

Changes And Drivers of Zooplankton Diversity Patterns In The Yangtze River Floodplain Lakes, China

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Abstract

Anthropogenic habitat alteration interfere the natural aquatic habitats and the system's hydrodynamics in the Yangtze River floodplain lakes, resulting in a serious decline in freshwater biodiversity. Zooplankton communities possess major position in freshwater ecosystems, which play essential parts in maintaining biological balance of freshwater habitats. Knowledge of processes and mechanisms for affecting variations in density, biomass and diversity of zooplankton are important for maintaining biological balance of freshwater ecosystems. Here, we analyzed that the temporal and spatial changes in the structure of zooplankton community and their temporal and spatial variations respond to changes in environmental factors in the Yangtze River floodplain lakes. The results showed that zooplankton samples were classified into 128 species, and rotifera was the most common taxa. Significant seasonal and spatial differences were found among the density, biomass and diversity of zooplankton. Similarly, we also found significant seasonal and spatial differences among the biomass of zooplankton functional groups. The spatial turnover component was the main contributor to the beta diversity pattern, which indicated that study areas should establish habitat restoration areas to restore regional biodiversity. The NMDS plot showed that structure of zooplankton community exhibited significant seasonal changes, where the community structure was significantly correlated with pH, water temperature, water depth, salinity, total nitrogen, chlorophyll-a and total phosphorus based on RDA. This study highlights that it is very important to ensure the floodplain ecosystem's original state of functionality for maintaining the regional diversity of the ecosystem as a whole.

Introduction

Freshwater ecosystems in the past few decades are heavily affected by anthropogenic disturbances, such as habitat degradation, dam construction, water pollution, species invasion, which have put these natural environments at risk and affected biodiversity (Dudgeon et al. 2006; Agostinho et al. 2009; Azan et al. 2015). For example, in the floodplains, anthropogenic habitat alteration interfere the natural aquatic habitats and the system's hydrodynamics (Agostinho et al. 2004), resulting in a serious decline in freshwater biodiversity (Dudgeon et al. 2006; Dudgeon 2019). To protect freshwater habitat, it is important to know the impact of different stressors on diversity, which provide key information on the temporal variation of diversity and the mechanisms by which ecosystems are altered, especially under intense anthropogenic disturbance (Altshuler et al. 2011; Dudgeon 2019).

Zooplankton plays a major role in freshwater ecosystems, and in the food webs, linking primary producers and consumers (Keister et al. 2012; Varadharajan and Soundarapandian 2013; Waidi et al. 2016; Compte et al. 2016). The functions performed by zooplankton in the freshwater ecosystem are closely related to ecosystem services (Dornelas et al., 2013), which is indispensable for the maintenance of human life. Zooplankton species can test hypotheses about the diversity variation through different spatial scales (Declerck et al. 2011; Melo and Medeiros 2013). Zooplankton are highly diverse and abundant in floodplain lakes, which have different functional traits and their distribution are influenced by environmental filters (Chaparro et al. 2011; Simões et al. 2013; Bozelli et al. 2015). Due to zooplankton

with different niche requirements (Allan 1976; Bozelli 2000; Bonecker et al. 2009), this community is used with investigating the impact of local factors on the community structure of floodplain lakes. Some studies showed the use of zooplankton communities as a useful tool to aid in the establishment of priority areas for conservation (Dodson et al. 2009; Louette et al. 2008; Palmer et al. 2013). Therefore, zooplankton communities possess major position in freshwater ecosystems, which play essential parts in maintaining biological balance of freshwater habitats (Loick-Wilde et al. 2016).

Species interactions are complex in floodplain ecosystems because periodic changes in the environmental characteristics of lakes and flood pulses (Bini et al. 2001; Lansac-Tôha et al. 2009; Górski et al. 2013; Simões et al. 2013). The dry periods can increase species differentiation of zooplankton among areas in response to changes in environmental conditions (Velho et al. 2004; Bozelli et al. 2015), whereas the floods can enhance biological homogenization among areas (Alves et al. 2005; Simões et al. 2013). In floodplain lakes, some studies showed that variation in zooplankton community was strongly related to flood pulse and environmental heterogeneity (Górski et al. 2013; Bozelli et al. 2015). The Yangtze River floodplain is one of the world's largest floodplains, containing about 3% of all freshwater fish species in global (Liu and Wang 2010). The floodplain has numerous shallow lakes connected with the Yangtze River mainstem (Wang and Dou 1998). From the 1950s to the 1970s, extensive lateral hydrological connectivity losses occurred in this area (Wang et al. 2016; Liu et al. 2018). Following the loss of lateral hydrological connectivity, the exploitation of lake resources has increased, and the water quality of most disconnected lakes continues to deteriorate, leading to a serious decline in freshwater biodiversity in this areas (Wang et al. 2016; Liu et al. 2018).

A major objective of ecologists is to define the factors that driver biodiversity, mainly in the case of environmental interference caused by human activities (Butchart et al. 2010; Lindenmayer and Likens 2010; Simoes et al. 2013). This information knows conservation actions, recommendations of environmental monitoring and management to reduce the loss of biodiversity (Butchart et al. 2010), and maximize the use of environmental services through ecosystem maintenance processes (Millennium Ecosystem Assessment 2005; Lindenmayer and Likens 2010; Simoes et al. 2013). Knowledge of processes and mechanisms for affecting variations in density and biomass of zooplankton are important for maintaining biological balance of freshwater ecosystems (Waidi et al. 2016; Compte et al. 2016). Understanding patterns and mechanisms can explain the community structure in various environments. Information on the species diversity of an ecosystem can better understand ecosystem functioning and biodiversity conservation (Magurran 2011; Legendre et al. 2005). Here, environmental parameters, and community composition of zooplankton, density, biomass, species diversity and diversity of functional taxa in the Yangtze River floodplain lakes, were monitored from 2019 to 2020. The aims of this study are as follows: (1) analyze the temporal and spatial zooplankton variations; and (2) evaluate the environmental parameters affecting zooplankton community structure. We hope our study will provide an important reference for the restoration and protection of freshwater ecosystems in the floodplain lakes.

Material And Methods

Study area

The study area (28°22'–29°45'N, 115°47'–116°45'E) are located in the southern bank of the Yangtze River in Jiangxi Province, China. Poyang Lake is connected to the Yangtze River, and Junshan Lake, Shahu Lake and Qinlan Lake are disconnected to the Yangtze River (Jin et al. 2012). It is a complex and highly interconnected river–lake–wetland system (Jin et al. 2012; Li et al. 2019). It is a humid subtropical climate with significant seasonal changes. The largest amount of precipitation is from April to June (Jin et al. 2012; Li et al. 2019). The study area has a higher water level in the summer and a lower water level in the winter. The average annual temperature and precipitation are 16.3–19.5°C and 1,350–2,150 mm, respectively.

Selection of sampling sites in this study considered habitat variation and anthropogenic activities in study area. Samples were collected from seven sampling sections (40 sampling sites; for details see Fig. 1 and Table S1): the middle reach of the Yangtze River (YR; 1–3), the connected river channel of Poyang Lake (TJ; 4–9), the main lake area of Poyang Lake (ML; 10–20), Nanjishan Lake (NJ; 21–25), Junshan Lake (JS; 26–30), Qinglan Lake (QL; 31–35) and Shahu Lake (SH; 36–40).

Sampling methods

Three repeated samples of zooplankton were collected using 25# zooplankton net (64 µm mesh size) in the study areas in April (spring), July (summer) and October (autumn) 2019 and January (winter) 2020. Zooplankton samples for qualitative analysis were collected using 25# zooplankton net and preserved with 4% formaldehyde. A 5 L sampler was used to collect 10 L of mixed surface water samples in six study areas and 25 L of mixed surface water samples in the Yangtze River at approximately 50 cm below the water surface. Zooplankton samples for quantitative analysis were filtered using a 25# zooplankton net and the sample volume was concentrated to 40 mL. The concentrated sample was preserved with 4% formaldehyde. In the laboratory, the concentrated sample was well-stirred for density calculations. To count the number of zooplankton, a 5-mL subsample was observed using a dissecting microscope (Leica S9i) at 10×10 magnification and a microscope (Leica DM500). Biomass of crustaceans was calculated according to the length–weight regression curve, and biomass of rotifers was calculated according to volume to determine their weight (Nakamura et al., 2017). The zooplankton taxonomic levels were mainly based on Zhang and Huang (1991), Wang (1961), Jiang and Du (1979), Institute of Zoology, Chinese Academy of Sciences (1979) and Han and Shu (1995).

Measurement of environmental factors

The environmental factors were measured in study area in April (spring), July (summer) and October (autumn) 2019 and January (winter) 2020. A Multi-Parameter Probe (YSI, USA) was used to measure the dissolved oxygen (DO; mg/L), hydrogen ions (pH), salinity (Sal; mg/L), turbidity (TURB; NTU), and water temperature (T; °C). A chlorophyll meter (HL-168C06, made in China) was used to measure the chlorophyll-a (Chl-a; mg/L). A velocity meter (FP111, Global Water, 0.1 m/s accuracy) was used to measure the water velocity (V; m/s). A digital sonar system (H22px handheld sonar system) was used to measure the water depth (WD; m). Water samples were collected and preserved with concentrated H₂SO₄,

and then refrigerated and transported to the Nanchang University laboratory. Total nitrogen (TN; mg/L) and total phosphorus (TP; mg/L) were analyzed using Ultraviolet Spectrophotometry (Wei et al. 1989; Huang et al. 1999).

Data analysis

Description and classification of zooplankton functional group was according to (Brandl 2005; Barnett et al. 2007; Sun et al. 2010; Benedetti et al. 2015; Shi et al. 2015; Wen et al. 2017; Ma et al. 2019). The zooplankton community was classified into eight functional groups: rotifers filter feeders (RF), rotifers carnivora (RC), small copepods and cladocerans filter feeders (SCF), small copepods and cladocerans carnivore (SCC), Middle copepods and cladocerans filter feeders (MCF), Middle copepods and cladocerans carnivore (MCC), Large copepods and cladocerans filter feeders (LCF), Large copepods and cladocerans carnivore (LCC).

To analyze the species diversity and richness of zooplankton in each sampling section, four biodiversity indices (Shannon-Wiener index: H' ; Simpson index: G ; Pielou evenness index: J' ; Margalef index: R) were assessed (Peet, 1974; Magurran, 1988). To analyze the difference in species composition between different communities, we used the beta diversity decomposition method (BAS frameworks; Baselga, 2010; Carvalho et al., 2012) based on the Sørensen index (β_{sor}), species spatial turnover (β_{sim}) and nestedness components (β_{sne}).

To explore the potential mechanisms of changes in species diversity, density and biomass, the correlations between the species diversity, density, biomass and environmental factors were analyzed using Mantel tests with 9999 permutations (Legendre and Legendre 2012). Beta diversity analyses and Mantel tests were performed in R 3.2.0 (R Development Core Team 2014) using the BETAPART package (Baselga and Orme 2012) and VEGAN (Oksanen et al. 2015).

One-way analysis of variance (ANOVA) was used to test significant variance (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$) between species diversity, density, biomass and environmental factors among each section and each season. The SPSS 22.0 was used to perform ANOVA tests.

The non-metric multidimensional scaling (NMDS) ordination plots was used to assess the variation in the composition of the zooplankton community among sampling sections. The ordination plots were based on Bray–Curtis index of the zooplankton taxa from sampling sections. The non-metric multidimensional scaling ordination plots and Bray–Curtis index were performed using PRIMER 6 (Clarke and Gorley 2006).

We analyzed the effect of environmental factors on the composition of zooplankton community using redundancy analysis (RDA) (ter Braak and Verdonschot 1995; Lep and Smilauer 2003). To determine whether linear or unimodal ordination, we performed a detrended correspondence analysis (DCA) for the composition of zooplankton community (Lep and Smilauer 2003). Monte Carlo permutation tests with 999 permutations were used to test significant variance ($p < 0.05$) of the RDA gradient (ter Braak and Verdonschot 1995). The environmental factors and the composition of zooplankton community were $\log_{10}(X + 1)$ transformed to meet assumptions of multivariate normality and moderate the influence of

extreme data (Borcard et al. 2011). Redundancy analysis was performed CANOCO Version 4.5 (ter Braak and Verdonschot 1995).

Results

Composition of zooplankton species

Zooplankton samples from the Yangtze River floodplain lakes were classified into 128 species, 61 genus and 26 families. Rotifera was the most common taxa, accounting for 68.8% (88) in the total number of species (Fig. 2). Significant seasonal differences were detected among the number of zooplankton species (ANOVA, $p < 0.05$), but no significant spatial differences (ANOVA, $p > 0.05$). The number of zooplankton in summer (104) was greater than it was in other seasons (Fig. 2a). The ML had the highest number of species, followed by the TJ, and the number of species in YR was the lowest (Fig. 2b). The dominating zooplankton groups had significant spatial variation (ANOVA, $p < 0.05$). The number of dominant groups in ML was the highest, followed by the TJ, and the number of species in YR was the lowest (Fig. 2).

Quantitative assessment of zooplankton

The mean density and biomass of zooplankton in the Yangtze River floodplain lakes were 221.1 ind/L and 1.14 mg/L, respectively. Significant seasonal and spatial differences were found among the density and biomass of zooplankton (ANOVA, $p < 0.05$). The density and biomass in summer and autumn was higher than those in other seasons (Fig. 3a). The density in NJ and SH was higher than those in other sampling sections (Fig. 3b), and the biomass in JS and NJ was higher (Fig. 3b). Similarly, we found significant seasonal and spatial differences among the density and biomass of taxonomic groups (ANOVA, $p < 0.05$). The density of rotifera in the seasonal and spatial changes was higher than those in other taxa (Fig. 4a and Fig. 4b). The biomass of cladocerans in spring and JS was higher than those in other taxa (Fig. 4c). The biomass of rotifera in summer, and ML and NJ was higher than those in other taxa (Fig. 4c and Fig. 4d). The biomass of copepods in autumn and winter, and YR, TJ, QL and SH was higher than those in other taxa (Fig. 4c and Fig. 4d).

Composition and biomass of zooplankton functional groups

Significant seasonal and spatial differences were found among the species number of zooplankton functional groups (ANOVA, $p < 0.05$). The number of RF species was the highest, followed by MCF and SCF, and the number of species in LCC and LCF was the lowest (Fig. 5a and Fig. 5b). Similarly, significant seasonal and spatial differences were found among the biomass of zooplankton functional groups (ANOVA, $p < 0.05$). In the seasonal changes, the biomass of MCF in spring, autumn and winter and RC in summer were higher than those in other functional groups (Fig. 5c and Fig. 5d). In the spatial changes, the biomass of MCF in YR, TJ, JS and QL and RC in ML and NJ were higher than those in other functional groups (Fig. 5c and Fig. 5d).

Diversity patterns of zooplankton

Significant seasonal and spatial differences were found among the diversity of zooplankton (ANOVA, $p < 0.05$). The highest abundance and diversity was found in summer, followed by autumn, and the abundance and diversity in winter was the lowest (Fig. 6). In the spatial changes, the highest abundance and diversity was found in TJ, followed by ML and QL, and the abundance and diversity in YR was the lowest (Fig. 6).

The composition dissimilarity of zooplankton had a lower value of 0.39. In the seasonal changes, the composition dissimilarity in autumn (0.44) was higher than it was in other seasons (Fig. 7a). In the spatial changes, the highest composition dissimilarity was found in JS (0.19), followed by YR (0.18), and the composition dissimilarity in TJ (0.16) was the lowest (Fig. 7b). In the composition dissimilarity changes of taxonomic groups, the highest composition dissimilarity were found in cladocerans (0.44), followed by rotifers (0.39), and the composition dissimilarity in copepods (0.33) was the lowest (Fig. 7c). The spatial turnover component was greater than the nestedness component in each season, each section and each taxonomic group (Fig. 7). In the composition dissimilarity changes of functional groups, the highest composition dissimilarity were found in LCF (0.56), followed by SCF (0.53), and the composition dissimilarity in RC (0.15) was the lowest (Fig. 7d). The spatial turnover component was greater than the nestedness component in RF, SCF and MCF, but the nestedness component in MCC was the mainly contributor to the beta diversity (Fig. 7d). In addition, the β_{sim} was zero in RC, SCC, LCF and LCC, which indicates that the nestedness component was the entire contributor to the beta diversity among them (Fig. 7d).

Temporal and spatial variation in zooplankton community

The NMDS plot showed that structure of zooplankton community exhibited significant seasonal changes. In spring, YR and JR formed one cluster, respectively, and structure of zooplankton community in other sampling sections was similar (Fig. 8 and Fig. S1). In summer, YR and NJ formed one cluster, respectively, and structure of zooplankton community in other sampling sections was similar (Fig. 8 and Fig. S1). In autumn, YR and SH formed one cluster, respectively, and structure of zooplankton community in other sampling sections was similar (Fig. 8 and Fig. S1). In winter, JS formed first cluster, SH and QL formed second cluster, and structure of zooplankton community in other sampling sections formed third cluster (Fig. 8 and Fig. S1). The Bray–Curtis similar showed that the structure of zooplankton community in total year from the Yangtze River floodplain lakes was divided into five areas, in which the first area included TJ and ML, the second area included NJ, QL and ML, and YR, JS and SH formed one cluster, respectively (Fig. S2).

Association of the structure of zooplankton community and environmental factors

Redundancy analysis (RDA) showed that value of eigenvalues along the first axis was 0.781, 0.461, 0.395 and 0.412 in spring, summer, autumn and winter, respectively. The cumulative percentage variance of the species–environment relation along the first axis was 78.1%, 46.1%, 39.5 % and 41.2% in spring, summer, autumn and winter, respectively (Table S6). The structure of zooplankton community in spring was significantly associated with chlorophyll-a and total phosphorus (Fig. 9). The structure of zooplankton community in summer showed a significantly correlation with pH, water depth and total nitrogen (Fig. 9).

The structure of zooplankton community in autumn presented a notably relationship with salinity and pH (Fig. 9). Additionally, the structure of zooplankton community in winter had a significantly correlation with pH and water temperature (Fig. 9). In addition, water depth and water velocity was significantly associated with density, biomass and α diversity, and salinity was significantly associated with α diversity and beta diversity of zooplankton, based on the Mantel test ($p < 0.05$; Table 1).

Table 1 Effects of physicochemical parameter on pairwise density, biomass, α diversity and β diversity in the Yangtze River floodplain lakes. Significant results are in bold ($*P < 0.05$; $**P < 0.01$). *B*: biomass; *D*: density; *H*: Shannon-Wiener index; *C*: Simpson index; *J*: Pielou evenness index; *R*: Margalef index; β_{sor} : compositional dissimilarity; β_{sim} : spatial turnover component; β_{sne} : nestedness component. DO: dissolved oxygen (mg/L); pH: hydrogen ions; Sal: salinity (mg/L); TURB: turbidity (NTU); T: water temperature ($^{\circ}$ C); Chl-a: chlorophyll-a (mg/L); V: water velocity (m/s); WD: water depth (m). TN: Total nitrogen (mg/L); TP: total phosphorus (mg/L).

		α diversity					β diversity			
		<i>B</i>	<i>D</i>	<i>H</i>	<i>J</i>	<i>R</i>	<i>C</i>	β_{sor}	β_{sim}	β_{sne}
T	<i>r</i>	0.15	0.01	-0.32	-0.33	-0.36*	-0.24	0.10	0.35	-0.19
	<i>p</i>	0.29	0.42	0.06	0.12	0.04	0.23	0.22	0.19	0.33
TURB	<i>r</i>	-0.30	0.02	-0.24	-0.29	-0.30	-0.18	0.21	0.31	-0.10
	<i>p</i>	0.07	0.40	0.18	0.14	0.11	0.30	0.13	0.21	0.38
Sal	<i>r</i>	0.51	0.41	0.91*	0.79**	0.21	0.96**	0.49*	-0.38	0.55*
	<i>p</i>	0.10	0.11	0.03	0.01	0.19	0.01	0.05	0.09	0.04
DO	<i>r</i>	-0.17	-0.03	-0.18	-0.22	-0.12	-0.13	0.01	0.38*	-0.26*
	<i>p</i>	0.30	0.53	0.17	0.13	0.39	0.47	0.29	0.02	0.02
V	<i>r</i>	0.50*	0.34*	0.58**	0.56*	-0.05	0.59*	-0.03	0.10	-0.02
	<i>p</i>	0.03	0.05	0.01	0.05	0.59	0.05	0.46	0.48	0.53
Chl-a	<i>r</i>	0.19	0.29	0.19	0.10	-0.26	0.27	0.31	0.12	0.09
	<i>p</i>	0.23	0.14	0.24	0.28	0.25	0.10	0.15	0.49	0.34
pH	<i>r</i>	0.37	-0.22	0.02	0.11	-0.20	-0.08	-0.02	-0.22	0.14
	<i>p</i>	0.08	0.21	0.55	0.41	0.23	0.57	0.52	0.11	0.28
TP	<i>r</i>	0.23	0.04	-0.13	-0.17	-0.35*	-0.10	0.49	0.04	0.25
	<i>p</i>	0.12	0.46	0.43	0.29	0.03	0.66	0.07	0.45	0.13
TN	<i>r</i>	0.38	-0.22	-0.08	-0.11	-0.21	-0.07	0.40	-0.34	0.47
	<i>p</i>	0.23	0.24	0.58	0.54	0.38	0.74	0.20	0.10	0.15
WD	<i>r</i>	0.49*	0.53*	0.70*	0.64*	-0.03	0.74*	0.08	-0.01	0.05
	<i>p</i>	0.05	0.04	0.05	0.04	0.56	0.03	0.37	0.46	0.34

Discussion

Temporal and spatial variations in zooplankton diversity

The Yangtze River Basin is one of the most human-influenced drainage basins worldwide (Liu and Diamond 2005; Yang et al. 2011; Zhang et al. 2020), and fisheries sustainability and biodiversity conservation in this basin have both faced great challenges during the past 70 years (Wu et al. 2004; Xie et al. 2003; Liu et al. 2019; Zhang et al. 2020). Anthropogenic activities have adversely affected the Yangtze River's aquatic organisms and their habitats with continual socio-economic development (Lu et

al. 2016; Zhang et al. 2017; Zhang et al. 2020). In this study, to determine the temporal and spatial zooplankton variations and association of water quality, the diversity and structure of zooplankton community were analyzed seasonally in the Yangtze River floodplain lakes. The results showed that significant seasonal and spatial differences were found among the diversity and community composition of zooplankton. In addition, this study also showed that environmental factors are important for affecting the structure of zooplankton community.

There was a significant seasonal variation in α diversity and community composition of zooplankton. The species number, density, biomass and α diversity of zooplankton were the highest in summer rather than during the other sampling periods. This may be attributed to the favorable summer temperatures, and phytoplankton was abundant in summer for increasing the number of zooplankton (Qin et al. 2020; Liu et al. 2020). In addition, the floodplain lake habitats became more complex in different seasons due to the presence of different morphological types of aquatic macrophytes (emergent, floating, rooted with floating leaves and submerged; Thomaz et al. 2009; Liu 2016). The diverse aquatic macrophytes could increase not only local, but also regional biodiversity (Lemmens et al. 2013), and played a major role in shaping the zooplankton communities (Bolduc et al. 2016; Nihwatiwa et al. 2017). Beta diversity of zooplankton declined from spring to summer, increased in autumn and decreased in winter with the lowest value. It indicated that zooplankton communities tended to homogenization in summer, which may be attributed to the flooding period increased connectivity and water area of lake habitats in summer, resulting in a decrease of beta diversity of zooplankton in species turnover (Alves et al. 2005; Gonzalez 2009; Simões et al. 2013).

We also found significant spatial variation in α diversity and community composition of zooplankton. The species number, density, biomass and α diversity of zooplankton in ML and TJ were higher than those in other sampling sections, which may be attributed to water area of lake habitats. Some studies also showed that the abundance of crustacean is usually positively correlated with lake area because habitat diversity usually increases with area (Stanley 1992; Hoffmann and Dodson 2005; Gooriah and Chase 2020). The concentrations of nutrients of ML and TJ may be higher than that of the other areas. The higher concentrations of nutrients increased in cladocera and copepoda density with a concurrent (Pace 1986; DeBoer et al. 2015). The species number, density, biomass and α diversity of zooplankton in JS was lower than those in other lakes, which may be related to lower primary productivity and higher predation pressure (Stanley 1992; Leibold 1999; Waide et al. 1999; Dodson et al. 2000). The ratio of macrophytes and phytoplankton is important for maintaining a favourable transparency in lakes (Scheffer, 1998; Zhang et al., 2016). Shallow lakes often exhibit alternative states with transparent water occupied by macrophytes, while turbid water occupied by phytoplankton (Scheffer 1998; Zhang et al. 2016). The diversity of zooplankton may vary with fish in different habitats (Gliwicz and Pijanowska 1989; Achenbach and Lampert 1997). The main fish of enclosure aquaculture in JS were four domestic Chinese carp species, and the pressure on zooplankton was prey by fish increased. The species number, density, biomass and α diversity of zooplankton in YR were the lowest, which may be attributed to the water flow of YR is relatively rapid, and is not good for the growth and survival of zooplankton (Thorp and Mantovani 2005).

Temporal and spatial variations in zooplankton functional groups

Functional traits, consider morphological, physiological, ecological and behavioral characteristics of species, which can determine the response of species to ecosystem processes and environmental characteristics (Violle et al. 2007; Braghin et al. 2018). In addition, functional traits detect processes that drive communities' changes, and evaluate and monitor environmental impacts (Arrieira et al. 2015; Laureto et al. 2015; Braghin et al. 2018; Oliveira et al. 2018). Zooplankton have different functional traits in floodplains, which its distribution is influenced by environmental filters, such as concentration of nutrient and chlorophyll-a, water depth and transparency (Simões et al. 2013; Lansac-Tôha et al. 2009; Chaparro et al. 2011; Bozelli et al. 2015). We found significant temporal and spatial variations in the species number and biomass of zooplankton functional groups. The biomass of RC in ML and NJ were higher than those in other functional groups, which may be attributed to they have abundant macrophyte and higher concentration of nutrient. Some studies showed that zooplankton like habitat in macrophyte beds because they may be affect the ratio of functional groups based on creating microhabitats and altering the top-down and bottom-up interactions (Natalia 2005; Heino 2008; Thomaz and Cunha 2010; Bolduc et al. 2016; Viana et al. 2016). In addition, the biomass of SCF and MCF in YR and TJ were higher than those in other functional groups, which may be attributed to they have the relatively rapid water flow. A higher water flow could reduce the density of rotifers, while crustacean are larger and could adapt to this environmental characteristics (Thorp and Mantovani 2005).

Key environmental factors for driving structure of zooplankton community

The temporal and spatial differences in the structure of zooplankton community may be affected by many environmental factors, such as water temperature, water depth, chlorophyll-a, total phosphorus, total nitrogen and pH in the floodplain lakes (Lacerot et al. 2013; Miron et al. 2014; Okogwu 2009; Du et al. 2014; Wang et al. 2017). The structure of zooplankton community in this study was significantly associated with chlorophyll-a, salinity, total phosphorus, water temperature, water depth, pH and total nitrogen. Water temperature is important environmental factor for affecting structure of zooplankton community (Kagalou et al. 2010; Jiang et al. 2015). For example, Helland et al. (2007) found that water temperature was the key environmental factors for determining structure of zooplankton community in Lake Stechlin of Germany. The increased in concentration of nutrient could promote the growth of phytoplankton, and indirectly affect the structure of zooplankton community based on the effect of top-down interactions from phytoplankton (Wu et al. 2011). In spring and summer, chlorophyll-a and nutrients was the main environmental factors affecting the diversity of zooplankton in this study. Additionally, some studies also showed that zooplankton taxonomic richness was significantly associated with pH (Shurin et al. 2009). Our study showed that pH was negatively affected the structure of zooplankton community.

Linking beta diversity patterns to habitat restoration and its driver factors

Beta diversity can determine the number of habitat restoration areas needed (Margules and Pressey 2000; Wiersma and Urban 2005; Anderson et al. 2006). If the spatial turnover component is the mainly contributor to beta diversity, a larger number of habitat restoration areas would be necessary to restore regional biodiversity (Baiser et al. 2012; Carvalho et al. 2012). On the contrary, the nestedness component is the mainly contributor to beta diversity, habitat restoration areas with a low species richness would be necessary to restore regional biodiversity (Baiser et al. 2012; Carvalho et al. 2012). This study showed that the spatial turnover component in the Yangtze River floodplain lakes was the main contributor to the beta diversity, which indicated that all study areas should establish habitat restoration areas to restore regional biodiversity.

The driver factors of spatial turnover component include habitat loss, geographical isolation, dispersal restrictions, environmental filter and competition (Angeler et al. 2013; Gutierrez-Canovas et al. 2013; Legendre et al. 2015), while nestedness component include selective extinction, selective colonization, passive sampling and habitat nestedness (Baselga 2010; Gonzalez-Oreja et al. 2012; Wang et al. 2012). This study showed that the spatial turnover component in the Yangtze River floodplain lakes was the main contributor to the beta diversity for each taxonomic group, which indicated that habitat loss, geographical isolation, dispersal restrictions, environmental filter and competition may be the main driver factors. For analysis of functional groups, the spatial turnover component was the main contributor to the beta diversity in RF, SCF and MCF, while the nestedness component in MCC was the main contributor. In addition, the nestedness component was the entire contributor to the beta diversity in RC, SCC, LCF and LCC, which indicates that selective extinction may be the main driver factors.

Conclusion

This study proved that the temporal and spatial changes in the structure of zooplankton community and their temporal and spatial variations respond to changes in environmental factors in the Yangtze River floodplain lakes. In addition, variations of habitat characteristics and seasonal change were also the main driver factors for variations of zooplankton communities. These results indicated that zooplankton species was increasingly vulnerable, and they could constitute a useful indicator for monitoring water quality. Additionally, anthropogenic activity posed a great threat to the freshwater ecosystem based on beta diversity pattern. Thus, more attention should be focused on anthropogenic habitat alteration in the Yangtze River floodplain lakes.

Declarations

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Data availability

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Author contribution

LQF, LXJ, OYS and WXP conceived the study. All authors contributed to the study design and data collection. LQF and LXJ analyzed the data. LQF, LXJ, OYS and WXP led the writing of the manuscript.

Ethics approval All necessary permits were obtained for the described field studies from the Yangtze River Fishery Administration of China. The handling of zooplankton was conducted in accordance with the guidelines on the care and use of animals for scientific purposes set by the Institutional Animal Care and Use Committee (IACUC) of Nanchang University, Jiangxi, China.

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Competing interests The authors declare that they have no competing interests.

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Figures

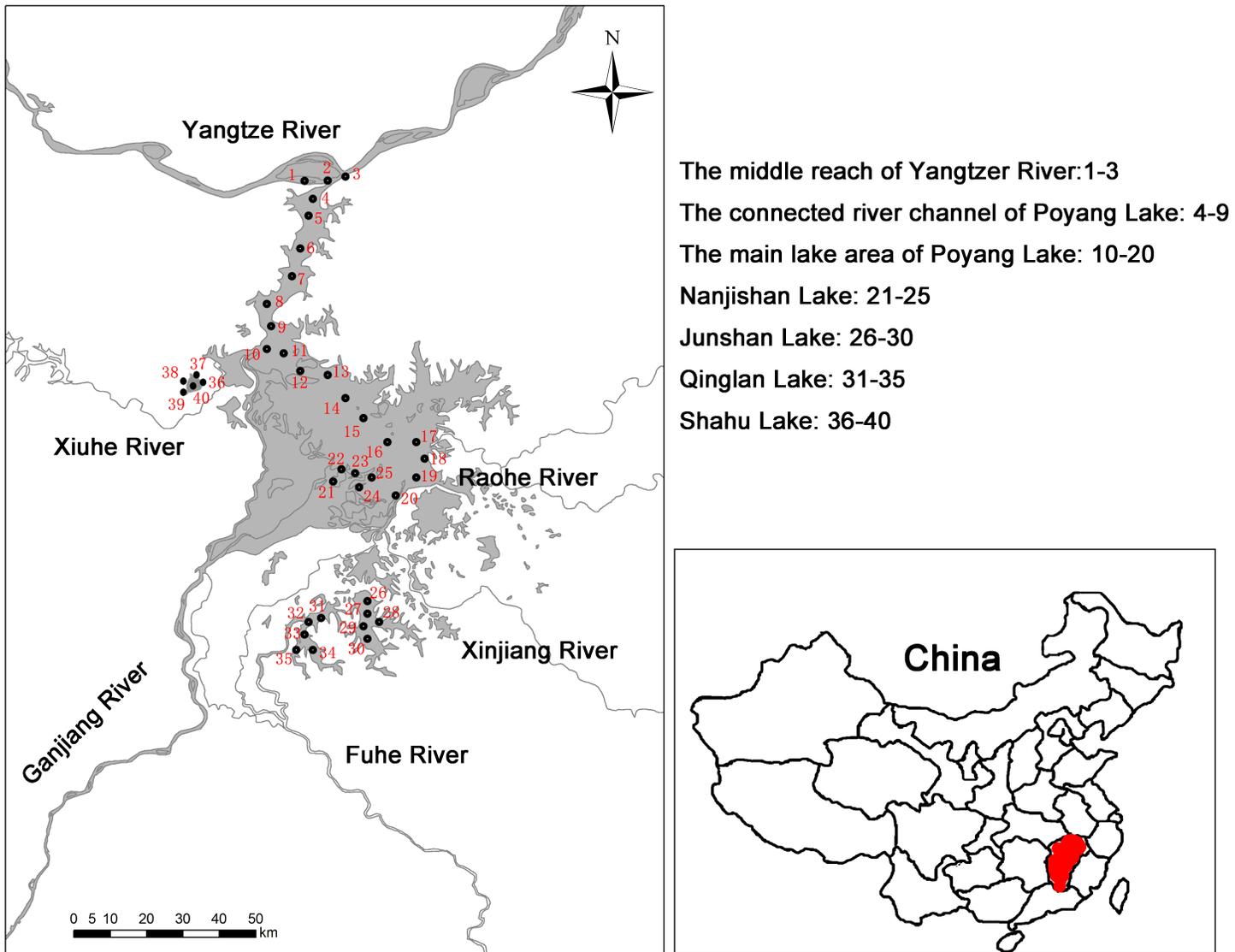


Figure 1

Map of the study area and sampling sites. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research

Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

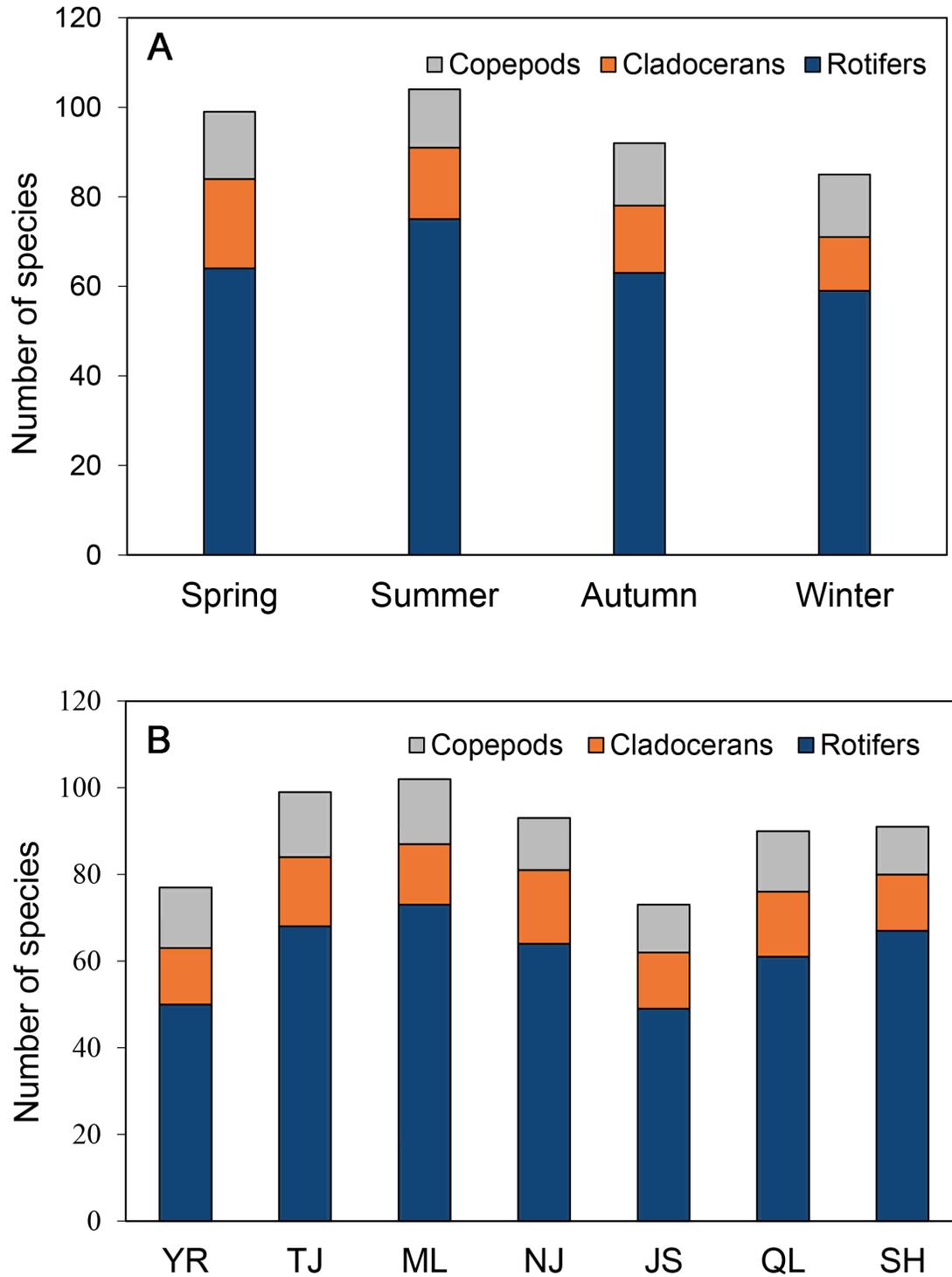


Figure 2

Seasonal (A) and spatial (B) variations in the number of zooplankton species in the Yangtze River floodplain lakes. YR: the middle reach of the Yangtze River; TJ: the connected river channel of Poyang

Lake; ML: the main lake area of Poyang Lake; NJ: Nanjishan Lake; JS: Junshan Lake; QL: Qinglan Lake; SH: Shahu Lake.

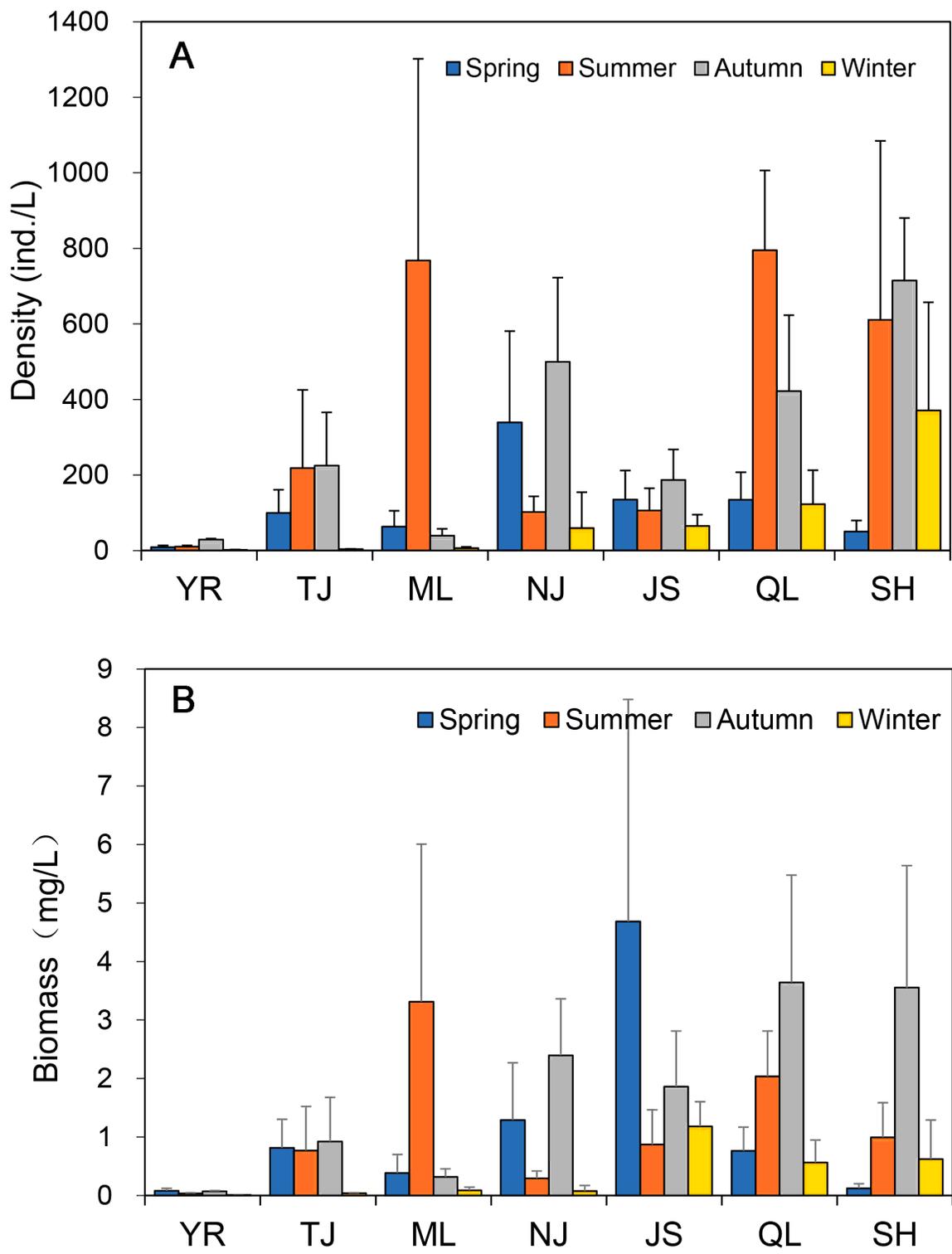


Figure 3

Seasonal variations in the density and biomass of zooplankton in the Yangtze River floodplain lakes. YR: the middle reach of the Yangtze River; TJ: the connected river channel of Poyang Lake; ML: the main lake area of Poyang Lake; NJ: Nanjishan Lake; JS: Junshan Lake; QL: Qinglan Lake; SH: Shahu Lake.

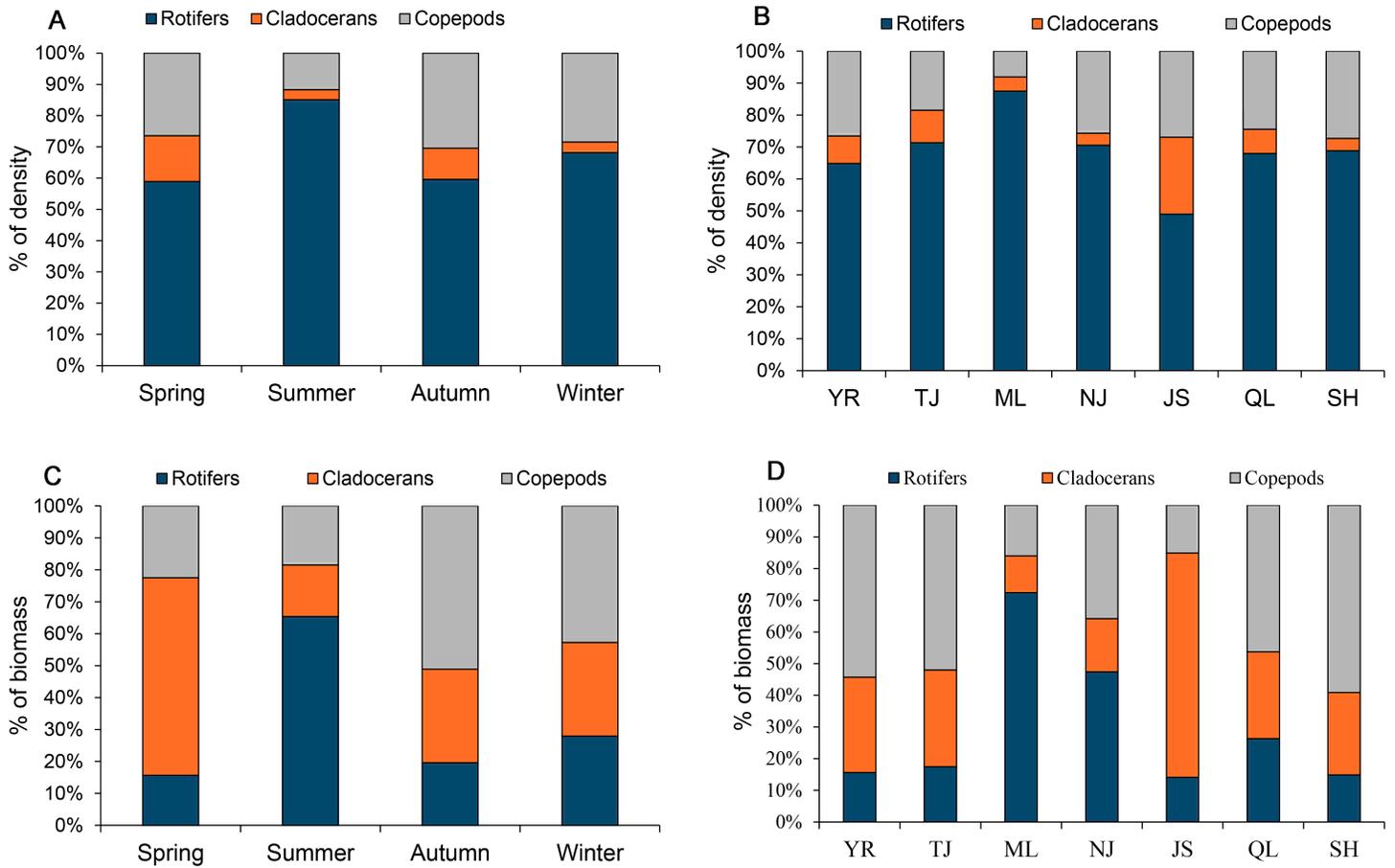


Figure 4

Seasonal (A, C) and spatial (B, D) variations in the density and biomass of zooplankton taxonomic groups in the Yangtze River floodplain lakes. YR: the middle reach of the Yangtze River; TJ: the connected river channel of Poyang Lake; ML: the main lake area of Poyang Lake; NJ: Nanjishan Lake; JS: Junshan Lake; QL: Qinglan Lake; SH: Shahu Lake.

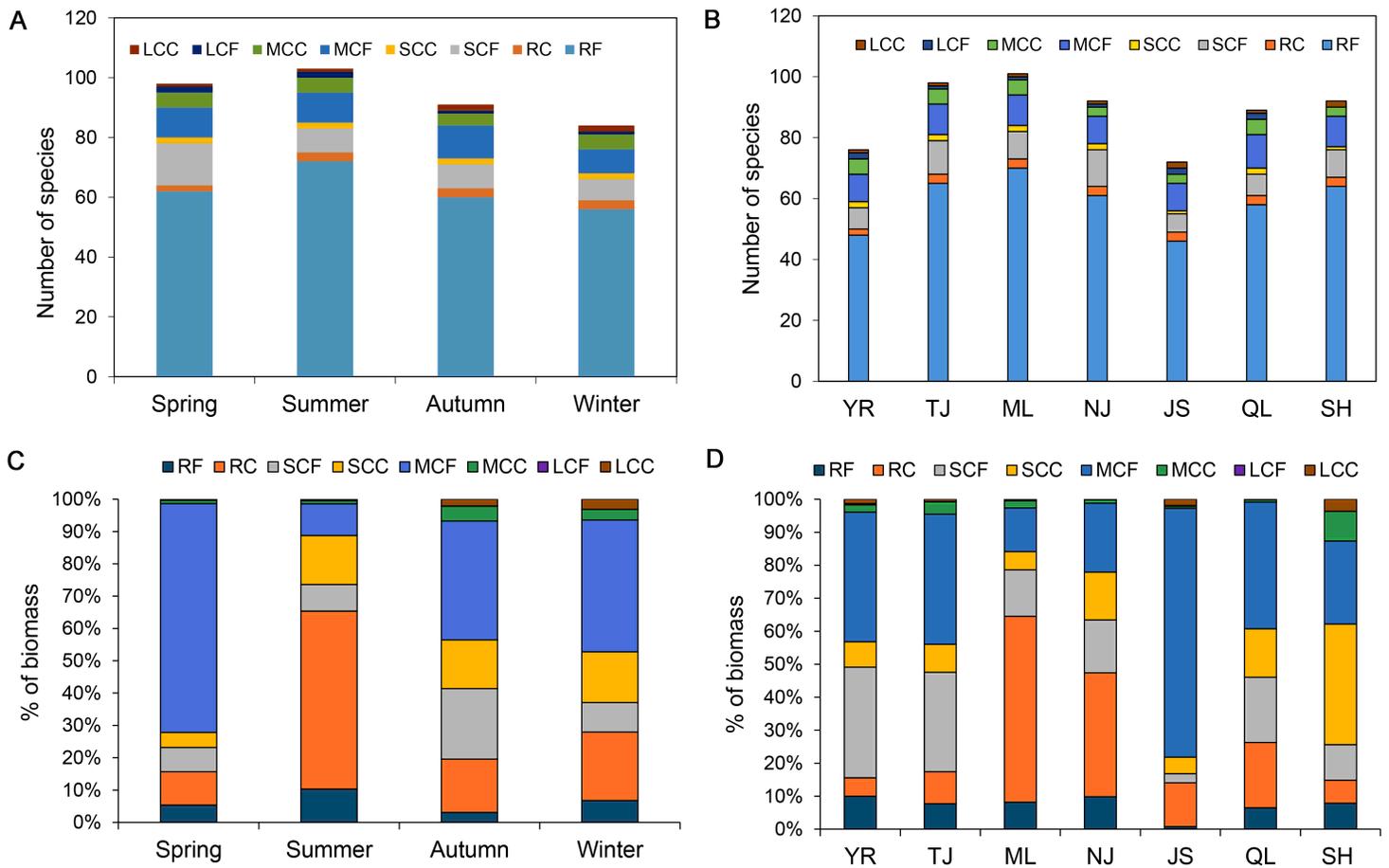


Figure 5

Seasonal (A, C) and spatial (B, D) variations in the density and biomass of zooplankton functional groups in the Yangtze River floodplain lakes. YR: the middle reach of the Yangtze River; TJ: the connected river channel of Poyang Lake; ML: the main lake area of Poyang Lake; NJ: Nanjishan Lake; JS: Junshan Lake; QL: Qinglan Lake; SH: Shahu Lake.

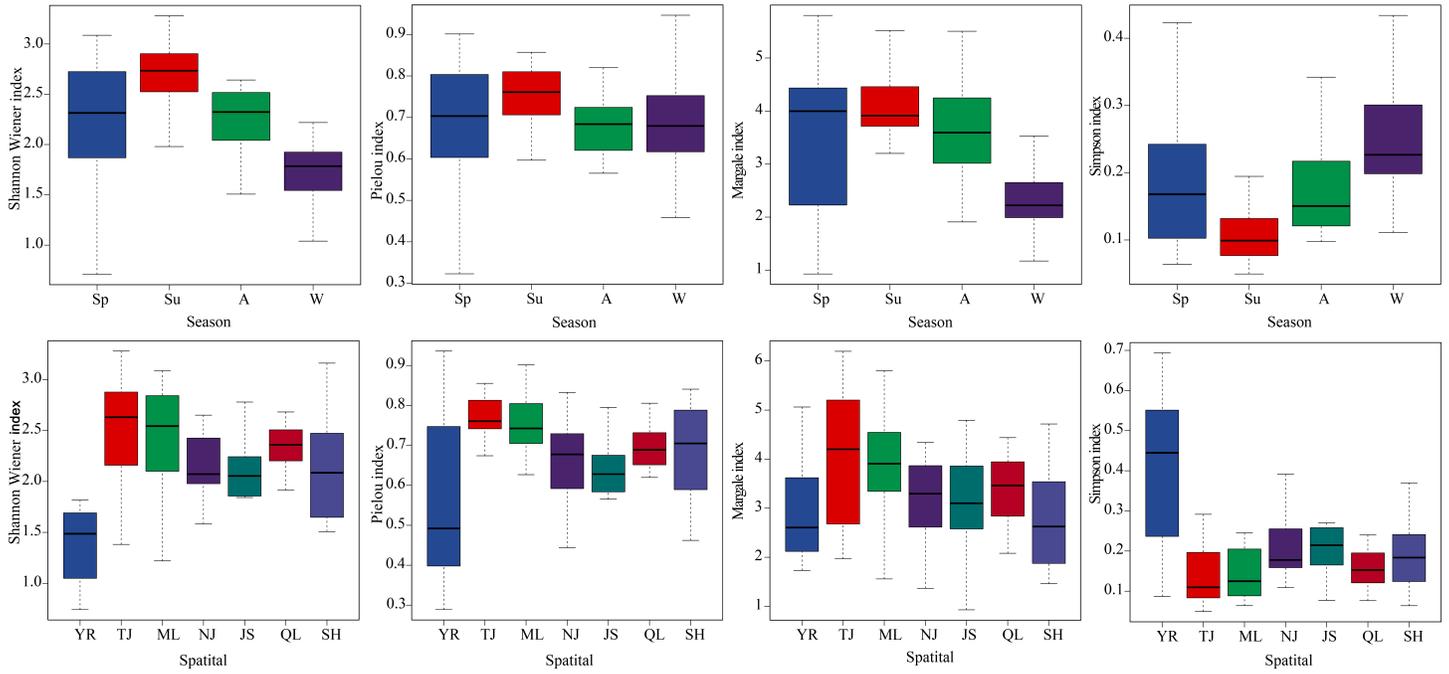


Figure 6

Seasonal and spatial variations in the α diversity of zooplankton in the Yangtze River floodplain lakes. YR: the middle reach of the Yangtze River; TJ: the connected river channel of Poyang Lake; ML: the main lake area of Poyang Lake; NJ: Nanjishan Lake; JS: Junshan Lake; QL: Qinglan Lake; SH: Shahu Lake.

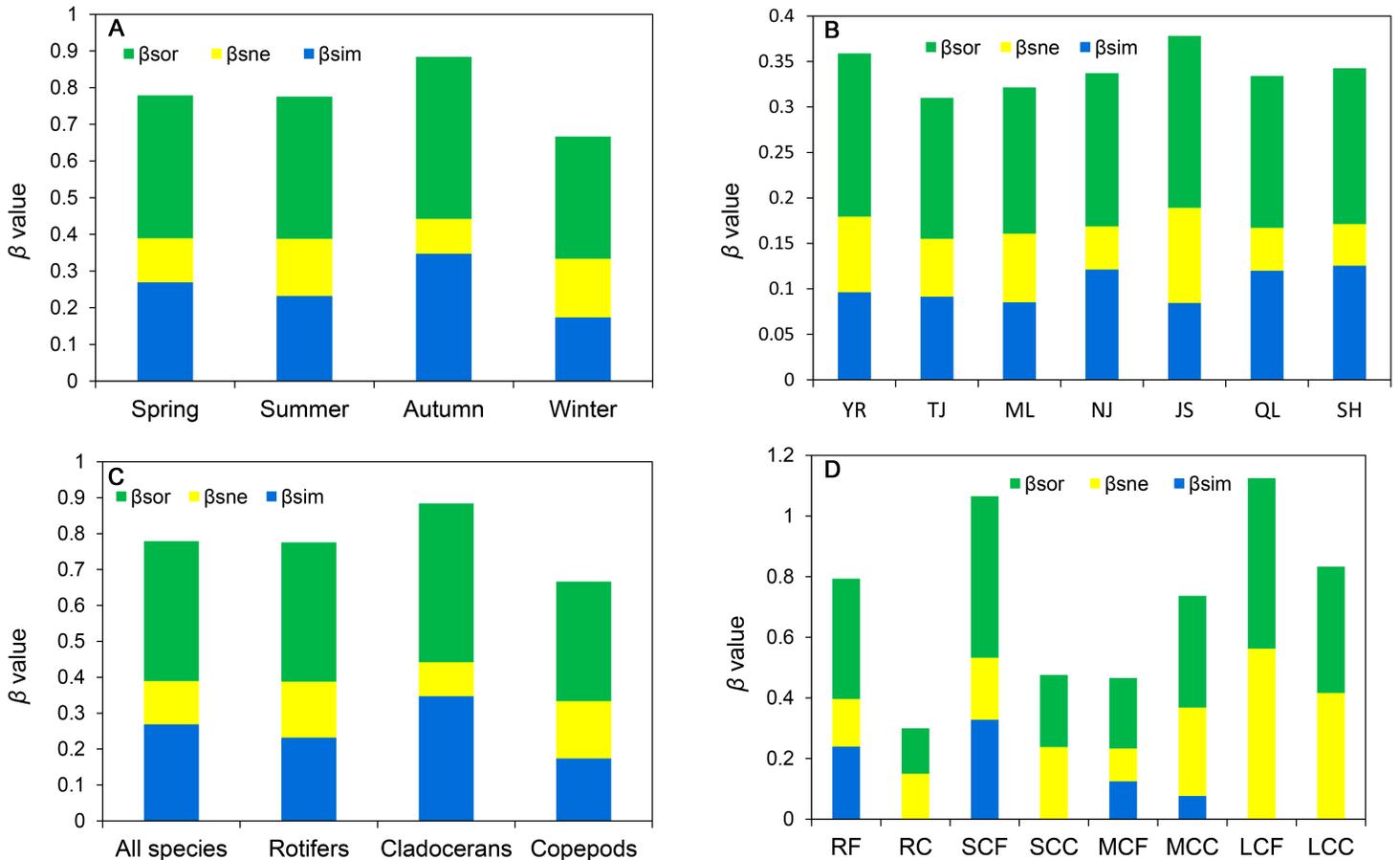


Figure 7

Seasonal (A) and spatial (B) variations in the beta diversity of zooplankton, and the beta diversity of taxonomic (C) and functional groups (D) in the Yangtze River floodplain lakes. YR: the middle reach of the Yangtze River; TJ: the connected river channel of Poyang Lake; ML: the main lake area of Poyang Lake; NJ: Nanjishan Lake; JS: Junshan Lake; QL: Qinglan Lake; SH: Shahu Lake. Sp: spring; Su: summer; A: autumn; W: winter.

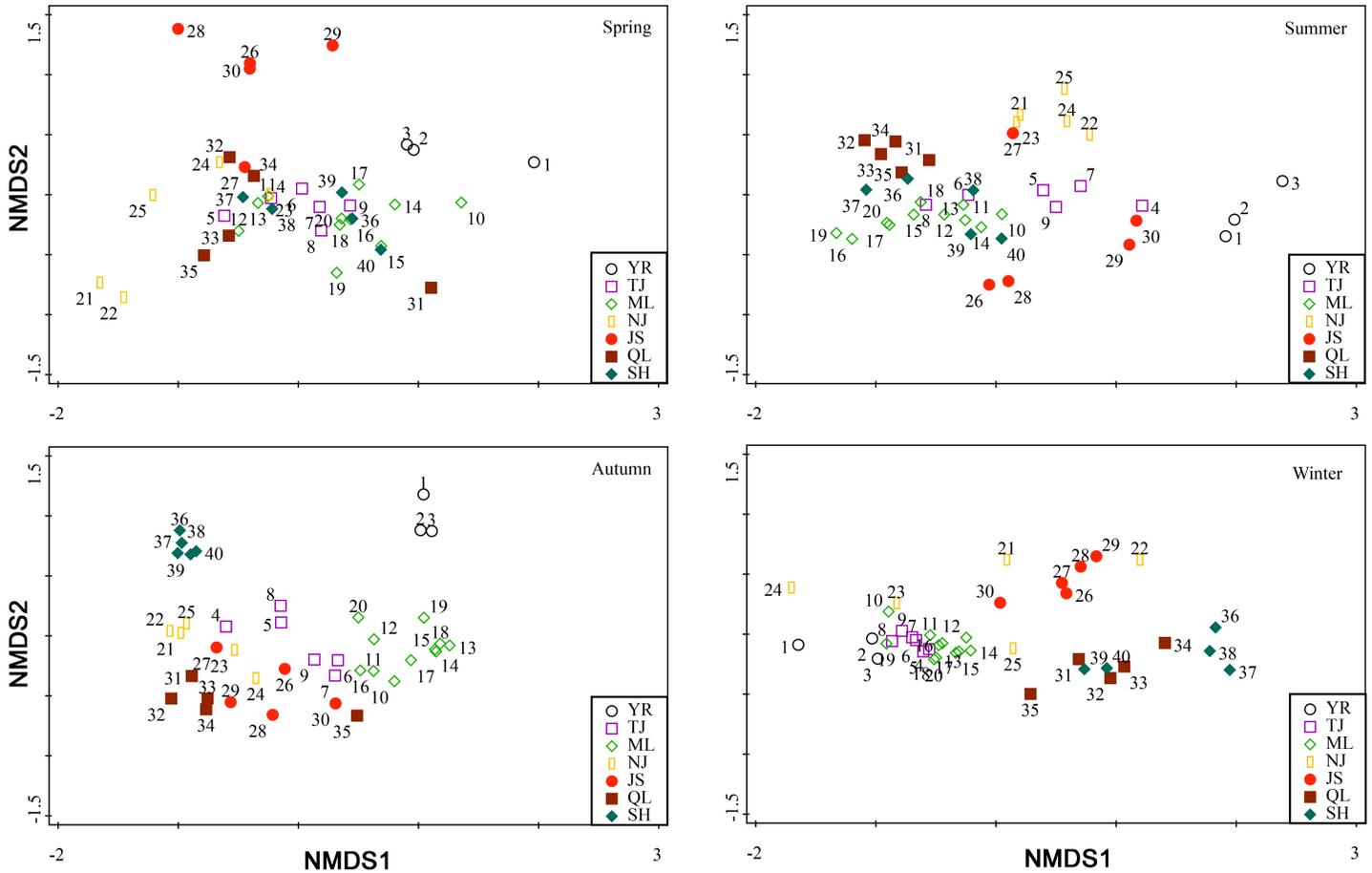


Figure 8

The non-metric multidimensional scaling (NMDS) ordination in the structure zooplankton community in the Yangtze River floodplain lakes. YR: the middle reach of the Yangtze River; TJ: the connected river channel of Poyang Lake; ML: the main lake area of Poyang Lake; NJ: Nanjishan Lake; JS: Junshan Lake; QL: Qinglan Lake; SH: Shahu Lake.

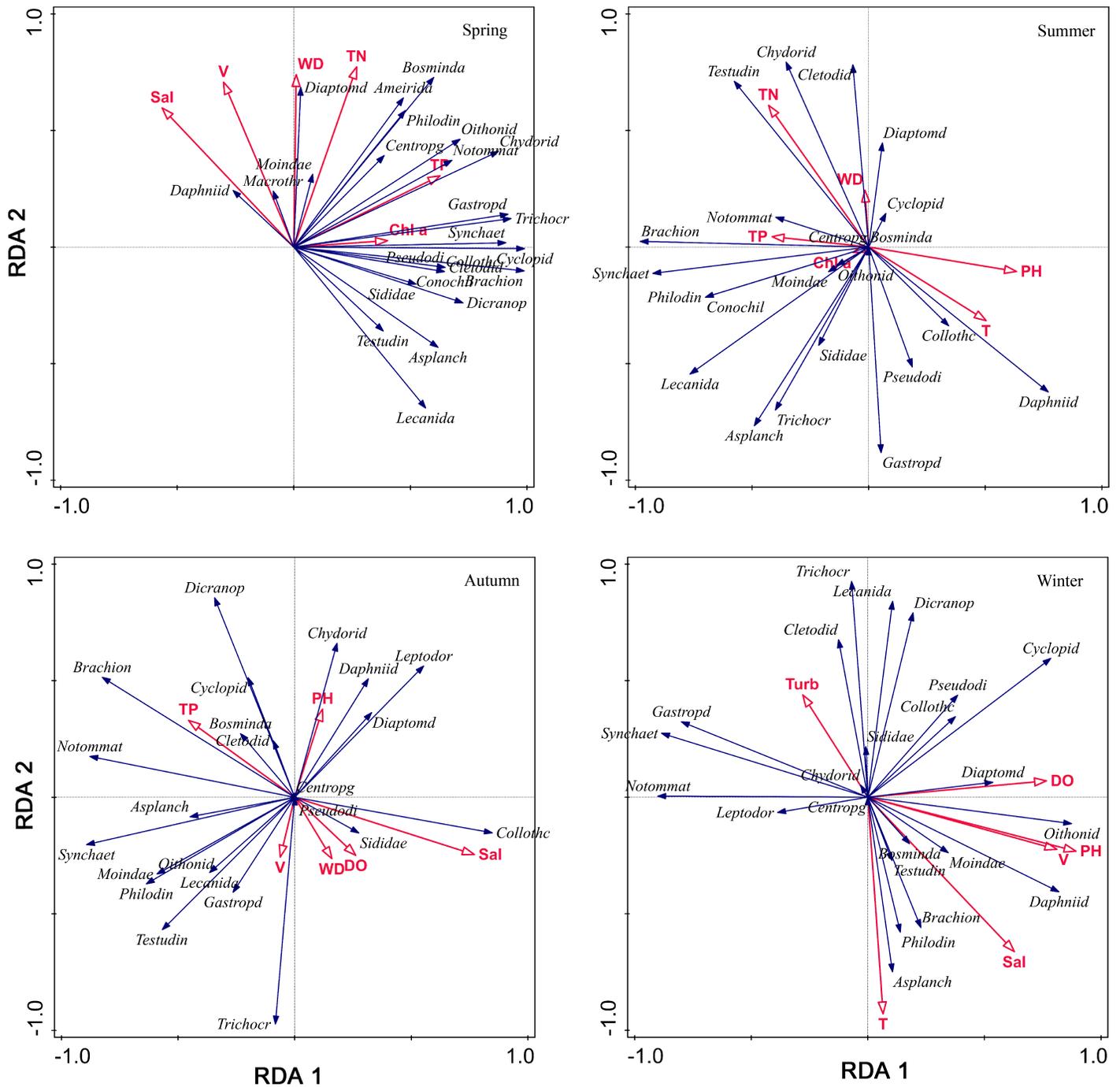


Figure 9

Ordination biplot of major zooplankton species and environmental variables based on Redundancy analysis in the Yangtze River floodplain lakes. DO: dissolved oxygen (mg/L); pH: hydrogen ions; Sal: salinity (mg/L); TURB: turbidity (NTU); T: water temperature (°C); Chl-a: chlorophyll-a (mg/L); V: water velocity (m/s); WD: water depth (m). TN: Total nitrogen (mg/L); TP: total phosphorus (mg/L).

Supplementary Files

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- [TableS1.docx](#)
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