Seasonal and inter-annual community structure characteristics of zooplankton driven by water environment factors in a sub-lake of Lake Poyang, China

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Background. Sub-lakes are important for the maintenance of the ecosystem integrity of Lake Poyang, and zooplankton play an important role in its substance and energy flow.

Methods. A seasonal investigation of zooplankton was conducted in spring (April), summer (July), autumn (October) and winter (January of the following year) from 2012 to 2016in a sub-lake of Lake Poyang. The aim of the present study was to understand the seasonal dynamics and interannual variation of zooplankton communities and their relationship to environmental factors.

Results. A total of 115 species were identified in all samples in the four years, which comprised of 87 Rotifera, 13 Cladocera and 15 Copepoda. Rotifera was the dominant group in terms of quantity, and its species richness and abundance were significantly higher when compared to Cladocera and Copepoda ($P<0.05$), while Cladocera dominated in terms of biomass. The species richness of Rotifera exhibited a significant seasonal difference ($P<0.05$). Both the density and biomass of zooplankton revealed significant seasonal differences ($P<0.05$). In general, the density and biomass of zooplankton were higher in summer and autumn, when compared to winter and spring. Biodiversity indices were dramatically lower in spring than in the other seasons. The non-metric multidimensional scaling (NMDS) analysis suggested that these zooplankton communities can be divided into three groups: spring community, summer–autumn community, and winter community. The seasonal succession of zooplankton communities did not have interannual reproducibility. In high water level years, the dominant species of zooplankton (Cladocerans and Copepods) in the wet season had a lower density, and the result in low water level years was exactly the opposite. The redundancy analysis revealed that water temperature (WT), conductivity, pH and dissolved oxygen (DO) had significant effects on the zooplankton community.

Conclusions. The community structure of zooplankton has a significant seasonal pattern, but has no interannual repeatability. In high water level years, the dominant species of zooplankton (Cladocerans and Copepods) in the wet season had a lower density, and the result in low water level years was exactly the opposite. The density, biomass and diversity indices of zooplankton were significantly different in different seasons. The present study was helpful in the further understanding of the ecosystem stability of lakes connected with rivers, providing scientific guidance for the protection of lake wetlands.

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Abstract

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Introduction

Lake Poyang, the largest freshwater lake in China, is a connected lake, in which water levels fluctuate widely in different seasons (Wu, 1994). In its low water period, more than 100 separated sub-lakes appear in Lake Poyang (Hu et al., 2015). When these sub-lakes connect with the main lake in the high water period, a close exchange of material, energy and biology occur among these water bodies. Sub-lakes are of significant ecological value due to the huge vegetation biomass (Huang & Guo, 2007; Li & Liu, 2001), high biodiversity (Wu, 1994; Ge et al., 2010), fish nurseries and reproduction sites in the high water period (Zhang & Wang, 1982), and ideal habitats provided for wintering birds (Qi et al., 2011; Hu and Ge et al., 2014). All these values play an important and unique role in maintaining the biological integrity and species diversity of the Lake Poyang wetland ecosystem.

As important biological parts and a link between the primary producer and higher consumers, zooplanktons are essential for maintaining the health and stability of aquatic ecosystems. These also indicate the trophic state of lakes, and can be accurately reflected by the spontaneous variation in zooplankton (Pereira et al., 2002; Krylov, 2015). Zooplankton communities have significant seasonal fluctuations under the influence of biotic and abiotic factors. Environmental factors, such as total nitrogen (TN), total phosphorus (TP), water temperature (WT), water clarity and the biomass of microalgae all play an important role in the succession of zooplankton communities (Yang et al., 2014; Hu and Yang et al., 2014). The periodical connection between lakes and rivers also affect the ecological structure and function of zooplankton communities. Different degrees of water level have different degrees of effect on zooplankton (Goździejewska et al., 2016). Planktivorous fish exerts high top-down control on zooplankton, especially on macro-zooplankton, which may lead to a decrease in the number of Daphnia (Scheffer et al., 1997) and miniaturization of the zooplankton community.

The increases in N and P levels in recent decades (Lv, 1996; Wang et al., 2008) have led to the eutrophication of Lake Poyang. In 2011, TN was 1.389 mg/L and TP was 0.067 mg/L on average (Chen et al, 2013), while the *Jiangxi Water Resources Bulletin* (2012–2015) indicated that the water of Lake Poyang exhibited moderate eutrophication (http://www.jxsl.gov.cn/). Although Lake Poyang has reached the level of eutrophication, fortunately, there was no outbreak of cyanobacteria bloom due to the connection of the lake with the Yangtze River and the seasonal fluctuations in water level (Hu & Zhu, 2014). However, cyanobacterial blooms have already taken place in its sub-lakes, due to unmanaged development and resource utilization (Dai et al., 2015). The ecological and environmental problems faced by sub-lakes are epitomes of the environmental deterioration of Lake Poyang, and the ecological decline in sub-lakes may eventually seriously affect its wetland ecosystem and the function of the whole lake.

The first study of zooplankton in Lake Poyang focused on the species in the 1960s (Deng et al., 1963). Subsequently, some discontinuous researches on zooplankton have been conducted, but these studies were relatively limited. For example, Xie et al. (1997, 1998 and 2000) carried out an annual dynamic research on zooplankton in Lake Poyang. Wang et al. (2003) catalogued 150 zooplankton species in spring and winter. Liu et al. (2016) characterized the characteristics of all crustaceans. According to records (Huang & Guo, 2007), there is a total of 207 zooplankton species in China, but reports on zooplankton in the sub-lakes of Lake Poyang remain very limited in the past decades. Zooplanktons in sub-lakes were reported only until the recent years (Zhang et al., 2014). Furthermore, there are very few reports on seasonal and annual variations in zooplankton communities in sub-lakes. Zooplankton are the main feeding target of many fishes, and its distribution and variation can be used as a scientific basis for exploring fish stocks and finding fishing grounds (Huang et al., 2010). At the same time, zooplanktons are also important indicators of aquatic environment change (Peter et al., 2010). The population structure, quantity, and dominant species can be an important indicator of water quality monitoring (Wang, et al., 2012). Therefore, the study on the spatial and temporal distribution pattern of zooplankton can provide a vital scientific basis for the protection and sustainable utilization of lake resources.

The present study carried out a preliminary research of the seasonal variations of zooplankton communities in Shahu Lake, a sub-lake of Lake Poyang. The samples were collected seasonally from April 2012 to January 2016. The specific aims were as follows: (1) investigate the seasonal and interannual variations of zooplankton communities in a sub-lake, and (2) identify the dominant physicochemical factors that affect the variation in zooplankton community structures.

Materials & Methods

Sampling site

Lake Poyang (28° 24'–29° 46'N, 115° 49'–116° 46') is located downstream of the Yangtze River (Fig. 1-A). It has an area of 3, 210 km^2 in the highest water level period and 146 km^2 in the lowest water level period (Zhang, 1988). Its catchment has a subtropical monsoon climate with an average annual rainfall of 1, 400–1, 900 mm, and an average annual temperature of 16.7–17.7 °C (Wu, 1994). Jiangxi Poyang Lake National Nature Reserve lies to the northwest of Lake Poyang (Fig. 1-B), and there are nine sub-lakes in the reserve. Shahu Lake, which has a surface area of 1.4 km^2, is one of these, and has a flat bottom and few submerged plants (Fig. 1-C). There is significant seasonal water level fluctuation in Shahu Lake. The maximum water fluctuation amplitude is approximately 6 m between flood and dry season. During the dry season, local fishermen fish in the lake using a method known as “lake enclosed in autumn”. This involves the fishermen discharging water through a water-gate, and fishing with a long mesh bag fixed at its gate from October to January of the next year. Through this process the water level gradually decreases to 0.2–0.3 m.

Sampling design

Zooplankton were seasonally sampled (spring = April, summer = July, autumn = October and winter = January) at three points in Shahu Lake from April 2012 to January2016. With the water level declining, the water only remained in deepest area, and the water depth was only approximately 0.2–0.3 m. Hence, these three sampling points in winter were set in the lake, in which the water depth was more than 1.4 m in autumn 2012 (Fig. 1-D). Zooplanktons were sampled three times at each point, and nine samples were collected in each season, resulting in a total of 144 samples over the four years. A 5-L modified Schindler–Patalas sampler was used to collect 10 L of mixed water at approximately 50 cm below the water surface for each sample. A plankton net (mesh size, 64 μm) was used to filter the water and collect the zooplankton, which gathered from the end of the net, and these were immediately preserved in 50 mL plastic bottles with 4% formalin. In the laboratory, the zooplanktons were counted and identified under a microscope (Olympus SZ61, Japan and Olympus CX23, Korea). When there were excessive individuals in one sample, a sub-sample method was used to estimate the actual quantity. In the present study, copepod nauplii were considered as one taxon. Four bibliographies, including three faunas, were used for zooplankton identification (Wang, 1961; Crustacean Research Group, 1979; Jiang & Du, 1979; Han & Shu, 1995).

The physicochemical parameters were simultaneously measured at the time of collection. WT, pH, conductivity (Cond), dissolved oxygen (DO) and turbidity (Turb) were measured using a multi-function water quality monitor (YSI6600V2, USA).

Data analysis

In the present study, the zooplankton community characteristics mainly include dominant species, diversity index, density, biomass and community clustering map.

The dominance index was calculated as follows:

$$Y = \mathrm{n}_i \times \mathrm{f}_i / N \quad \text{(Eqn. 1)}$$

In which Y represented the dominance index, n_i represented the individual number of i species, f_i represented the occurrence frequency of i species and N represented total numbers of individuals. When Y was greater than or equal to 0.02, this species was defined as dominant species. In the present study, N referred to the total density of zooplankton in each season (Wen et al., 2015).

The Shannon–Weiner diversity index (H'), Margalef richness index (D) and Pielou evenness index (J') calculation formulae were as follows:

$$H' = -\sum P_i \ln (P_i)$$

$$D = (S-1)/ \ln N$$

$$J' = H' / \ln S \quad \text{(Eqn. 2)}$$

Where S represented the species number and P_i represented the proportion of i species densities in the total zooplankton density in the sample (Wen et al., 2015).

The densities of zooplankton were calculated by dividing the individual numbers of zooplankton that gathered in each collection by the sample volume, and this was expressed by ind./L. The biomass of zooplankton (wet weight) was evaluated according to the method reported by Zhang and Huang (1991). The weight of each nauplii was estimated to be approximately 0.003 mg (Xie & Li, 1998).

The seasonal variance of water physicochemical factors, zooplankton density and biomass were analysed by one-way ANOVA, using STATISTICA 7.0 (StatSoft Inc., Tulsa OK, USA). The seasonal variation in zooplankton communities was tested by non-metric multidimensional scaling analysis (NMDS) and analysis of similarities (ANOSIM). Zooplankton individual number data were analysed using a ranked similarity matrix based on Bray–Curtis similarity measures. Rare species, which had an average density of less than 1.0 ind./L, were excluded during NMDS and ANOSIM analyses. NMDS ordination and ANOSIM analyses were performed with the PRIMER 5 computer package (Clarke & Warwick, 1994). The indicator value method (IndVal) was used to detect how strongly each species discriminated among the NMDS groups. The indicator value of a taxon varied from 0 to 100, and the indicator value attained its maximum value when all individuals of a taxon occurred at all sites within a single group (Szulc et al., 2010). The significance of the indicator value for each species was tested with a Monte Carlo randomization procedure with 1, 000 permutations. IndVal was performed using the *indval* function in R package *labdsv* (R version 3.4.1, R Development Core Team2017).

The correlation between water physicochemical factors and zooplankton dominant species was analysed through redundancy analysis (RDA), and the significance was determined using the Monte Carlo test. The RDA and Monte Carlo tests were performed using Canoco for Windows

4.5 software (Ter Braak & Smilauer 2002). Except for the NMDS analysis, all variables were transformed by ln(x + 1) prior to analysis.

Results

Physical-chemical variables

The seasonal mean values of physicochemical factors in Shahu Lake from April 2012 to January 2016 are presented in Table 1. The one-way ANOVA revealed that all physicochemical factors had significant seasonal differences (P<0.05). WT rose from spring, reaching a maximum (~29.4 °C) in summer, falling in autumn and dropping to the minimum (~9.2 °C) in winter. Conductivity had an average range (±SE) from 90.2±15.4 to 532.6±446.2 μS/cm with a minimum value of 60.7 μS/cm in April 2013 and a maximum value of 1049 μS/cm in October 2013. DO and water turbidity were highest (11.0±1.2 mg/L, and 142.1±75.2 NTU, respectively) in winter and lowest (5.9±2.1 mg/L, and 35.1±27.4 NTU, respectively) in summer. In contrast, pH was lowest (6.7±0.6 mg/L) in winter and highest (7.6±0.7 mg/L) in summer.

Species composition

Species richness

A total of 115 species of zooplankton were found (Appendix Table 1). There were 87 species of Rotifera, 13 species of Cladocera and 15 species of Copepoda. The species of these three main groups comprised of 76.1%, 11.1% and 12.8% of the total species number, respectively. Zooplankton species richness had no significant interannual variation. There were 56 species captured in 2012, 65 species in 2013, 61 species in 2014 and 72 species in 2015 (Fig. 2). Merely 24 species occurred simultaneously over the four years: 18 rotifera species, two cladocera species and four copepoda species. Zooplankton species richness exhibited significant seasonal differences (P=0.041). In every season, rotifers, which comprised 36.4–81.3% of the total species number, were the dominant component. A total of 58 species was found in spring with the minimum (11 species) in 2014 and the maximum (34 species) in 2015. There were 88 species collected in summer, with the minimum (33 species) in 2014 and the maximum (48 species) in 2013 and 2015. In autumn, 72 species were captured, and the minimum (23 species) were found in 2012 and the maximum (42 species) were found in 2014. In winter, 65 species were identified, and the minimum (23 species) were found in 2012 and the maximum (35 species) were identified in 2015.

Dominant species

From 2012 to 2015, there were 13 dominant species, 10 dominant species, 16 dominant species and eight dominant species in each year (Table 2). *Bosmina longirostris*, copepod nauplii and *Microcyclops varicans* dominated in four years. In spring, *Keratella cochlearis* and *Conochilus unicornis* were dominant species. Especially in spring 2014, the outbreak of *C. unicornis* leading to the highest density (1908.8 ind./L) of rotifers. In summer and autumn, the dominant genera of rotifers were *Brachionus*, *Keratella*, *Polyarthra*, *Asplanchna* and *Trichocerca*. In winter, the dominant species were replaced by *Polyarthra dolichoptera*, *Synchaeta oblonga*, *K. cochlearis*, *C. unicornis* and *A. priodonta*.

Zooplankton density and biomass

Seasonal variation

Total density of zooplankton showed similar trend with species richness (Fig.3-A). In general, the maximum density occurred in summer or autumn and the minimum density appeared in spring or winter. Zooplankton density was highest in autumn (140.0 ind./L), followed by summer (83.0 ind./L) and spring (56.9 ind./L). The minimum density was found in winter (1.3 ind./L). Rotifers density showed no significant seasonal difference (P= 0.123). However, the densities of cladocerans and copepods in winter were significantly lower, when compared to the other seasons (P<0.001). The maximum density of cladocerans was observed in October 2014 (219.2 ind./L), while the maximum density of copepods was observed in July 2014 (137.6 ind./L).

The biomass of zooplankton was significantly lower in winter (Fig. 3-B), when compared to the other seasons (P<0.05). The highest biomass of rotifers was in autumn, and the lowest was in winter. The biomass of both cladocerans and copepods was highest in spring and lowest in winter. Although the density of cladocerans was lower than rotifers and copepods, this contributed 50% of the total biomass of zooplankton and was 1.7 times and 1.9 times the biomass of rotifers and copepods.

Interannual variation

The interannual variation in zooplankton density was significant (P = 0.012). The density of 2014 was significantly higher than in the three other years (Fig.4-A). The outbreak of *C. unicornis* resulting in highest density of rotifer in spring 2014 than in the other years (P=0.018). The density of cladocera in 2014 was significantly higher than in 2012 and 2015 (P=0.039). The biomass of zooplankton in 2015 was significantly lower than in the other three years (P=0.036,

Fig. 4-B). The density and biomass of zooplankton in spring 2015 was very low (18.2 ind./L, 0.16 mg/L, respectively), and the density and biomass of 2015 were lower than in previous years.

Species diversity index

There was some fluctuation in the zooplankton diversity index over the sixteen seasons (Fig.5). The Shannon–Weiner index (H') was in the range of 0.2–3.1 (Fig.5-A), with average was 2.37. The Margalef index (D) was in the range of 1.1–7.6 (Fig.5-B), with an average of 4.2. Pielou's evenness index (J') was in the range of 0.09–0.85 (Fig.5-C), with an average of 0.69. The results of the one-way ANOVA revealed that the Shannon–Wiener index and Pielou's index had significant seasonal variation (P<0.001, and P=0.002, respectively). The seasonal variation in the Margalef index was not significant.

Community structure

The NMDS results revealed that, apart from July 2012, zooplankton in July and October in all four years were at high density, and had similar dominant species. In addition, these combined as a summer–autumn community (Fig. 6). Zooplankton in January was categorized as a low-density winter community. The zooplankton community of July 2012 and April in all four years were separated into independent branches, because the species composition and density of zooplankton in these seasons were quite different from those in the other seasons. During the month, the species composition and diversity of zooplankton were quite different and formed separate communities. However, the inter-annual zooplankton communities could not be distinguished from each other. This result indicated that the seasonal variation of the zooplankton community structure in Shahu Lake was greater than the interannual variety. In order to identify the key indicator species of the three main NMDS groups (i.e., spring, summer-autumn and winter), the indicator value method (IndVal) was used, and it was revealed that the three groups were characterized by different indicator species (Appendix Table 2).

Redundancy analysis of zooplankton and environmental factors

Before the redundancy analysis (RDA), a preliminary detrended correspondence analysis (DCA) on species-sample data produced a longest gradient length of 3.184, suggesting that both RDA and canonical correspondence analysis (CCA) were appropriate. The RDA was selected to illustrate the relationships between the dominant species of zooplankton and environment factors (Fig.7). The first axis explained the 15.6 % of the variance in species data, and the 50 % of the variance in species–environment relationship (Table 3). The second axis explained the 7.4 % of the variance in species data, and the 23.7% of the variance in species–environment relationship. The Monte Carlo permutation test revealed that WT (P=0.002), conductivity (P=0.002), pH (P=0.018) and DO concentrations (P=0.026) had significant effects on zooplankton communities. WT had a higher correlation with Axis 1 (R=0.695), and Spearman rank correlation analysis indicated that WT had significant positive correlation with zooplankton (R=0.722, P<0.05).

Discussion

Temporal pattern of zooplankton communities in the sub-lake

Rotifera are an important component of zooplankton community in a freshwater lake. The small size, fast growth rate and parthenogenetic reproduction (Gilbert, 1999; Inaotombi et al., 2016) means that the abundance is generally dominant (Romo, 1990). In the present study, rotifers were also the dominant group in Shahu Lake. The quarterly survey in 2012–2015 identified 87 Rotifers, 13 Cladocerans and 15 Copepods, with an average of 63 species each year. Nevertheless, the species richness was lower, when compared with the historical research records in Lake Poyang (Xie et al., 1997, 1998; Wang et al., 2003; Huang & Guo, 2007). The density of three species (*B. longirostris*, Copepod nauplii and *M. varicans*) of zooplankton were separately analyzed, which were dominant species in four years, and it was found that the density changes have similar patterns (Fig. 8). Both in the flood season (summer) and retreat period (autumn), the density of these three zooplanktons were significantly less in high water level years than in low water level years. The comparative analysis revealed that these changes were closely correlated to the inter-annual hydrological situation (Gal et al., 2014), and that these might have correlations with the number variation of fishes entering the lake under different water levels. Usually, these three dominant species (both crustaceans zooplankton) are food resources for planktonic feeding fishes (Mamani et al., 2019). Hence, the predation pressures of fishes might be the direct cause of changes in zooplankton density. As a sub-lake of the Lake Poyang, the habitat diversity in Shahu Lake is lower than that of Lake Poyang. Furthermore, the samples in the present study were only taken in the open water area. In addition, the lake has faced intensive human activities, such as beach grazing, fishing, eutrophication caused by pollution, etc. These objective factors may have led to species richness decrease. The NMDS analysis suggested that seasonal variation was more significant than interannual in the zooplankton community structure, and that this could be divided into three community groups associated with distinct indicator species (Fig. 6, Appendix Table 2). According to the previous studies of zooplankton in Lake Poyang (Xie et al., 1997, 1998; Liu et al., 2016), the seasonal dynamics of zooplankton community structure can be roughly observed. Rotifers peaked in summer and autumn. Cladocerans and copepods achieved their peaks in spring, summer and autumn. However, all three groups were at minimum levels in winter. The present study also had the same seasonal dynamic patterns. Though the sub-lake was separated from the Lake Poyang in the dry season, the seasonal dynamics of the zooplankton community in Shahu Lake was similar to those of Lake Poyang. Similar patterns of seasonal changes in zooplankton community have been reported in other lakes (Hu & Yang, 2014; Lin et al., 2014).

The density and biomass of zooplankton exhibited a significant difference among seasons (P=0.035, P=0.002). Over the four years, rotifers were the main component of zooplankton, which represented 72.3% of the total zooplankton abundance, and had 6.5 times and 4.4 times the density of cladocerans and copepods, respectively. Zooplankton density was highest in autumn and lowest in winter. With one exception, the maximum density (1971.0 ind./L) occurred in spring 2014due to the outbreak of *C. unicornis*. The biomass of zooplankton was significantly lower in winter than in other seasons (P<0.05). The highest biomass of rotifers was in autumn and lowest in winter. An earlier study reported that cladocerans and copepods are the main component of zooplankton productivity due to the larger body size (Castro & Gonçalves, 2007). In the present study, it was also found that the biomass of both cladocerans and copepods was highest in spring. Although the density of cladocerans was lower than rotifers and copepods, this contributed to 50% of the total biomass of zooplankton.

In the present study, it was found that the seasonal succession characteristics of the zooplankton community in Shahu Lake were consistent with the reported previous model (Sommer, 1986). In winter, the cold temperature and lack of food resulted in a decline in zooplankton reproductive capacity. Thus a minimum zooplankton density was observed in this period. In spring, the phytoplankton biomass increased with rising temperatures and provided more food resource to phytoplanktivorous zooplankton (Cladocera and Calanoida). Simultaneously, the hatching of dormant eggs and copepods diapause ontogeny developed into supplementary populations. The result was an increase in zooplankton abundance in spring (Hairston et al., 2000). The numbers of *Daphnia* gradually decreased after midsummer, and this was replaced by smaller species and copepods (Threlkeld, 1979; Steiner, 2004; Deng et al., 2008). After autumn, with fishing causing less vulnerability to fish predation, the abundance of rotifers rapidly increases, becoming the dominant groups in Shahu Lake.

Some studies have found that the spring-summer zooplankton community is not a complete repetitive succession in small sub-lakes due to the difference in interannual water temperature and rainfall (Rettig et al., 2006). There was a large variation in the spring zooplankton community of the Shahu Lake among the four years, while the other seasons the community structures tended to be similar. In early spring, Shahu Lake and Lake Poyang were still not connected. Zooplankton communities in Shahu Lake were mainly affected by rainfall, human disturbance and other unspecified factors. Therefore, zooplankton community succession in this period may not have a uniform direction. In summer, Shahu Lake was connected with the main lake. The material and biological exchanges between the sub-lake and main lake resulted in a similarity in water environment and biological community structure. Therefore, the zooplankton community succession was back to the early stages (Baranyi et al., 2002).

Effects of environmental factors on zooplankton community

Water physicochemical factors can affect species composition and the abundance of a zooplankton community. The significant differences in physicochemical factors in different seasons lead to seasonal zooplankton dynamics (Deyzel 2004). Some studies have pointed out that the seasonal dynamics of zooplankton can be influenced by temperature (Hu et al., 2014; Hussain et al., 2016). Water temperature has an important effect on dormant eggs hatching, growth and reproduction of zooplankton (Korpelainen, 1986; Hu et al., 2008). For example, the net reproduction rate of *Brachionus diversicornis* is highest when the temperature is 30 °C (Ning et al., 2013), which might be the main reason why *B. diversicornis* is the dominant species in summer in the Shahu Lake. Temperature also affects phytoplankton as well as zooplankton. High temperature was favourable for the growth of phytoplankton, and the biomass of phytoplankton in Lake Poyang was highest in summer (Wu et al., 2013). Low temperature limits the predation of zooplankton on phytoplankton (Zheng et al., 2015). Hence, zooplankton has a high density in summer and a low density in winter in the Shahu Lake.

Different zooplankton species have different adaptations to temperature (Tao et al., 2008). The number of resting eggs increases in both higher and lower temperatures (Shi & Shi, 1996). In the present study, it was found that the dominant species in summer were thermophilic species, such as *Brachionus* spp. and *Trichocerca* spp., and wide suitable temperature species, such as

Keratella spp. The dominant species in winter were those suitable for low temperature species, such as *Polyarthra dolichoptera* and *Synchacta* spp. and so on. Therefore, the seasonal variation of temperature is one of the reasons for the substitution of zooplankton dominant species. The WT variation was significant in Shahu Lake, which was highest in summer and lowest in winter (Table 1). The RDA suggested that there was a positive correlation between temperature and most of the dominant species. The Spearman rank correlation analysis also revealed that temperature has a positive correlation with the species richness (R=0.376, P=0.009), density (R=0.401, P=0.005) and biomass (R=0.480, P=0.001) of zooplankton.

The results of the redundancy analysis revealed that conductivity, pH and dissolved oxygen also had a significant effect on the seasonal variation of the zooplankton community. Berzins and Pejler (1987) reported that some species of rotifers, which could instruct the water oligotrophic conditions, generally appeared in water at pH 7.0 or at a slightly lower pH value. Some other species of Rotifera indicated that eutrophic conditions prefer water with a pH value higher than 7.0. The pH value of Shahu Lake was higher than 7.0, and its water was at a certain degree of eutrophication. Among its dominant species, such as *Brachionus* spp., *A. brightwelli*, *S. oblonga*, *Filinia longiseta*, *Daphnia pulex*, *Bosmina longirostris* and *Bosmina coregoni*, most were commonly found to be indicator species of eutrophication. Phytoplankton blooms can lead to higher water pH values. There is a correlation between the water pH value in summer and phytoplankton. In the present study, the Spearman rank correlation analysis revealed that significant positive correlations existed between pH and zooplankton species richness (R=0.644, P<0.001) and the Shannon–Weiner diversity index (R=0.487, P<0.001). In the present study, it was found that there was a significant positive correlation between conductivity and copepods (R=0.463, P<0.001), but there was a weakly positive correlation between conductivity and cladocerans (R=0.078, P<=0.597). This was consistent with a previous study (Soto & Rios, 2006).

Water level fluctuation was also one of the important factors that affected the zooplankton community structure. It was found that the density and community structure of zooplankton changes as water level fluctuates (Goździejewska et al., 2016). As the fluctuation intensified, the former dominant species, *Daphnia*, was replaced by rotifers (Zhou et al., 2016). The zooplankton composition of the Shahu Lake in summer was dominated by small individual rotifers, copepod nauplii and *Bosmina longirostris*. The main reason was that the Lake Poyang was in the rising water level period from April to July, and the water level changes resulting in a disturbance to zooplankton. When the water level rose, the Shahu Lake was connected with the main lake (Fig 8-C). As a consequence, nutrients and other biological communities (such as fishes, Fig 8-D) poured into the sub-lake along with the flood, and interactions occurred among zooplanktons and other aquatic organisms from rivers. This probably was one of the reasons for the great shift in zooplankton community in Shahu Lake from spring to summer. Interval water level differences can also lead to annual zooplankton differences. In the summer of 2012, the water level was significantly higher than in previous years (Fig. 8-C). The continuing high water level could be the reason why the zooplankton community structure in summer 2012 was significantly different from other years.

Evaporation, seepage flow and the opening water-gates for fishing from the middle of October resulted in the water level gradually decreasing in Shahu Lake. The water depth was only 20-30cm at the end of fishing. Then most of the lake basin was exposed. The lake bottom sediment and its attachments fully contacted with the atmosphere and the sun. The digestion of organic matter in the sediment was accelerated and the soil structure improved (Hu, 2012). However, the water-gate was not opened during the winter of 2013. Hence, the water depth remained more than one meter in at that period (Fig. 8-C).The stability of the water level maintained a relatively stable environment, coupled with nutrient enrichment and temperature recovery in spring, which led to the outbreak of *Conochilus unicornis* population.

Effects of aquatic organisms on zooplankton community

In addition to environmental factors, biological factors are also important in causing zooplankton community seasonal dynamics (Castro & Gonçalves, 2007). Fish have choices in the process of predation (Dodson, 1970) and most fish prefer bigger zooplankton (Wang, 2010). Filter-feeding fishes such as silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*Aristichthys nobilis*), have an important place in Shahu Lake (Zeng et al., 2015). After the lake has been fished in winter by being enclosed, zooplankton face lower predation pressure from fish at the start of spring. When the water level rose, the floods not only changed the zooplankton community structure, but also brought many migrating fishes from the rivers and other lakes. These two factors have led to miniaturization of zooplankton species. The larger zooplankton, *Daphnia hyalina*, *D. pulex* and *Sinocalanus dorrii*, were dominant in spring. However, the abundance of these species declined sharply in summer, and some species even disappeared from the lake. This presented a close correlation with fish predation (Scheffer et al., 1997; Steiner, 2004; Deng et al., 2008). Therefore, the outbreak of small *C. unicornis* in spring 2014 may have had a certain relationship with the absence of *Daphnia* at that time, which was caused by the end of fishing in winter 2013.

In addition to predation relations between fish and zooplankton, some other aquatic organisms have contributed to zooplankton seasonal dynamics by affecting the water environment. In winter, the grasslands, mudflats and shallow waters provide an excellent habitat for wintering migratory birds and a large number of migratory birds live in the Lake Poyang. The feces of winter migratory birds led to an increase in nitrogen and phosphorus concentrations, which increased the eutrophication level of the sub-lakes. The study of the water quality of Shahu through the zooplankton diversity index revealed that spring water quality was worse than other seasons (Zhu et al., 2014; Nie et al., 2018). The dynamics of the zooplankton community is a complex ecological process, and some factors have not been involved in this experiment. The composition and biomass of phytoplankton, interspecific and intraspecific competition, and nutrient concentration all had effect on the succession of zooplankton community.

Conclusions

The community structure of zooplankton has a significant seasonal pattern, and has no interannual repeatability. The differences in zooplankton density, biomass and diversity indices were significant in different seasons and years. This study was helpful in further understanding the ecosystem stability of lakes connected with rivers, and providing scientific guidance for the protection of lake wetlands.

Overall, ecological civilization construction is very important for the national decision-making of the present Chinese government. Hence, promoting green development and strengthen ecological system protection is imperative. As the largest lake in China, the ecological states of Lake Poyang is of great importance for the whole Yangtze catchment, and is a vital part of the ecological civilization construction of China, such as biodiversity conservation, and water resource planning and management. The results of the present study can thereby provide vital scientific basis for lake ecosystems protection and the sustainable utilization of biodiversity resources.

Acknowledgements

We are grateful to Liu GH, Yan JY, Zeng ZG, Zhang XC, Zeng T, AN CT, Guo GY, Huang WG, Lv Q, Hou JJ, Zhang XL for their assistance in the field and laboratory. We are grateful to Waigen Huang for the touch of the manuscript in English. This project was funded by National Natural Science Foundation of China (31560133, 41501028), International Crane Foundation (11001903) and Key Laboratory of Ministry of Education, Nanchang University (13006457).

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Figure 1

Location of Shahu Lake and the zooplankton sampling points (water depth map based on the water level of October 2012)

(A) Location of the Poyang Lake. (B) Location of Jiangxi Poyang Lake National Nature Reserve.

(C) Location of Shahu Lake. (D) Zooplankton sampling points in Shahu Lake.

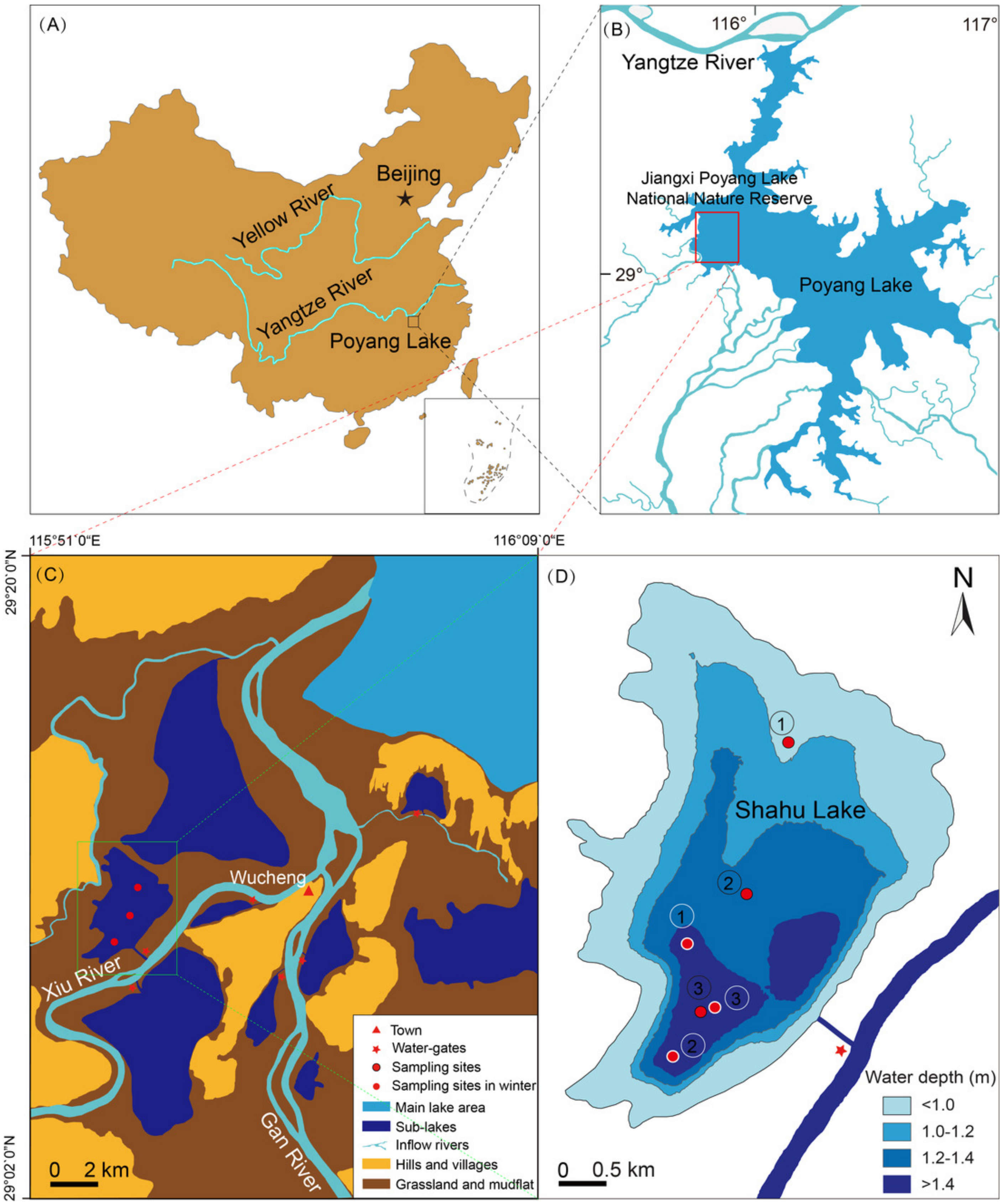
(A)
Beijing
Yellow River
Yangtze River
Poyang Lake
(B)
116°
117°
Yangtze River
Jiangxi Poyang Lake
National Nature Reserve
29°
Poyang Lake
115°51'0"E
116°09'0"E
29°20'0"N
29°02'0"N
(C)
Wucheng
Xiu River
Gan River
0 2 km
Town
Water-gates
Sampling sites
Sampling sites in winter
Main lake area
Sub-lakes
Inflow rivers
Hills and villages
Grassland and mudflat
(D)
N
Shahu Lake
Water depth (m)
<1.0
1.0-1.2
1.2-1.4
>1.4
0 0.5 km

Figure 2

Seasonal variation in species richness of main zooplankton groups in Shahu Lake from April 2012 to January 2016

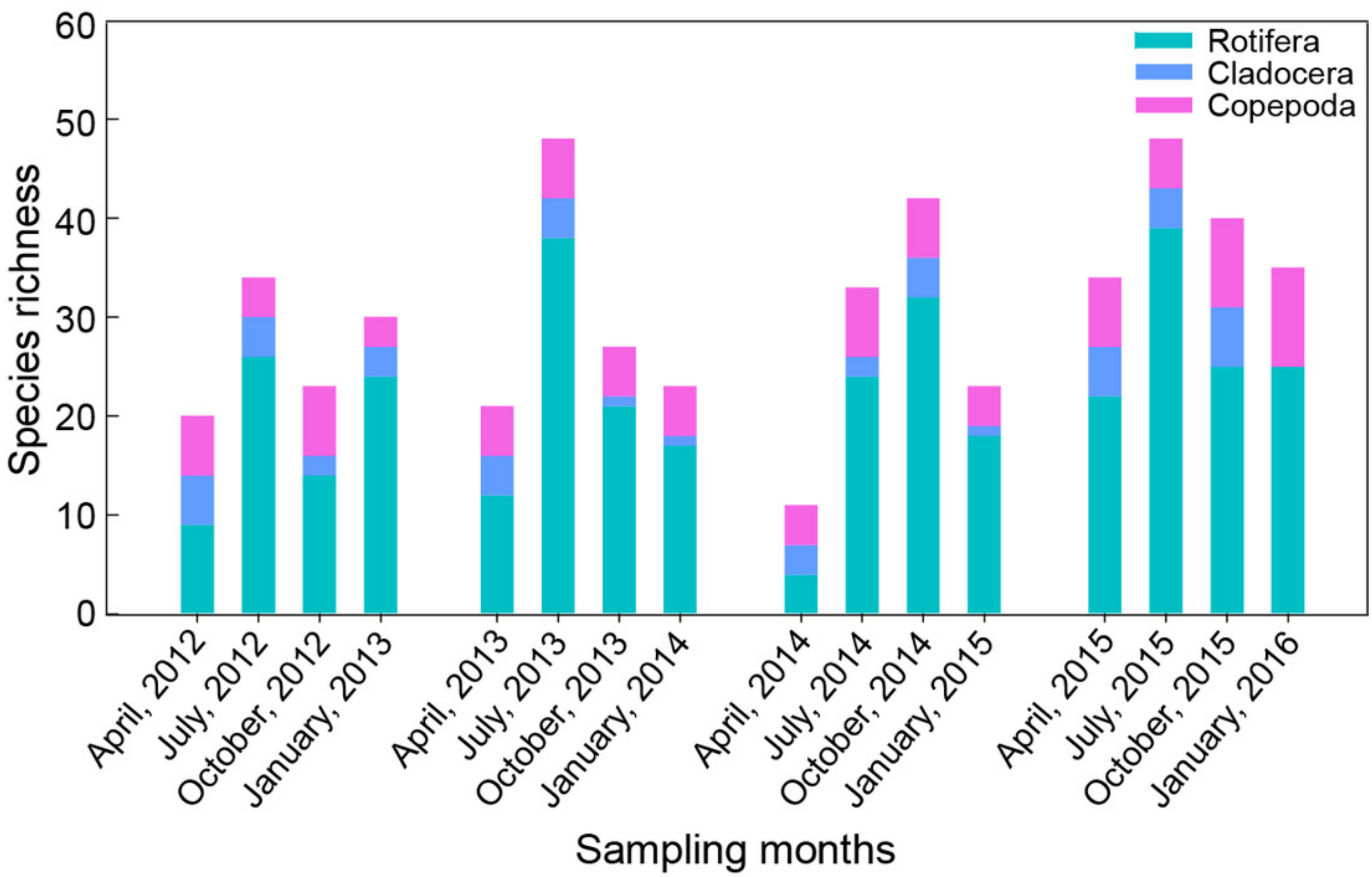

Figure 3

Seasonal variation in mean density (ind./L) and biomass (mg/L), relative density and biomass (%) of each group (Rotifera, Cladocera and Copepoda) in Shahu Lake during 2012–2015

(A) Density variation. (B) Biomass variation.

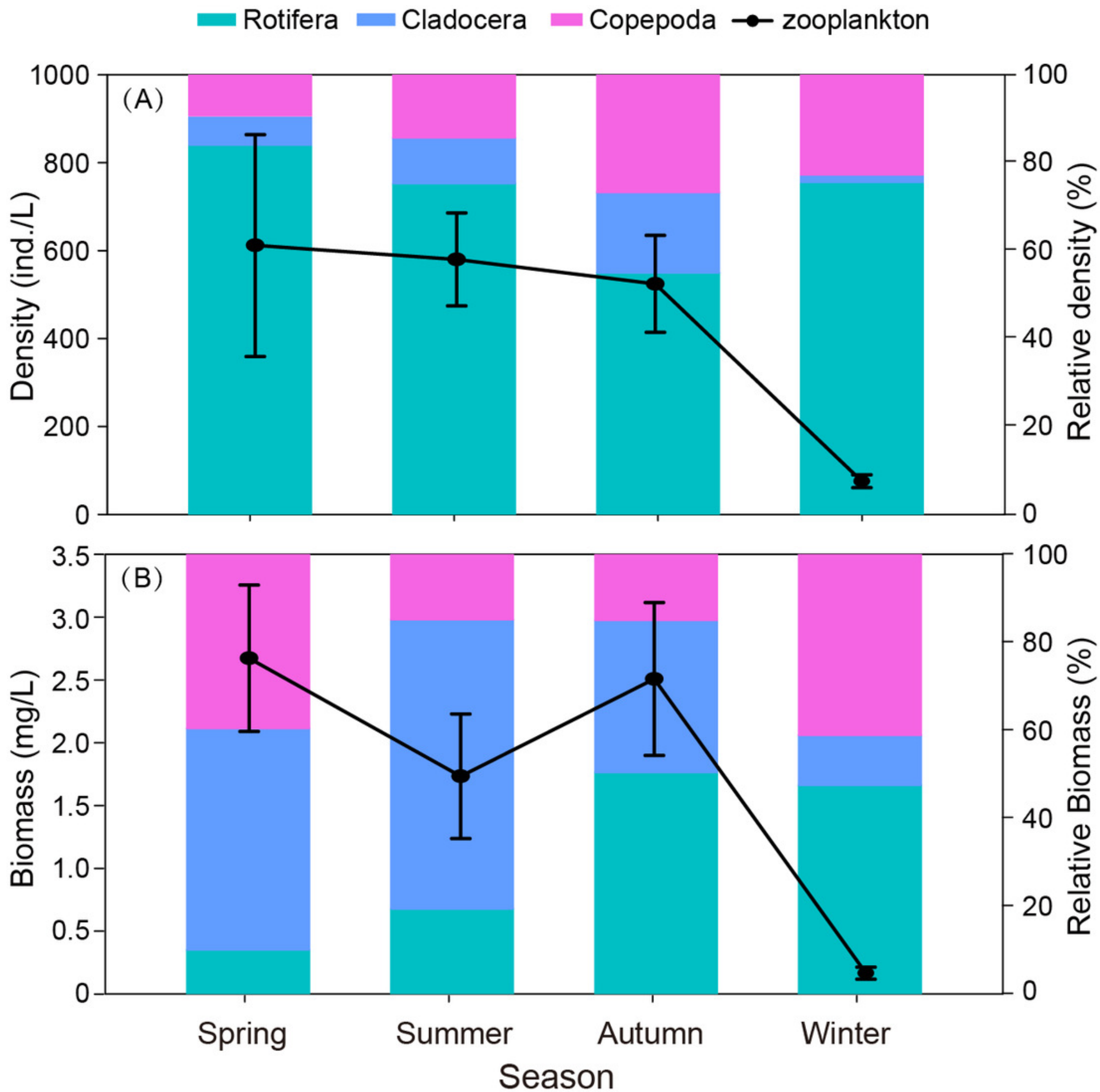
Rotifera
Cladocera
Copepoda
zooplankton
(A)
Density (ind./L)
Relative density (%)
0
200
400
600
800
1000
0
20
40
60
80
100
(B)
Biomass (mg/L)
Relative Biomass (%)
0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
Spring
Summer
Autumn
Winter
Season

Figure 4

Interannual differences in density (ind./L) and biomass (mg/L), relative density and biomass (%) of zooplankton in Shahu Lake during 2012–2015

(A) Density variation. (B) Biomass variation.

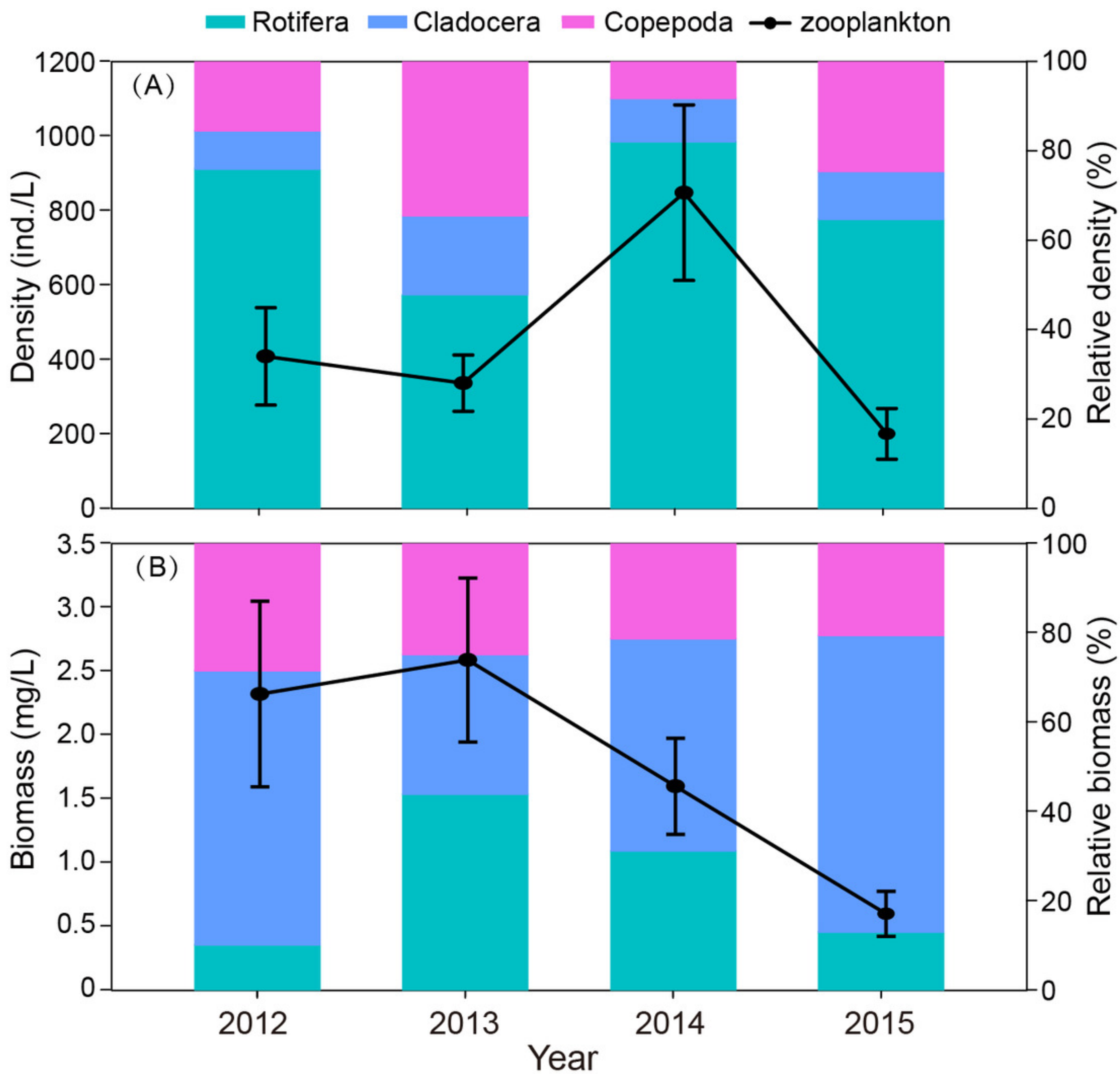

Figure 5

Seasonal variation in biodiversity index in Shahu Lake during 2012–2015

(A) Shannon–Weiner index, H' . (B) Margalef index, D. (C) Pielou’s index, J'.

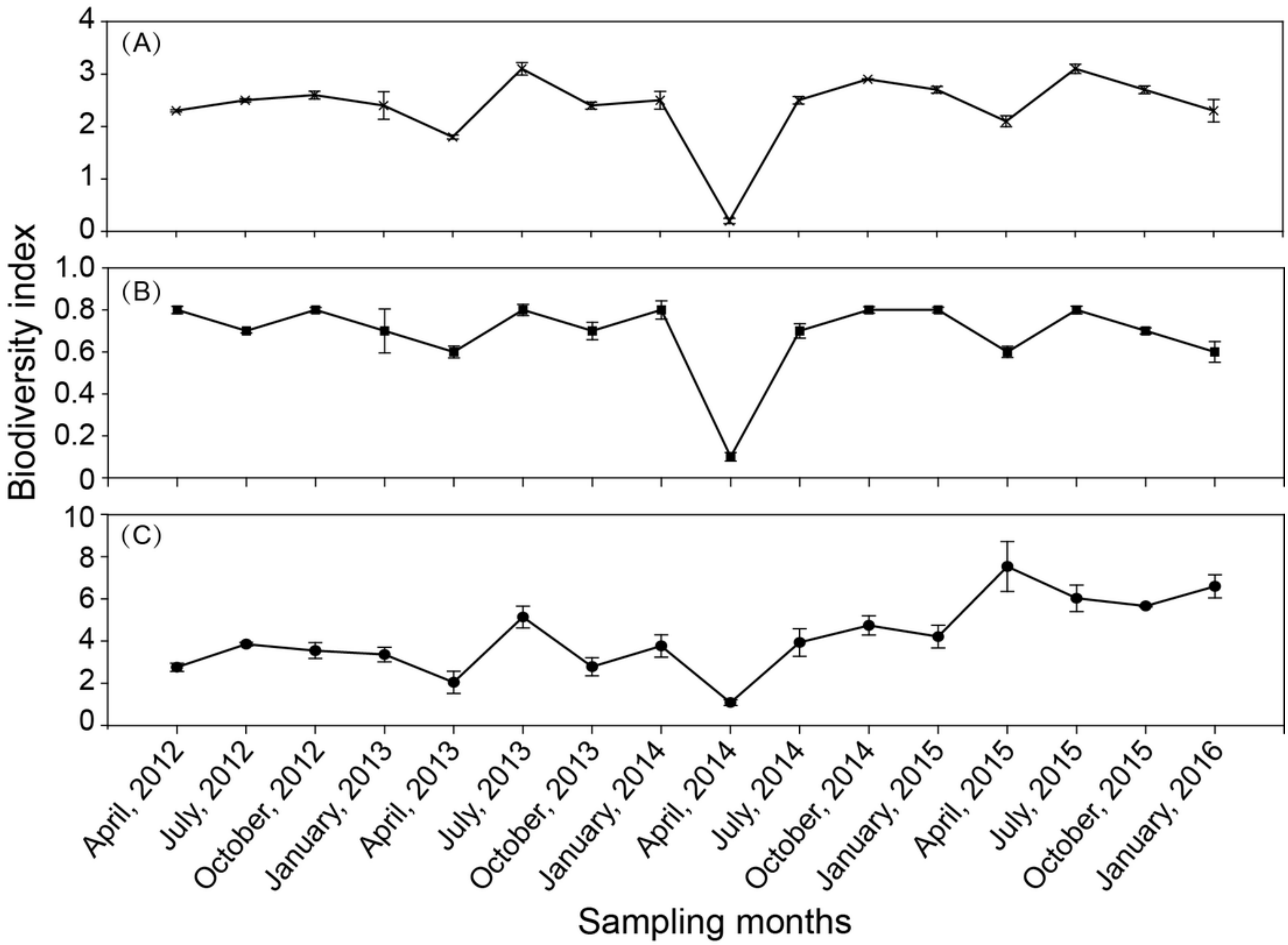

Figure 6

Non-metric multidimensional scaling ordination (NMDS) of zooplankton communities

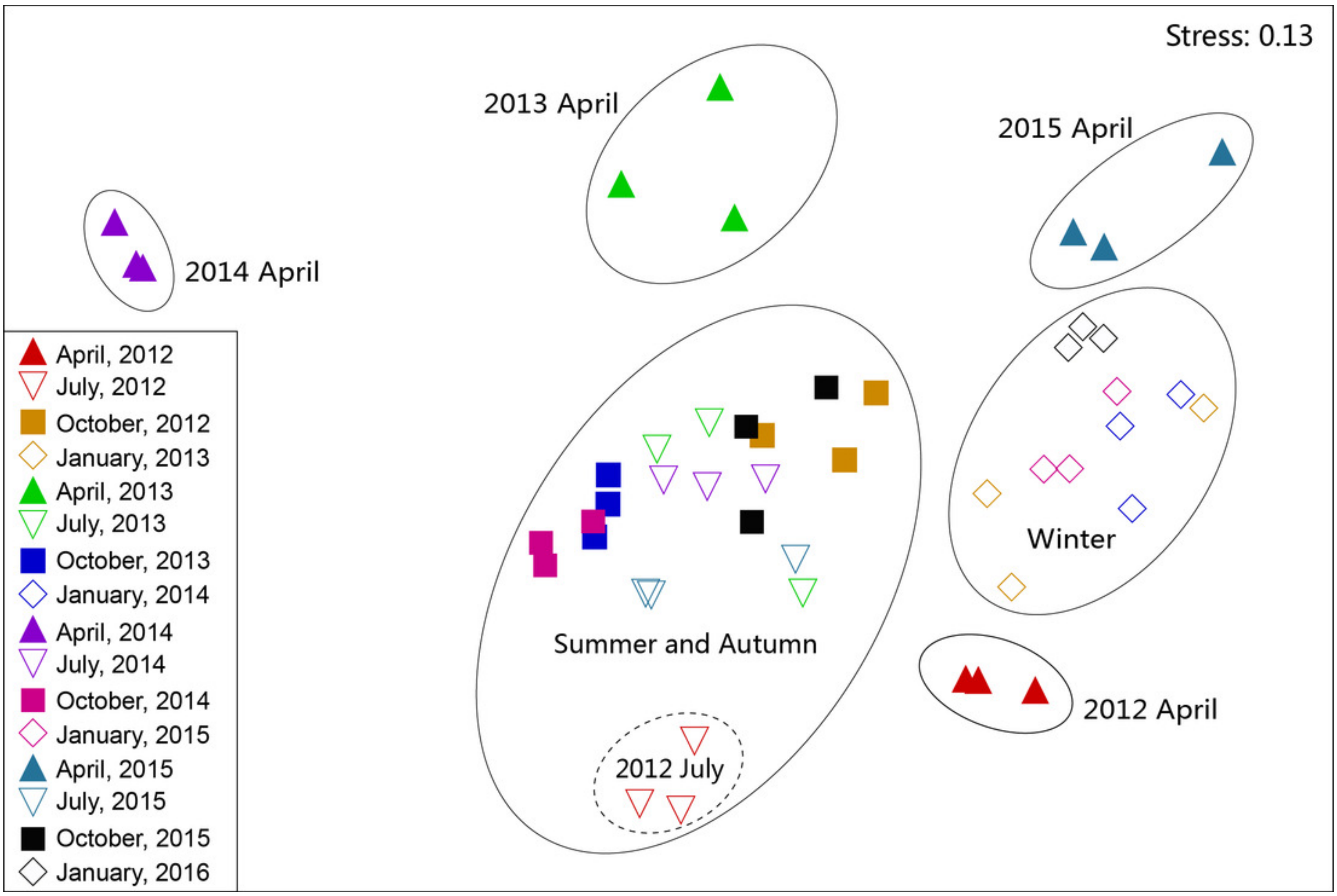

Figure 7

Redundancy analysis (RDA) of zooplankton dominant species and environmental factors in Shahu Lake (WT, water temperature; Cond, conductivity; DO, dissolved oxygen; Turb, turbidity)

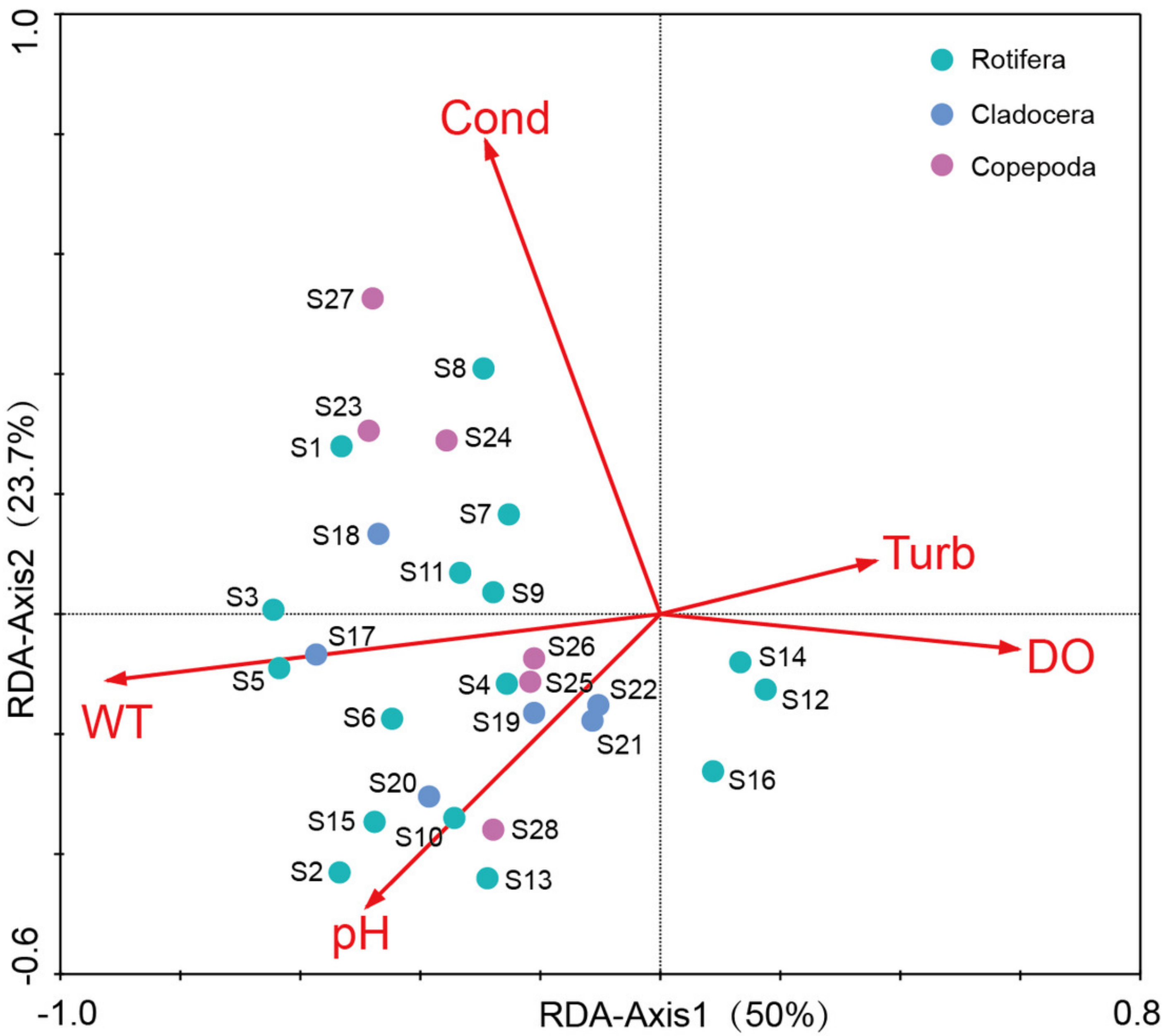

Figure 8

Interannual variation of zooplankton dominant species density in summer and autumn and diurnal variation of water level in 4 years of Shahu Lake.

(A) Interannual variation of zooplankton dominant species density in summer. (B) Interannual variation of zooplankton dominant species density in autumn. (C) diurnal variation of water level in 4 years. (D) Differences in the number of fishes that may enter the sub-lake after hydrological connectivity.

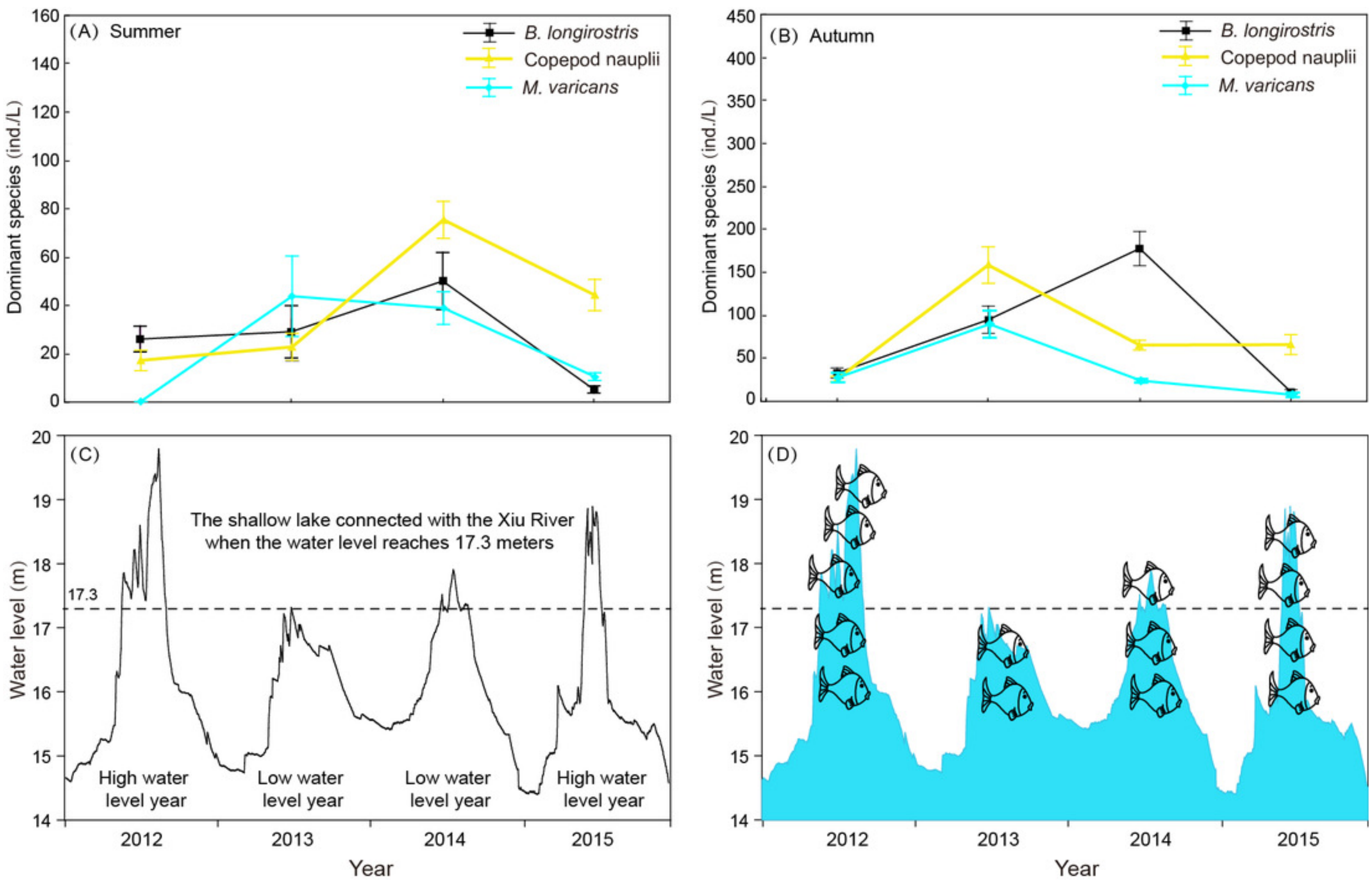

Table 1 (on next page)

Mean values (± standard error) of physicochemical factors and their effects on the density of zooplankton in Shahu Lake (n=48)

Table 1. Mean values (± standard error) of physicochemical factors and their effects on the density of zooplankton in Shahu Lake (n=48).

	April	July	October	January	F	P
Water temperature (℃)	20.8±1.13[a]	29.4±0.39[b]	21.3±0.21[a]	9.2±0.58[c]	152.48	<0.001
Conductivity (μS/cm)	90.2±4.35[a]	229.0±68.51[ab]	532.6±128.79[b]	279.3±94.28[ab]	4.52	0.008
Dissolved oxygen (mg/L)	8.8±0.15[a]	5.9±0.60[b]	8.9±0.20[a]	11.0±0.35[c]	32.74	<0.001
pH	7.1±0.20[ab]	7.5±0.21[a]	7.1±0.20[ab]	6.7±0.16[b]	3.08	0.037
Turbidity (NTU)	82.1±15.37[ab]	35.1±7.92[a]	112.4±23.84[b]	142.1±21.69[b]	6.24	0.001

Table 2 (on next page)

Dominant species, mean density (ind./L) and dominance (Y) for each year in Shahu Lake during 2012–2015

Table 2. Dominant species, mean density (ind./L) and dominance (Y) for each year in Shahu Lake during 2012–2015.

Dominant species	2012 ind./L (Y)	2013 ind./L (Y)	2014 ind./L (Y)	2015 ind./L (Y)	Code
Rotifera					
Brachionus angularis	0.9 (0.001)	**12.6 (0.024)**	8 (0.006)	**5.7 (0.023)**	S1
Brachionus forficula	5.1 (0.004)	3.2 (0.004)	1.1 (0.000)	**5.8 (0.023)**	S2
Brachionus diversicornis	7.6 (0.013)	3 (0.006)	0.5 (0.000)	**5.6 (0.022)**	S3
Keratella cochlearis	**35.1 (0.066)**	**17.7 (0.052)**	**28 (0.030)**	1.8 (0.011)	S4
Keratella. valga	5.8 (0.008)	**16.5 (0.049)**	13.1 (0.009)	**22.7 (0.088)**	S5
Asplanchna priodonta	4.8 (0.003)	**12 (0.035)**	25.6 (0.018)	**5.1 (0.034)**	S6
Asplanchna. girodi	**9.3 (0.021)**	1 (0.001)	0.1 (0.000)	0.1 (0.000)	S7
Asplanchna. brightwel	1 (0.000)	**19.6 (0.037)**	1.9 (0.001)	0.2 (0.000)	S8
Ascomorpha ecaudis	-	**30.9 (0.134)**	6.5 (0.003)	0.2 (0.000)	S9
Trichocerca cylindrical	11.3 (0.013)	0.1 (0.000)	12.9 (0.009)	**4.9 (0.020)**	S10
Polyarthra trigla	-	4.9 (0.013)	23.5 (0.017)	**4.2 (0.023)**	S11
Polyarthra dolichoptera	**57.2 (0.139)**	3.6 (0.007)	3.9 (0.001)	2.3 (0.009)	S12
Polyarthra vnlgaris	**81.9 (0.133)**	-	10 (0.004)	-	S13
Synchaeta oblonga	**24.6 (0.031)**	3.7 (0.006)	2.4 (0.001)	0.6 (0.002)	S14
Filinia longiseta	3.4 (0.002)	0.3 (0.000)	-	**10.3 (0.042)**	S15
Conochilus unicornis	-	0.8 (0.001)	**495.6 (0.654)**	**22.1 (0.167)**	S16
Cladocera					
Diaphanosoma brachyurum	**2.8 (0.034)**	3.3 (0.009)	**6.5 (0.042)**	**8.5 (0.210)**	S17
Bosmina longirostris	**15.2 (0.267)**	**43.3 (0.551)**	**66.4 (0.808)**	**4.7 (0.160)**	S18
Bosmina. coregoni	-	**10.9 (0.026)**	**8.6 (0.043)**	**-**	S19
Bosminopsis deitersi	1.5 (0.007)	-	-	**5.3 (0.083)**	S20
Daphnia pulex	**8.4 (0.053)**	-	-	-	S21
Daphnia hyalina	**5.5 (0.030)**	-	-	-	S22
Copepoda					
Copepods nauplii	**18.6 (0.264)**	**48.7 (0.374)**	**37.4 (0.479)**	**33.1 (0.677)**	S23
Limnoithona sinensis	-	13.6 (0.078)	**5.1 (0.038)**	**3.1 (0.033)**	S24
Macrocyclops fuscus	**18.6 (0.198)**	-	-	0.2 (0.001)	S25
Tropocyclops prasinus	**6 (0.048)**	-	-	-	S26
Microcyclops varicans	**12.8 (0.090)**	**33.6 (0.161)**	**16.6 (0.179)**	**4.7 (0.072)**	S27
Mesocyclops leuckarti	-	-	4.3 (0.015)	**5.3 (0.066)**	S28

-, the species density is very small or does not appear.

Table 3 (on next page)

Eigenvalues of the first and second axes in the redundancy analysis

Table 3. Eigenvalues of the first and second axes in the redundancy analysis.

Axes	RDA1	RDA2	Total variance
Eigenvalues :	0.156	0.074	1
Species-environment correlations :	0.754	0.806	
Cumulative % variance			
of species data :	15.6	23	
of species-environment relation :	50	73.7	
Sum of all eigenvalues			1
Sum of all canonical eigenvalues			0.313

Table 4(on next page)

Species list of zooplankton in Shahu Lake, 2012–2015

1 **Appendix Table 1.** Species list of zooplankton in Shahu Lake, 2012–2015.

Zooplankton species	2012				2013				2014				2015			
	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter
Rotifera																
Anarthra aptera										+						
Argonotholca foliacea														++		
Ascomorpha ecaudis					+++	+++	+++			+	+++			+		+
Ascomorpha ovalis							+			+	++		+	+	+	+
Ascomorpha saltans		+++			+	+		+			+			+		
Asplanchna brightwel		+		+		+	+++		++	+				+		
Asplanchna girodi		+++	+++	+++		+	+	+				+		+		
Asplanchna priodonta		++			+	+++	+++				+++	+++	+++	+++	++	+++
Asplanchna sieboldi		+														
Brachionus angularis	+		++			++	+++			+++	++		+	+++	++	+
Brachionus budapestiensis	+		+++	+		+	+	+++		+	++	+++		+++	+	
Brachionus calyciflorus	+	+	++	+		+					+			+		+++
Brachionus capsuliflorus											+	+++	+	+	+	
Brachionus caudatus						+						+++				
Brachionus diversicornis	+	++	+++	+	+	+	+	+			+	+	+	+++	++	
Brachionus falcatus		+++								+++		+++		+++		
Brachionus forficula		++				+		+			+	++		+++	+++	
Brachionus leydigi													+			+
Brachionus urceus				+		+		+				++	+++	++	+	+++
Cephalodella catellina								+								
Cephalodella gibba	+			+												
Cephalodella sterea														+		
Collotheea mutabilis						+			+							

Conochiloides dossuarius										++	++					
Conochilus unicornis								+++	+++	++	+++	+++	+++	+++	+++	+++
Eosphora thoa						+	+									+
Eothinia elongata						+										
Epiphanes senla		++					+									
Euchlanis dilatata											+		+	+		
Filinia longiseta		+				+							+	+++	+++	
Filinia maior		+					+				+++					
Filinia passa		+	+++			+	+							+++	+	
Gastropus hyplopus		++	+		+	+		+								
Gastropus stylifer		+	+	+						+						
Harringia eupoda				+			+									
Kellicottia longispina		+														
Keratella cochlearis	+++	+++		+		+	+++	+++		++	+++	+++	++	++	++	+
Keratella quadrata								+		+		+			+	
Keratella ticinensis														+	++	
Keratella valga		++	+			+++	+++	+		+	+++	++	+	+++	+++	
Lecane luna						+										
Lecane nodosa																+
Lecane ungulata																+
Lepadella apsida				+												
Lindia truncata											+					
Monostyla crenata							+									
Monostyla elachis														++		
Monostyla lunaris													+	+		
Monostyla unguitata										+	+					
Mytilina ventralis						+						+++				
Notholca labis								+								+
Notommata tripus						+										

Pedalia mira				+		+				+	++					
Ploesoma hudsoni			++		+	+			+	++			+++			
Ploesoma truncatum				+		+				+						
Polyarthra dolichoptera	+++	+++	++	+++		+	+	+++				+++	++	+	+	+
Polyarthra euryptera										++	+		+			
Polyarthra trigla					+	+	+++	+		+++	+++		+	+++	+++	+++
Polyarthra vnlgaris	++	+++	+	+							+++		+			
Pompholyx complanata				+			+									
Pompholyx sulcata										+	+					
Proales daphnicola					+											
Pseudoharringia semilis						+										
Resticula gelida						+										
Resticula melandocus						+										
Scaridum longicaudum		++			++	+								+		
Synchacta atylata				+							+					
Synchacta tremula				+				+				+				
Synchaeta oblonga		+++		+++	+	+		+++				+++	+			+++
Synchaeta pectinata													+	+		+++
Trichocerca bicristata					+	+					+					
Trichocerca bicuspes														+	+	
Trichocerca capucina		+	+++	+		+++				+	+++			++	+	
Trichocerca cylindrical	+	+++		+	+					+++	+++			++	+++	+
Trichocerca dixon-nuttalli														+		
Trichocerca elongata											+			+	+	
Trichocerca gracilis						+								+++	+	+
Trichocerca longiseta		++		+								+				
Trichocerca lophoessa		++	+			+					+			++	+	+
Trichocerca pusilla											++			++	+	+
Trichocerca rattus														+		+

Trichocerca rousseleti											+					
Trichocerca similis													+	+	+	
Trichocerca stylata						+				+	+++					
Trichocerca tenuior										+				+		
Trichocerca weberi				+		+	+									+
Trichotria tetractis													+			+
Cladocera																
Alonella rostrata		+														
Bosmina coregoni						+++			++		+++					
Bosmina fatalis													+		++	
Bosmina longirostris	+	+++	+++	+	+++	+	+++	+	++	+++	+++	++	+++	++	+++	
Bosminopsis deitersi		+		+										+++	+	
Daphnia cucullata				+									+++			
Daphnia hyalina	+++															
Daphnia pulex	+++												+			
Diaphanosoma brachyurum	+	+	+++			+++			+	++	++		+	+++	+++	
Diaphanosoma leuchtenbergianum					+	+								+	+	
Leptodora kindti		+			+											
Moina micrura					+											
Sida crystallina	+										++				++	
Copepoda																
Copepod nauplii	+++	++	+++	+++	++	+++	+++	+++	+	+++	+++	+++	+++	+++	+++	+++
Cyclops vicinus													+			+
Limnocletodes behningi					+	+										
Limnoithona sinensis						+++	+	+++	+	+++	+			++	+++	+
Macrocyclops fuscus	+++	++	++										+++			
Mesocyclops leuckarti											++			+++	+++	+
Microcyclops varicans	+++		+++	+++		+	+++	+		+++	+++	+++	+	+++	+++	++

Neodiaptomus schmackeri													++		++	+
Paracyclops fimbriatus													+			+
Schmackeria forbesi	+		+						++	++	+				+	+
Sinocalanus dorrii	++	+	+		+++	+	+	+	++	+		+	++		+	+
Thermocyclops hyalinus				+						+						
Thermocyclops kawamurai	+++		+		++	+	+	+		++	+	+			+	+
Thermocyclops taihokuensis														+	++	
Tropocyclops prasinus	+++	+	++													

Note: + means appeared; ++ means common species (occurrence frequency greater than 0.65); +++ means dominant species (dominance index greater than 0.02).

Table 5 (on next page)

Summary of indicator species analysis showing indicator value (IV) and p values for each group. S= spring, SA= summer and autumn, W= winter

Appendix Table 2. Summary of indicator species analysis showing indicator value (IV) and p values for each group. S= spring, SA= summer and autumn, W= winter.

	Group	IV	*P* values
Sinocalanus dorrii	S	90.62	0.001
Daphnia pulex	S	33.33	0.004
Macrocyclops fuscus	S	45.22	0.012
Daphnia hyalina	S	25.00	0.032
Brachionus angularis	SA	86.71	0.001
Brachionus forficula	SA	56.50	0.001
Brachionus diversicornis	SA	73.05	0.001
Keratella valga	SA	90.29	0.001
Asplanchna priodonta	SA	68.48	0.001
Ascomorpha ovalis	SA	52.65	0.001
Trichocerca cylindrical	SA	58.97	0.001
Trichocerca capucina	SA	63.77	0.001
Pedalia mira	SA	56.78	0.001
Diaphanosoma brachyurum	SA	72.27	0.001
Bosmina longirostris	SA	69.57	0.001
Copepod nauplii	SA	75.76	0.001
Limnoithona sinensis	SA	63.97	0.001
Microcyclops varicans	SA	71.50	0.001
Polyarthra trigla	SA	72.21	0.002
Filinia longiseta	SA	41.64	0.007
Keratella cochlearis	SA	64.85	0.009
Mesocyclops leuckarti	SA	37.17	0.009
Collotheea mutabilis	SA	33.33	0.014
Brachionus falcatus	SA	34.57	0.019
Asplanchna brightwel	SA	46.87	0.021
Trichocerca stylata	SA	29.17	0.022
Scaridum longicaudum	SA	31.97	0.023
Filinia maior	SA	29.17	0.027
Bosminopsis deitersi	SA	28.12	0.039
Brachionus budapestiensis	SA	44.18	0.05
Synchaeta oblonga	W	62.10	0.001