

4.2 Responses of rotifers

Unlike the protection provided by macrophytes to crustaceans, the effects of macrophyte restoration on rotifers mainly depended on their sizes. Specifically, the abundance of large sized rotifers increased, while moderate and small-sized rotifers were suppressed during the restoration. Moreover, these size-dependent differences led to decreased total rotifer density, but increased biomass.

However, the positive correlations between small and moderate sized rotifers and COD or Chl-*a* might indicate that their growth inhibition resulted from a shortage of food resources. Based on the negative correlations between macrophytes and COD or Chl-*a*, restored macrophytes might indirectly suppress the growth of rotifers in G1 and G2 by decreasing their food concentrations.

In shallow lakes, COD is most likely to be affected by suspension of sediments in response to waves caused by wind and boats (Miranda, 2008). The Xihu Lake is affected by typhoons from the East China Sea every year, and patrol and cruise boats frequently cross the lake, all of which results in large waves, and therefore increased COD levels. However, reconstructed macrophytes have been shown to effectively reduce wave energies, protecting the sediment from erosion and resuspension and promoting sedimentation (Kufel and Kufel, 2002; Pluntke and Kozerski, 2003; James et al., 2004; Li et al., 2008). These changes ultimately lead to decreased concentrations of organic matter. Furthermore, the negative correlation between macrophytes and Chl-*a* might indicate that phytoplankton biomass was also suppressed by restored macrophytes. Accordingly, two mechanisms might contribute to this inhibition. Specifically, macrophytes may directly suppress phytoplankton and periphyton by producing allelopathic substances (Chang et al., 2012; Espinosa-Rodríguez et al., 2016) and competing for limited nutrients. Conversely, they may indirectly decrease phytoplankton levels by strengthening the predation of large-sized zooplankton on phytoplankton (Lacerot et al., 2013). Therefore, reconstructed macrophytes could significantly decrease the food resources (COD and Chl-*a*) for rotifers in G1 and G2, and thus indirectly suppress their growth.

4.3 Zooplankton community variations

In this study, the overall density of total zooplankton decreased significantly every year. Within this group, rotifer density decreased significantly, but that of crustaceans increased significantly every year, as did the crustacean-to-rotifer-density ratio. However, the crustacean-to-rotifer-biomass ratio and the biomass of total zooplankton, rotifers and crustaceans in 2012 were significantly higher than those in 2010 and 2011.

In shallow, subtropical lakes, fish predation is an important factor controlling large-sized zooplankton, such as crustaceans and large rotifers (Fernandes et al., 2009; Teixeira-de Mello et al., 2009). As discussed above, dense macrophytes could effectively decrease fish predation of large zooplankton, thereby promoting their growth. Moreover, once predation by fish predators was no longer the main factor limiting large-sized zooplankton growth, the inherent competitive advantages (e.g., large body size) of large-sized zooplankton compared to small rotifers (e.g., stronger starvation tolerance, higher potential fecundity and broader food spectrum) contributed to their significant increases (Cyr and Curtis, 1999).

During the restoration, the main food resources (phytoplankton and organic detritus) for zooplankton were significantly decreased by macrophytes. Thus, limited resources made large-sized zooplankton more competitive while suppressing the growth of small rotifers because of a lack of available food. Based on the above analysis, it was not difficult to infer that submerged macrophyte restoration could encourage large-sized zooplankton and suppress small rotifers, leading to a significant increase in crustacean-to-rotifer ratio in the zooplankton community.

5 CONCLUSION

This study showed that submerged macrophyte restoration increased the ratio of large-sized zooplankton in the zooplankton community in a subtropical shallow lake. Specifically, crustaceans and large-sized rotifers exhibited vigorous growth, while small-sized rotifers were significantly suppressed. However, the main mechanisms responsible for these effects might be different. Macrophytes primarily accelerated the growth of large-sized zooplankton by providing effective refuge effects against predator predation. Conversely, the growth inhibition of small-sized rotifers in response to restored macrophytes was likely a result of bottom-up control of nutrients. Overall, these findings indicated that an important mechanism by which macrophyte restoration leads to remarkable improvements in aquatic ecosystems is via increased predation of phytoplankton by large-sized zooplankton in subtropical shallow lakes.

6 ACKNOWLEDGEMENT

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