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

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Shallow lakes are important for the maintenance of Lake Poyang ecosystem integrity, and zooplankton play an important role in its substance and energy flow. We investigated zooplankton in spring (April), summer (July), autumn (October) and winter (January of the following year) from 2012 to 2016 in a sub-lake of Lake Poyang with seasonal water level fluctuations. The study aims to understand their seasonal dynamics and interannual variation of zooplankton community in relation to environmental variables. A total of 115 species were identified in all samples of the 4 years, comprising 87 Rotifera, 13 Cladocera and 15 Copepoda. Rotifera was the dominant group in quantity and its species richness and abundance were significantly higher than Cladocera and Copepoda ($P<0.05$, by ANOVA), while Cladocera dominated in biomass. Species richness of Rotifera showed a significant seasonal difference ($P<0.05$ by ANOVA). The clear decline of zooplankton species richness in spring was mainly due to the dramatic decrease of Rotifera species. Furthermore, both density and biomass of zooplankton showed significant seasonal differences ($P<0.05$). Generally, the density and biomass of zooplankton were higher in summer and autumn than in winter and spring. Biodiversity indices e.g., Shannon-Wiener index and evenness were dramatically lower in spring than in other seasons. Non-metric multidimensional scaling (NMDS) analysis suggested that the zooplankton communities can be divided into three groups: spring community, summer–autumn community and winter community associated with distinct indicator species. The results of species richness and community analysis showed that the seasonal succession of zooplankton communities did not have interannual reproducibility. Redundancy analysis revealed that water temperature (WT), conductivity, pH and dissolved oxygen (DO) had significant effects on the zooplankton community. In addition, water level fluctuations, disturbance by wintering waterbirds and artificial water level control during dry season have potential effects on zooplankton community structure too. This study is helpful to further understand

the ecosystem stability of lake connected with rivers and provide scientific guidance for protection of lake wetlands.

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

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Abstract

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

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

Results. A total of 115 species were identified in all samples of the 4 years, comprising 87 Rotifera, 13 Cladocera and 15 Copepoda. Rotifera was the dominant group in quantity and its species richness and abundance were significantly higher than Cladocera and Copepoda (*P*<0.05), while Cladocera dominated in biomass. Species richness of Rotifera showed a significant seasonal difference (*P*<0.05). Both density and biomass of zooplankton showed significant seasonal differences (*P*<0.05). Generally, the density and biomass of zooplankton were higher in summer and autumn than in winter and spring. Biodiversity indices were dramatically lower in spring than in other seasons. Non-metric multidimensional scaling (NMDS) analysis suggested that the 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. Redundancy analysis revealed that water temperature (WT), conductivity, pH and dissolved oxygen (DO) had significant effects on the zooplankton community. In addition, water level fluctuations, disturbance by wintering waterbirds and artificial water level control during dry season have potential effects on zooplankton community structure

Conclusions. The community structure of zooplankton has a significant seasonal pattern and no interannual repeatability. The differences in zooplankton density, biomass and diversity indices were significant in different seasons and years. Water environmental factors, water level fluctuations, wintering migratory bird activities and human disturbances have a direct or indirect impact on zooplankton community structure. This study is helpful to further understand the ecosystem stability of lake connected with rivers and provide scientific guidance for protection of lake wetlands.

Introduction

Lake Poyang, the largest freshwater lake in China, is a connected lake where water levels fluctuate widely in different seasons (Wu, 1994). In its low water period, there can be more than 100 separated shallow lakes appearing in Lake Poyang (Hu, 2015). When these sub-lakes connect with the main lake in the high water period, there is a close exchange of material, energy and biology among those water bodies. Shallow lakes are of significant ecological value due to their 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 the ideal habitats that provided for wintering birds (Qi et al, 2011; Hu et al, 2014), etc. All these values play an important and unique role in maintaining the biological integrity and species diversity of the Lake Poyang wetland ecosystem.

As an important biological part of the water ecosystem and the link between the primary producer and higher consumers, zooplankton cannot be absent if the health and stability of the water ecosystem is to be maintained. They also indicate the trophic state of lake water. It can be accurately reflected by the spontaneous variation in zooplankton (Pereira et al., 2002; Krylov, 2015), because their community structure and the standing crop relate closely to the water nutrient state. When water eutrophication becoming worsens, the number of zooplankton species will decrease, while their abundance has increased (Yang & Huang, 1994; Lin, 2013).

Zooplankton communities have significant seasonal fluctuations under the influence of biological and abiotic factors. Environmental factors, such as total nitrogen (TN), total phosphorus (TP), water temperature (WT), water clarity and the biomass of small algae all play an important role in the succession of zooplankton communities (Yang et al., 2014; Hu et al., 2014). Periodical connection between the lakes and rivers also affects the ecological structure and function of zooplankton communities. Different degrees of water level have different degrees of effect on zooplankton (Goździejewska, 2016). Planktivorous fish exerts high top-down pressure 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.

Increasing N and P levels in recent decades (Lv et al, 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), and the *Jiangxi Water Resources Bulletin* (2012–2015) indicated that the water of Lake Poyang showed moderate eutrophication (http://www.jxsl.gov.cn/). Although the Lake Poyang has reached the level of eutrophication, fortunately, there was no outbreak of cyanobacteria bloom due to the characteristics of lake connected with the Yangtze River and repeated water changes (Hu & Zhu, 2014). However, cyanobacterial blooms have already taken place in its sub-lakes, because of unmanaged development and resource utilization (Dai et al, 2015). The ecological and environmental problems faced by shallow lakes are epitomes of the environmental deterioration of Lake Poyang, and the ecological decline in sub-lakes may eventually affect its wetland ecosystem and the functioning of the whole lake seriously.

The first study of zooplankton in Lake Poyang was focused on the species in the 1960s (Deng, 1963). Subsequently, some of discontinuous researches on zooplankton have been conducted, but those studies were relatively limited. For example, Deng (1963) made a preliminary investigation on Cladocera. Xie et al. (1997, 1998 and 2000) carried out 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 the crustaceans. According to records (Huang, 2007) there is a total of 207 zooplankton species in China, but reports on zooplankton in the shallow lakes of Lake Poyang were still very limited in past decades. Zooplankton in sub-lakes was reported only until recent years (Zhang, 2014). Moreover, reports on seasonal and annual variations in zooplankton communities in shallow lakes remain rarely reported. Zooplankton is 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, zooplankton is also an important indicator of water environment change (Peter et al., 2010), its population structure, quantity, dominant species can be an important indicator of water quality monitoring (Wang, et al., 2012). Therefore, the study of zooplankton's spatial and temporal distribution pattern can provide vital scientific basis for the protection and sustainable utilization of lake resources.

This study has carried a preliminary research into seasonal variations in zooplankton communities in Shahu Lake, a sub-lake of Lake Poyang. Samples were collected seasonally from April 2012 to January 2016, and our specific aims were to: (1) investigate the seasonal and interannual variations of zooplankton community in the shallow lakes, and (2) identify the dominant environmental factors that affect the variation in zooplankton communities.

Materials & Methods

Sampling site

Lake Poyang (28° 24'–29° 46'N, 115° 49'–116° 46'), located downstream in the Yangtze River. 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 average annual rainfall of 1400–1900 mm and 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), and there are nine sub-lakes in the reserve. Shahu Lake with a surface area of 1.4 km^2 is one of these and has a flat bottom and few submerged plants. 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 by the 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 sampled seasonally (spring = April, summer = July, autumn = October and winter = January) at three points in Shahu Lake from April 2012 to January 2016. With the water level declining, the water only remained in deepest area, so three sampling points were set in the more than 1.4 m area in winter (Fig. 1). Zooplankton were sampled three times at each point, and so nine samples were collected in each season resulting in a total of 144 samples over the 4 years. A 5-L modified Schindler–Patalas sampler was used to collect 10 L mixed water at about 50 cm below the water surface for each sample. A plankton net (mesh size, 64 μm) was used to filter the water and to collect zooplankton, which were gathered from the end of the net and immediately preserved in 50 ml plastic bottles with 4% formalin. In the laboratory zooplankton were counted and identified under 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 this study, copepod nauplii was considered as one taxon. Four bibliographies, including three faunas, were used for zooplankton identification (Crustacean Research Group, 1979; Jiang & Du, 1979; Wang, 1961; Zhou & Chen, 2011). Their density was calculated by dividing the individual numbers of zooplankton gathered in each sample by the sample volume and expressed by ind./L. The biomass of zooplankton (wet weight) was evaluated according to the method of Zhang and Huang (1991). The weight of each nauplii was estimated to be about 0.003 mg (Xie & Li, 1998).

Physicochemical parameters were measured simultaneously at the time of collection. WT, pH, conductivity (Cond), dissolved oxygen (DO) and turbidity (Turb) were measured using a Multi-function Water Quality Monitor (YSI 6600 V2, US).

Data analysis

The dominance index was calculated as follows:

$$Y = n_i \times f_i / N \quad \text{(Eqn 1)}$$

where 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 a dominant species. In this study, N referred to the total density of zooplankton in each season.

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 species number and P_i represented the proportion of i species densities in the total zooplankton density in the sample.

The seasonal variance of water physicochemical factors, zooplankton density and biomass were analysed by one-way ANOVA, using the STATISTICA 7.0 (StatSoft Inc, Tulsa OK, USA). The seasonal variation in zooplankton communities was tested by non-metric NMDS analysis and analysis of similarities (ANOSIM). Zooplankton individual number data were analysed using a ranked similarity matrix based on Bray–Curtis similarity measures. Rare species, whose average density was less than 1.0 ind./L, were excluded during NMDS and ANOSM analyses. NMDS ordination and ANOSIM analyses were performed with the PRIMER 5 computer package (Clarke and Warwick, 1994). The indicator value method (IndVal) was then 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. We tested the significance of the indicator value for each species with a Monte Carlo randomization procedure with 1000 permutations. IndVal was performed by the *indval* function in R package *labdsv* (R version 3.4.1, R Development Core Team 2017).

The correlation between water physicochemical factors and zooplankton dominant species was analysed through redundancy analysis (RDA) and significance was determined by the Monte Carlo test. RDA and Monte Carlo tests were performed by use of Canoco for Windows 4.5 software (ter Braak & Smilauer 2002). All variables were ln (x+1) transformed prior to analysis.

Results

Physical-chemical variables

The seasonal mean values of physicochemical factors in Shahu Lake from April 2012 to January 2016 are shown in Table 1. One-way ANOVA showed that all the physicochemical factors had significant seasonal differences ($P<0.05$). WT rose from spring, reaching the 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, 142.1±75.2 NTU, respectively) in winter and lowest (5.9±2.1 mg/L, 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. Species of these three main groups comprised 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). Only 24 species occurred simultaneously over the four years: 18 rotifera species, 2 Cladocera species and 4 Copepoda species. Zooplankton species richness showed significant seasonal differences ($P=0.041$). In every season, rotifers, which comprised 36.4–81.3% of total species numbers, 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; the minimum (23 species) were found in 2012 and the maximum (42 species) in 2014. In winter 65 species were identified; the minimum (23 species) were found in 2012 and the maximum (35 species) in 2015.

Dominant species

From 2012 to 2015, there were 13 dominant species, 10 dominant species, 16 dominant species and 8 dominant species in each year (Table 2). *Bosmina longirostris*, copepod nauplii and *Mesocyclops leuckarti* 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). Generally, 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 significant lower than other seasons (P<0.001). The maximum density of cladocerans was observed in October 2014 (219.2 ind./L) while copepods in July 2014 (137.6 ind./L).

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. 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, it 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. The outbreak of *C. unicornis* resulting in highest density of rotifer in spring 2014 than in other years (P=0.018). The density of Cladocera in 2014 was significantly higher than in 2012 and 2015 (P=0.039). Biomass of zooplankton in 2015 was significantly lower than in the other three years (P=0.036, Fig. 4). 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. The Shannon–Weiner index (H') was in the range of 0.2–3.1, with average of 2.37. The Margalef index (D) was in the range of 1.1–7.6, with average of 4.2. Pielou's evenness index (J') was in the range of 0.09–0.85, with average of 0.69. The results of one-way ANOVA showed that the

Shannon–Wiener index and Pielou's index had significant seasonal variation (*P*<0.001; *P*=0.002, respectively). The seasonal variation in the Margalef index was not significant.

Community structure

NMDS results showed that, apart from July 2012, zooplankton in July and October in all 4 years were at high density and had similar dominant species. And they 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 as independent branches, because the species composition and density of zooplankton in these seasons were quite different from the other seasons. The interannual differences of the communities were not found indicating that the seasonal variation in zooplankton community structure in Shahu Lake was much greater than the interannual variation. 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 showed 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. We selected the RDA to illustrate the relationships between the dominant species of zooplankton and environment factors (Fig.7). The first axis explained 15.6 % of the variance in species data, and 50 % of the variance in species–environment relationship (Table 3). The second axis explained 7.4 % of the variance in species data, and 23.7 % of the variance in species–environment relationship. Monte Carlo permutation test showed 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 Pearson correlation analysis indicated that WT had significant positive correlation with zooplankton (R=0.722, *P*<0.05).

Discussion

Temporal pattern of zooplankton communities in a shallow 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, 2016) means their abundance is generally dominant (Romo, 1990). In our 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 in each year. Nevertheless the species richness was lower in comparison with the historical research records in Lake Poyang (Xie et al., 1997, 1998; Huang et al, 2003; Huang et al., 2007). Besides, we found that species richness of zooplankton had significant seasonal difference (*P*=0.041). This variation was mainly caused by the species numbers of rotifers changed in different seasons (*P*=0.012). During the four years, there were 16 species of rotifers becoming dominant species. While only 6 species of cladocerans and copepods were dominant species, respectively. In spring, the dominant species are usually larger body size species, such as *D. pulex*, *D. hyalina* and *Sinocalanus dorrii*.

As sub-lake of the Lake Poyang, habitat diversity in Shahu Lake is lower than that of Lake Poyang. Moreover, the samples in this study were only taken in the open water area. In addition, the lake has faced intensive human activities, e.g. beach grazing, fishing, eutrophication caused by pollution etc. These objective factors may lead to species richness decrease. NMDS analysis suggested that seasonal variation were more significant than interannual in zooplankton community structure, and 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), we can roughly see the seasonal dynamics of zooplankton community structure. Rotifers peaked in summer and autumn. Cladocerans and copepods achieved their peaks in spring, summer and autumn. But all the three groups were at minimum levels in winter. Our 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 had been reported in other lakes (Hu, 2014; Lin, 2014).

The density and biomass of zooplankton showed significant difference among seasons (*P*=0.035, *P*=0.002). Over the 4 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 2014 due 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. Early research reports that cladocerans and copepods are the main component of zooplankton productivity due to the larger body size (Castro & Gonçalves, 2007). In this study, we 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, but it contributed 50% of the total biomass of zooplankton.

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

Some studies have found that spring-summer zooplankton community is not a complete repetitive succession in small shallow 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 4 years, while in 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 main lake. The material and biological exchanges between the sub-lake and main lake resulting in a similarity 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 (Hussain et al., 2016; Hu et al., 2013). Water temperature has an important effect on dormant eggs hatching, growth and reproduction of zooplankton (Korpelainen H, 1986; Hu, 2008). For example, the net reproduction rate of *Brachionus diversicornis* is highest when the temperature is 30℃ (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), and so zooplankton has a high density in summer and a low density in winter in the Shahu Lake.

Different zooplankton species have different adaptation to temperature (Tao et al., 2008). Numbers of resting eggs increase in both higher and lower temperatures (Shi & Shi, 1996). In this study, we 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.. Winter dominant species 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, highest in summer and lowest in winter (Table 1). RDA suggested that there was a positive correlation between temperature and most of the dominant species. Pearson correlation analysis also showed that temperature had a positive correlation with 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 redundancy analysis showed that conductivity, pH and dissolved oxygen also had significant effect on the seasonal variation of zooplankton community. Berzins and Pejler (1987) pointed out that some species of rotifers, which could instruct the water oligotrophic conditions, generally appeared in water at pH 7.0 or slightly lower pH value. Some other species of Rotifera indicating 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 this study, Pearson correlation analysis showed that significant positive correlations between pH and zooplankton species richness (R=0.644, P<0.001) and Shannon–Weiner diversity index (R=0.487, P<0.001). In our research, we found that there was a significant positive correlation between conductivity and Copepods (R=0.463, P<0.001), but a weakly positive correlation between conductivity and Cladocerans (R=0.078, P<=0.597). This was consistent with a previous study (Soto & De los Rios, 2006).

Water level fluctuation is also one of the important factors affecting zooplankton community structure. It was found that the density and community structure of zooplankton changes as water level fluctuates (Goździejewska, 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 rising, the Shahu Lake connected with the main lake As a consequence, nutrients and other biological communities poured into the sub-lake along with the floods, interactions occurred among zooplankton 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 lead to annual zooplankton differences as well. In the summer of 2012, the water level was significantly higher than in previous years (Appendix Fig. 1). 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 is only 20-30 cm at the end of the 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 is accelerated and the soil structure is improved (Hu, 2012). However, the water-gate was not opened during the winter of 2013, and so the water depth remained more than 1 meter in at that period (Appendix Fig. 1). 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 (Hall et al., 1976) and most fish prefer bigger zooplankton. Filter-feeding fishes such as silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*Aristichthys nobilis*) have an important place in Shahu Lake (Zeng, 2015). After the lake had been fished in winter by being enclosed, zooplankton face lower predation pressure from fish at the start of spring. When the water level rising, 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. While their 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 lake eutrophication. The study of the water quality of Shahu by zooplankton diversity index found that spring water quality was worse than other seasons (Zhu et al., 2014). The dynamics of 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 no interannual repeatability. The differences in zooplankton density, biomass and diversity indices were significant in different seasons and years. Water environmental factors, water level fluctuations, wintering migratory bird activities and human disturbances have a direct or indirect impact on zooplankton community structure. This study is helpful to further understand the ecosystem stability of lake connected with rivers and provide scientific guidance for protection of lake wetlands.

Overall, ecological civilization construction is a very important national decision-making of the current Chinese government and promoting green development and strengthen the 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 will be a vital part of the ecological civilization construction of China, such as biodiversity conservation, water resource planning as well as management, etc. The results from this study can thus provide vital scientific basis for lake ecosystems protection and sustainable utilization of lake biodiversity resources.

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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)

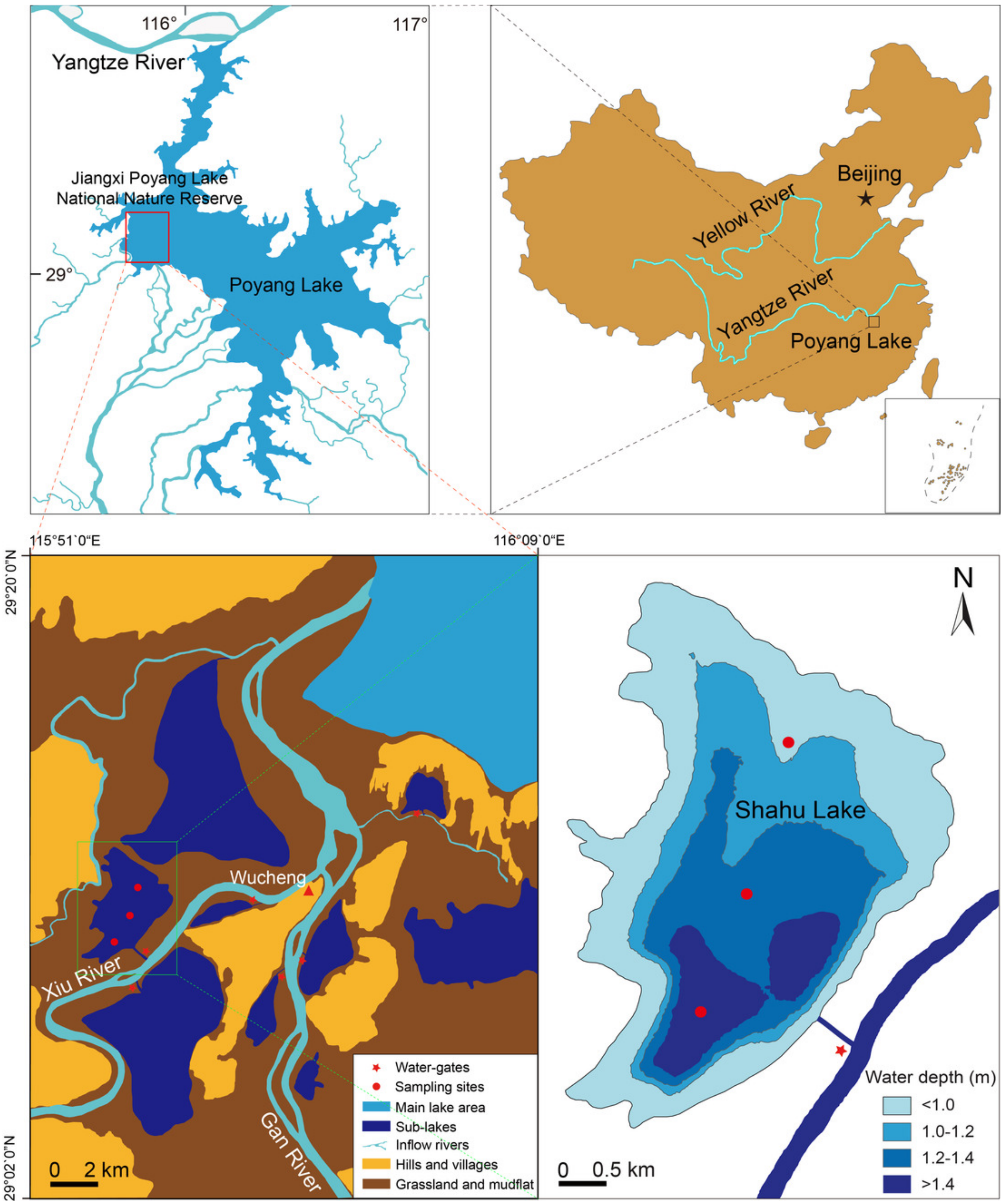
116°
117°
Yangtze River
Jiangxi Poyang Lake
National Nature Reserve
29°
Poyang Lake
Beijing
Yellow River
Yangtze River
Poyang Lake
115°51`0"E
116°09`0"E
29°20`0"N
29°02`0"N
Wucheng
Xiu River
Gan River
Water-gates
Sampling sites
Main lake area
Sub-lakes
Inflow rivers
Hills and villages
Grassland and mudflat
0 2 km
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

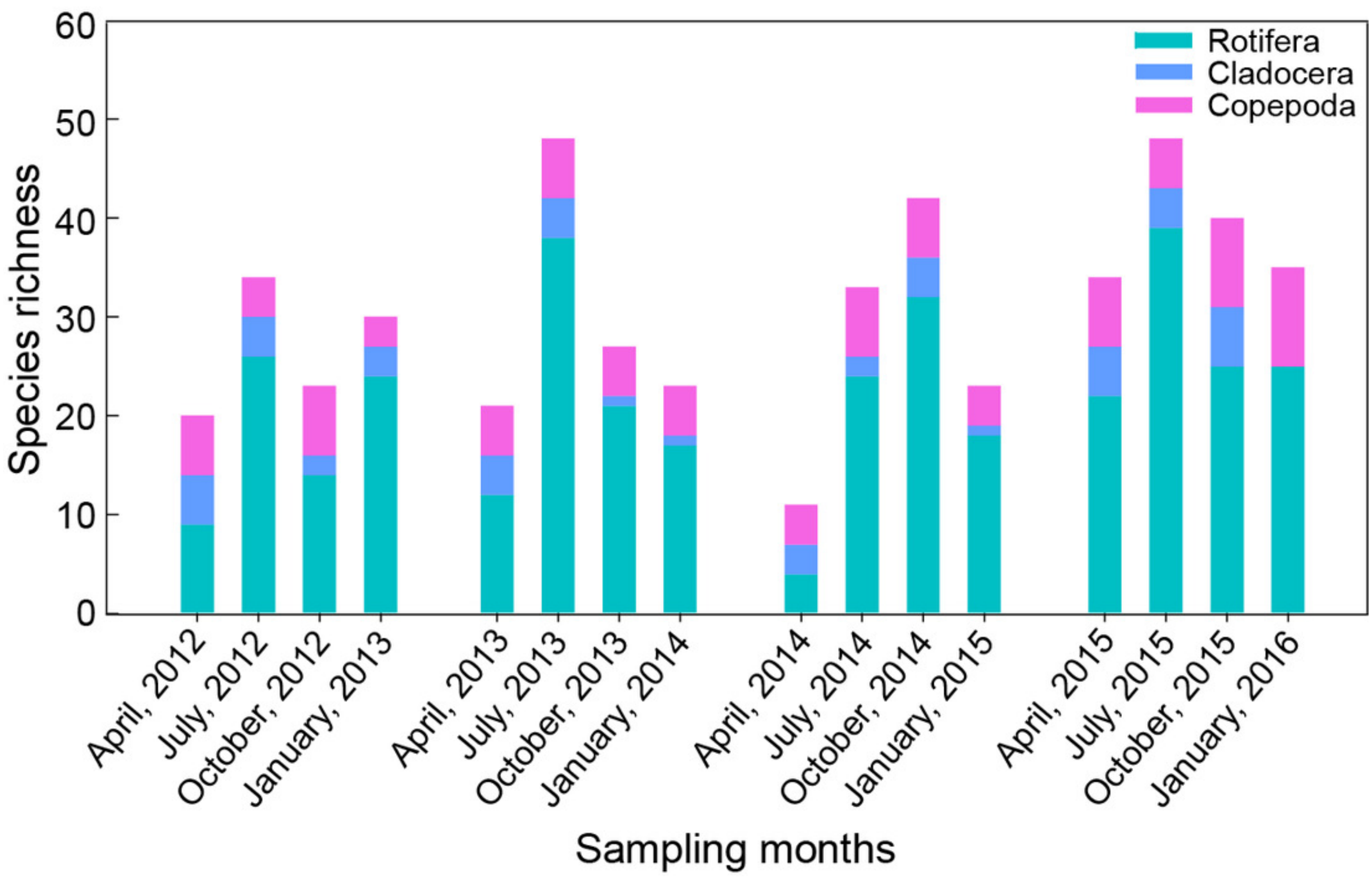

Figure 3

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

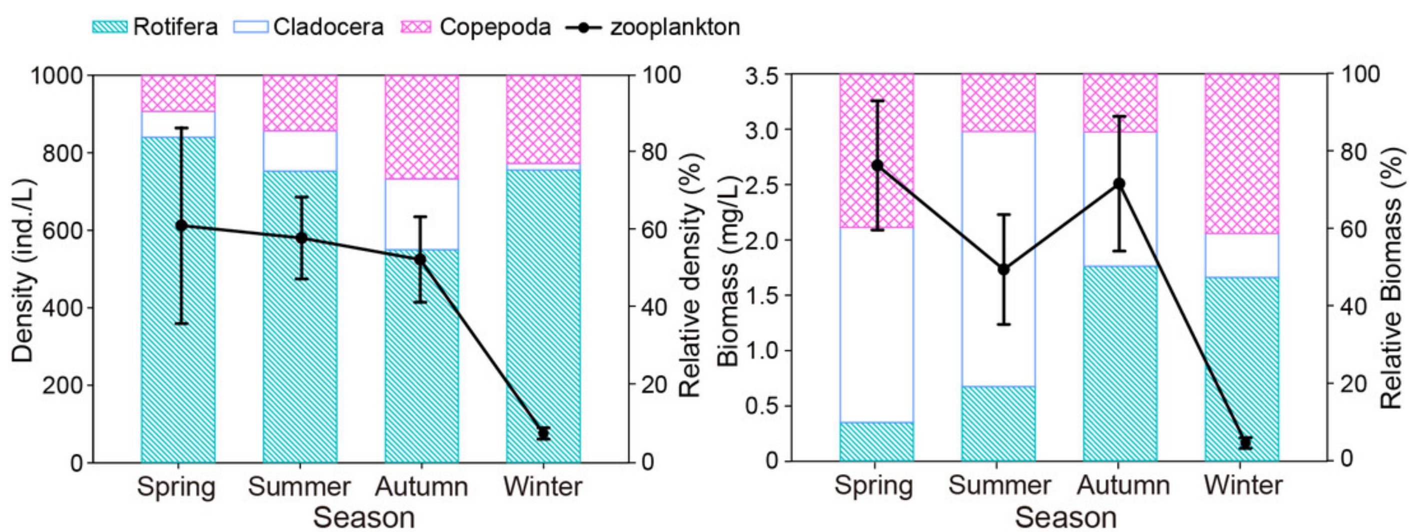

Figure 4

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

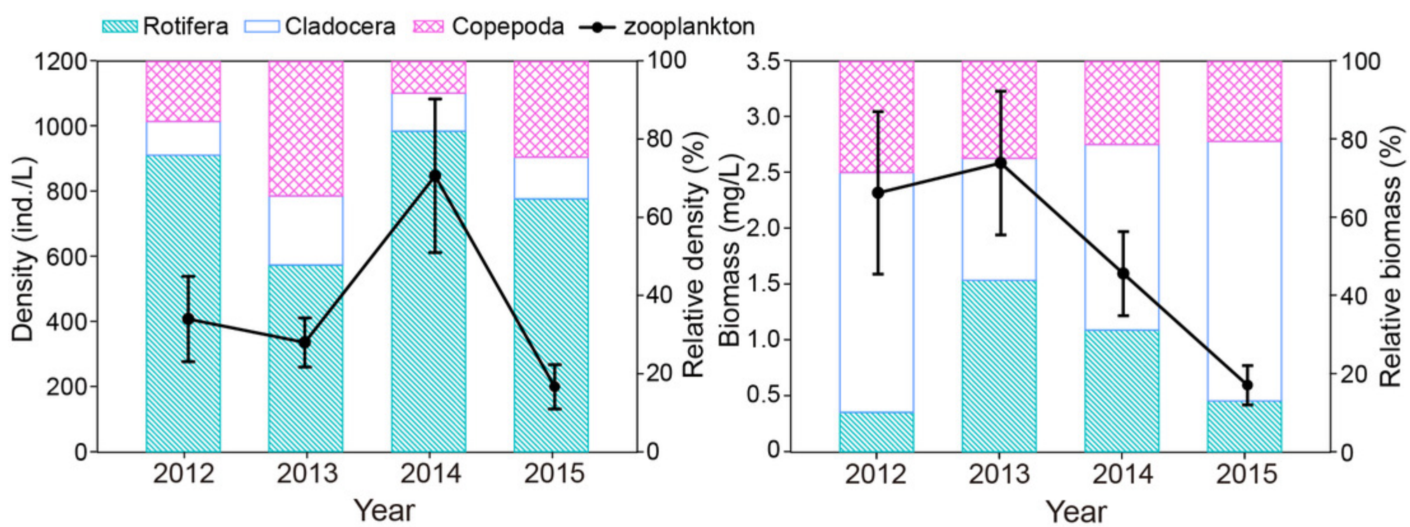

Figure 5

Seasonal variation in H' (Shannon–Weiner index), D (Margalef index) and J' (Pielou's index) in Shahu Lake during 2012–2015

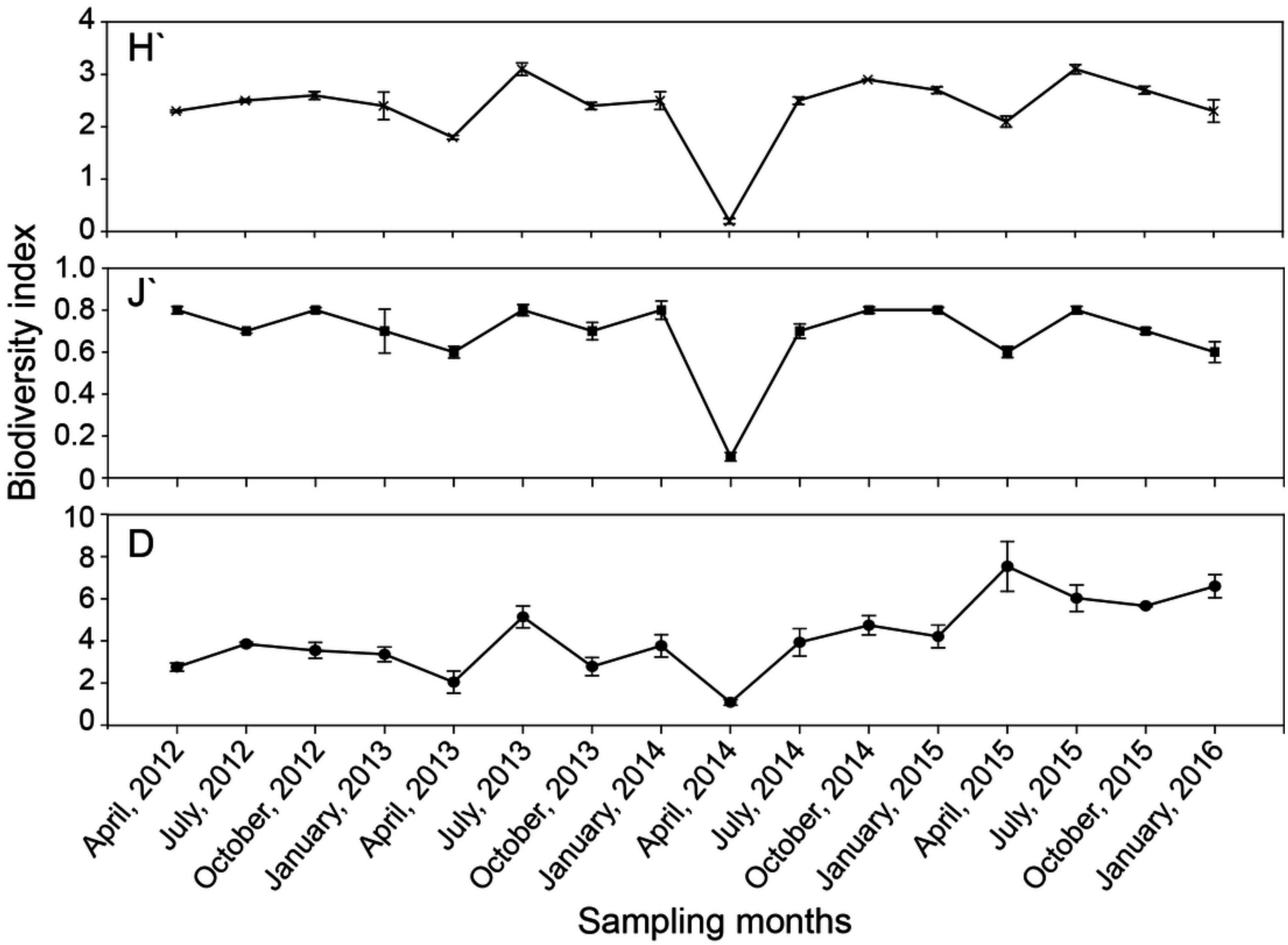

Figure 6

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

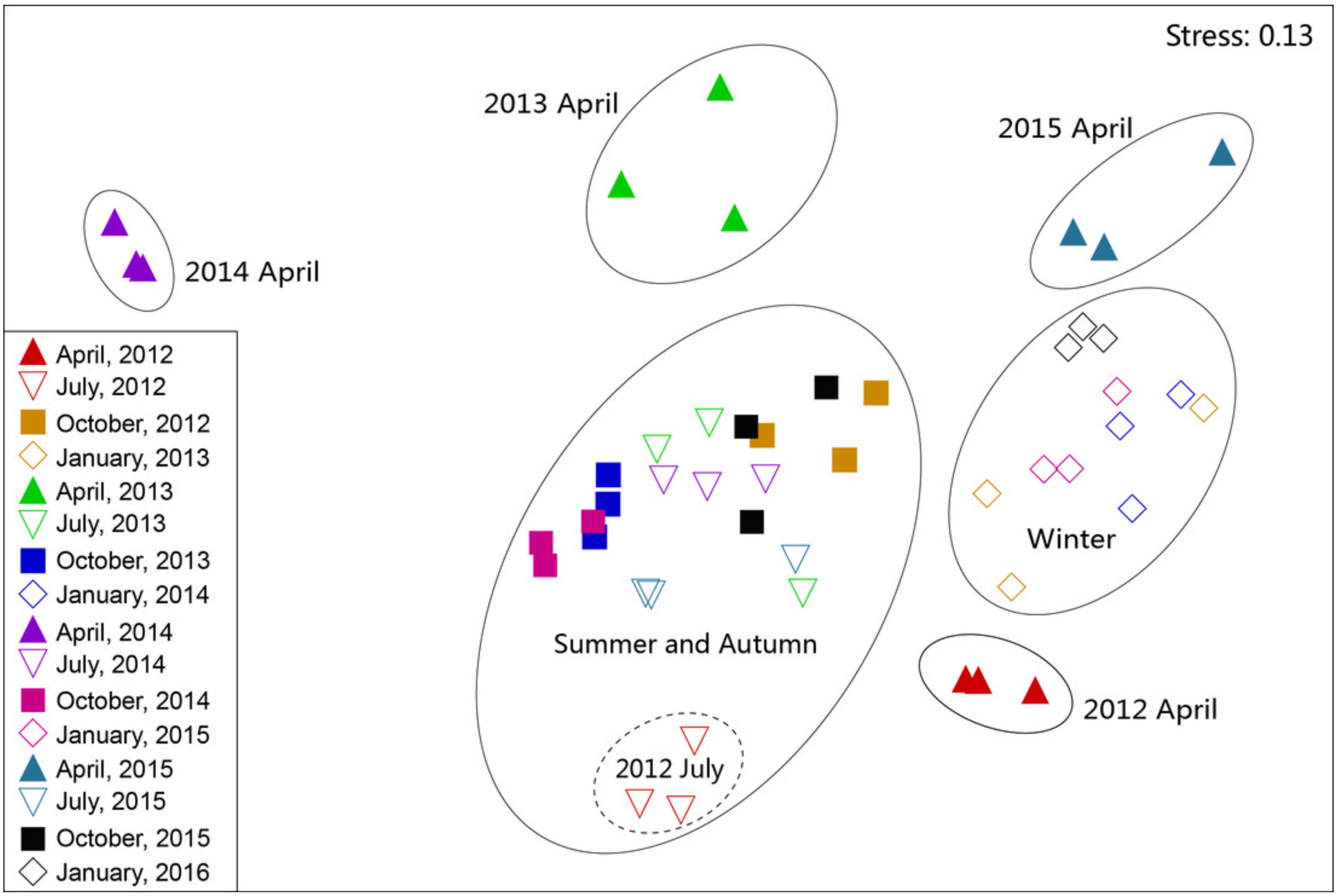

Figure 7

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

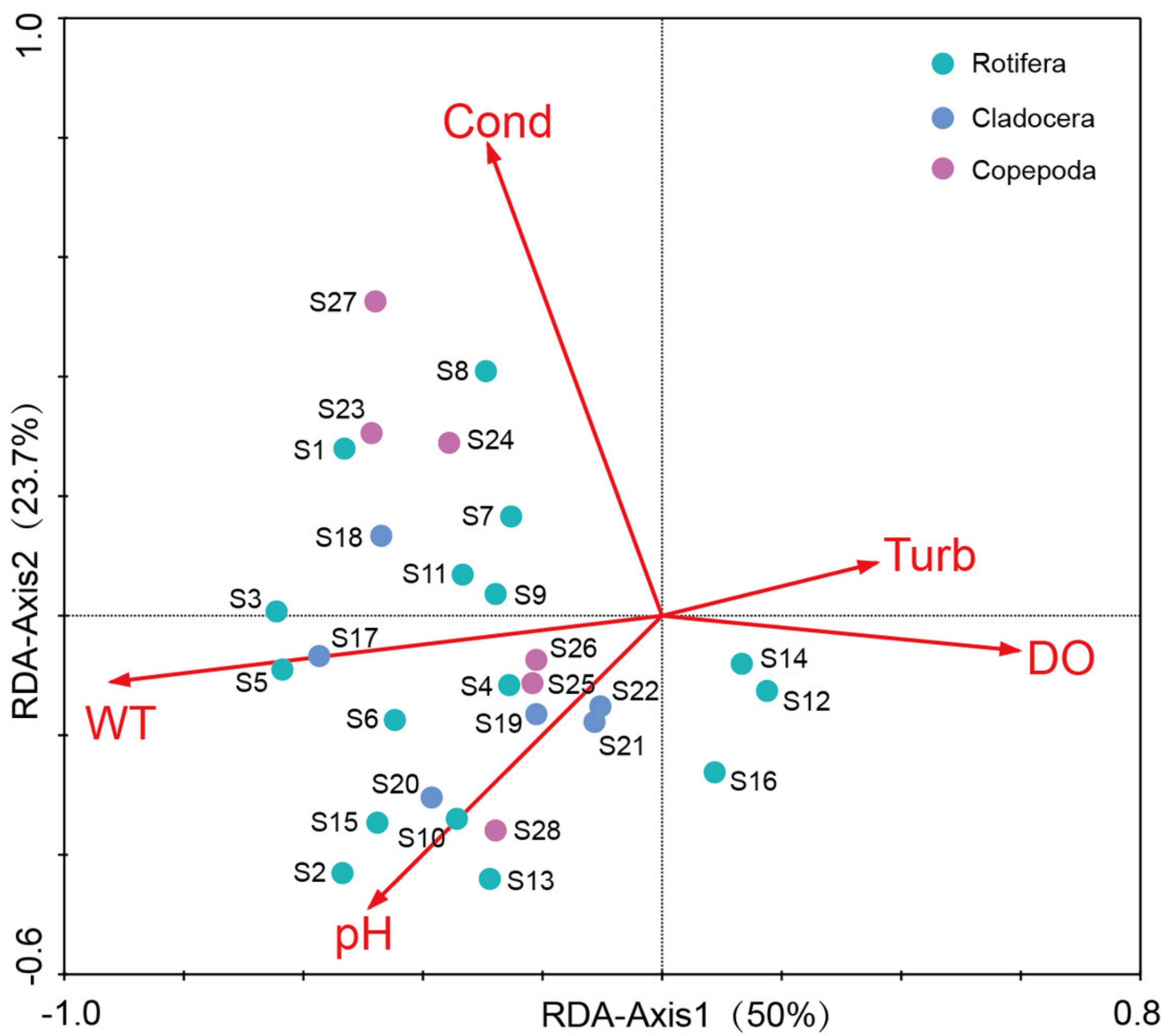

Table 1(on next page)

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.

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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