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PRIMARY RESEARCH PAPER

Comparative analysis of rotifer community structure in five subtropical shallow lakes in East China: role of physical and chemical conditions

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Abstract Worldwide, there have been few comparative studies on rotifer communities in subtropical lakes. We studied changes in rotifer community structure over 1 year and its relationship to several physicochemical variables in five subtropical shallow lakes in East China, covering a nutrient gradient from mesotrophy to moderate eutrophy. In these lakes, the genera *Brachionus*, *Lecane*, and *Trichocerca* dominated the rotifer species composition, and *Polyarthra dolichoptera*, *Keratella cochlearis*, *Filinia longiseta*, *T. pusilla*, and *Anuraeopsis fissa* were the dominant species. With increased nutrient loading, total rotifer abundance and species dominance increased, indicating that rotifer abundance might be a more sensitive indicator of trophic state than species composition. Comparative analyses of the six rotifer community indices calculated in this study and redundancy analysis (RDA) revealed that the two slightly eutrophic lakes and the other two moderately eutrophic lakes exhibited a high degree similarity in community structure. This suggests that the trophic state of a lake determines the rotifer community structure. In contrast, in the two moderately eutrophic lakes, the mass ratios of TN:TP and the contents of TP suggested N-limitation and cyanobacteria dominance in phytoplankton communities might be possible. In these lakes TN played a more important role in shaping the rotifer community according to stepwise multiple regression and RDA. RDA analysis also suggested that rotifer species distribution was strongly associated with trophic state and water temperature, with water temperature being the most important factor in determining seasonality.

Keywords Rotifers · Community structure · Dominant species · Physicochemical conditions · Shallow lakes · Redundancy analysis

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Introduction

Studies on changes in zooplankton community structure during seasonal succession in water bodies are of great scientific and practical significance. They can reveal the relationship between zooplankton community structure and the trophic status of a water body (Andronikova, 1993). Numerous studies on zooplankton ecology have focused more on the temporal variation in community structure, but the research on spatial patchiness of the zooplankton has received relatively less attention (Zhou et al., 2009), although the spatial pattern of a community is of crucial importance for understanding ecosystem function (Rosenzweig, 1991; Romare et al., 2003).

As the principal constituents of freshwater zooplankton communities, cladocerans have received most of the attention in aquatic systems, since they are efficient filter feeders and account for a large fraction of zooplankton biomass (Castro et al., 2005). However, rotifers are an important link between pico- and nanoplankton carbon and macrozooplankton, and can be responsible for 25–30% bactivory in freshwater. In contrast, microcrustaceans generally account for less than 1% of this energy flow in some lakes (Wallace et al., 2006). Nevertheless, rotifers probably play more important roles in the energy flow in aquatic systems than cladocerans, especially when the abundance of large cladocerans is low (Sanders et al., 1989; Jeppesen et al., 1990a; Tadonléké et al., 2004; Wallace et al., 2006).

Regulation of the seasonal succession and spatial structure of rotifer assemblages has been attributed to both abiotic factors including temperature, pH, dissolved oxygen, etc., and biotic factors such as food resource, competition, and predation (e.g. Herzig, 1987; Devetter, 1998; Arora & Mehra, 2003; Wallace et al., 2006). Trophic state is regarded as the most important characteristic of aquatic ecosystem (Andronikova, 1993) and has commonly been found to be important in determining the composition of rotifer communities. However, Etilé et al. (2009) has suggested that the role of trophic state in determining the communities of zooplankton including rotifers has not been clearly demonstrated. Among the nutrients related to the trophic state, phosphorus is often a key factor in eutrophication studies as the most common limiting nutrient in freshwater lakes. It is widely reported that total phosphorus (TP) has great effects on rotifer distribution and abundance (Berzins & Pejler, 1989a; Kuczyńska-Kippen & Nagengast, 2006), and rotifer species richness and diversity declined considerably with increasing TP (Jeppesen et al., 2000). However, some other studies found that phosphorus was not a limiting nutrient, rather nitrogenous nutrients (Devetter, 1998; Castro et al., 2005; Wang et al., 2010), transparency (Yang et al., 2009), and chlorophyll-*a* (Chl-*a*) combined with other factors (Contreras et al., 2009) were found to regulate the dynamics of rotifer assemblages. Additionally, water temperature is likely to be a key factor in determining rotifer community structure in subtropical climates because of dramatic seasonal changes. Hence, the question that we asked in this study was whether the effect of phosphorus on rotifer community structure was larger than that of nitrogen, Chl-*a*, or water temperature in subtropical lakes in China?

Rotifer species composition, which varies from lake to lake (May & O'Hare, 2005), can be used as an indicator of lake trophy (e.g. Mäemets, 1983; Berzins & Pejler, 1989a; Duggan et al., 2001a). However, because rotifer species composition can be affected by physical, chemical, and biological factors including the macrophyte covering in lakes (Duggan et al., 2001b, 2002; Green, 2003; Kuczyńska-Kippen, 2001, 2009), and is sensitive to sample size (Macarthur & Wilson, 1967), rotifer abundance may be a more sensitive indicator of trophic state than species composition (May & O'Hare, 2005). This idea can be tested by comparing the rotifer communities in some lakes with similar climate conditions and macrophytes.

Worldwide, relatively less data on rotifer species distribution in subtropical lakes are available (Wallace et al., 2006; Wang et al., 2010), and less attention has been paid to comparative studies on rotifer distribution in Chinese lakes (Wang et al., 2010), and the relationship between rotifer community structure and trophic states of lakes. In this study, a comparative study on rotifer community structure in five lakes in the same region with different trophic states was carried out to: (a) test the hypotheses that trophic state was important in determining rotifer community structure, and rotifer abundance was a more sensitive indicator of trophic state than species composition; (b) assess the contribution of physicochemical variables, especially total nitrogen (TN) and TP, to the indices of rotifer community structure.

Materials and methods

Study sites

The five lakes, including Longwo, Jinghu, Tingtang, Fengming, and Yinhu studied in this paper are all shallow lakes with the average depth of 4.0, 1.3, 2.0, 1.5, and 1.5 m, respectively. They are located near Wuhu city on the south bank of Yangtze River

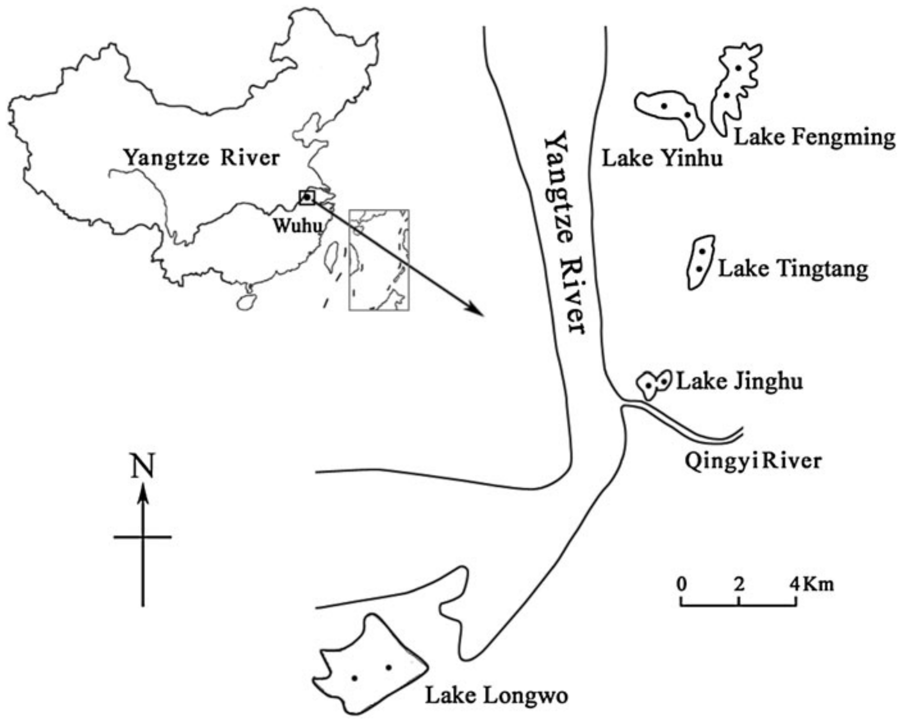

Fig. 1 Sampling locations for rotifers in the five lakes (*solid circle* indicates sampling station in each lake)

(between 119°21′ longitude and 31°20′ latitude) (Fig. 1).

Lake Longwo is located in the south of Wuhu, has a surface area of 337 ha, and has functioned as a reservoir for aquaculture. Lake Jinghu and Lake Tingtang are located in the center of the city, and have a water surface area of 7.9 ha and 13.47 ha, respectively. Both of them are strongly subjected to recreational activities. Lake Yinhu and Lake Fengming are located in the north of Wuhu, and have a surface area of about 23 ha and 40.27 ha, respectively. Both are surrounded by several factories and farmlands. Only in Lake Yinhu among the five lakes, do submerged macrophytes cover most parts of its basin and severe cyanobacteria blooms were observed in the water column in late spring and summer.

Based on the index of trophic state, Lake Jinghu and Lake Tingtang can be characterized as slightly eutrophic, Lake Fengming and Lake Yinhu represent moderately eutrophic lakes, whereas Lake Longwo is considered mesotrophic (Qian et al., 2007).

Rotifer sampling

Sampling was performed from July 2005 to June 2006 at two sites in each lake. Rotifers were collected monthly at approximately the same time (about 0900 to 1200) each day. On each sampling date, more than 20 l water was collected and filtered through a 64-μm net for identification of rotifer species. In addition, 15.0 l water was collected using a 2.5 l modified Van-Dorn sampler at three depths of 0, 0.5, and 1.0 or 1.5 m (if water depth permitted) at each sampling site and mixed. A 1.0 l subsample of this sample was fixed with 5% formalin solution and concentrated to 30 ml after 48 h sedimentation for quantification of rotifers. Rotifers were counted in at least five Sedgewick-Rafter sub-samples. Rotifer densities were determined for discrete species, and species identification was carried out on living materials according to Koste (1978).

Environmental analysis

Surface water temperature was measured using a mercury thermometer, and pH was recorded with a HI-8424 acidometer (Hanna, Italy) once a month. Water transparency was determined and average depth was estimated using secchi-disk. A 1.0 l water sample of the 15.0 l pooled samples was filtered through Whatman GF/C glass-fiber filters (1.2 μm pore size), and Chl-*a* content was spectrophotometrically measured after extracting the filters overnight at dark using 90% acetone and calculated without correcting for phaeopigments (Huang, 1999). TN, TP, and dissolved oxygen (DO) contents were measured once bimonthly according to Huang (1999).

Data analyses

Shannon–Wiener index (H') and evenness index (E) calculated using the formulas $H' = -P_i \Sigma \log_2 P_i$ and $E = H/H_{\max}$, where P_i means density percentage of the ith species (Arora & Mehra, 2003), were both used to estimate the changes in biodiversity. The dominance grade was calculated as $K = N_{\max}/N$, where $N_{\max}$ and N indicate the abundance of the first dominant species and the total rotifers in a community, respectively (Qian et al., 2007). One-way ANOVA and LSD test were conducted to detect the significant differences in environmental parameters and the indices of rotifer community among lakes.

Pearson correlation was carried out between species number (R), H', E, abundance of total rotifers (N_t), dominant species abundance (N_d), as well as K and the environmental variables including water temperature (Wt), Chl-*a*, TN, TP, DO, transparency, as well as pH value of the water with SPSS 11.5 software. To examine the factors that may determine rotifer community structure in the lakes, linear regression analyses were performed between each of seven environmental variables recorded for each lake and H', R, E, K, N_d, as well as N_t with SPSS 11.5 software. Multiple regression analyses were performed to compensate for covariance, using the forward stepwise selection procedure to select those variables with a significant F-value that significantly increase the regression of sum of the squares.

The relationships between the rotifer data matrix and the environmental variables were computed using canonical correspondence analysis (CCA; ter Braak, 1986) with CANOCO 4.5 (SCIENTIA Software) for detecting important physicochemical variables associated with underlying trends. CCA was performed on the rotifer species whose abundance >0.1% of the total numbers being taken into account to eliminate rarest taxa which provide little or no information for the community structure, when their spatial–temporal variations are considered in the analysis (Etilé et al., 2009). Species composition data was $\log(x + 1)$ transformed and environmental variables were standardized. Species data was analyzed by means of detrended correspondence analysis (DCA) (Hill & Gauch, 1980) to determine the length of the gradient. DCA revealed that the gradient (2.9) was less than 3 standard deviation units in the regional study; therefore, unimodal ordination techniques would be more appropriate (ter Braak & Smilauer, 2002). Hence, redundancy analysis (RDA) was used to relate rotifer assemblage structure to all predictor environmental variables and to explore the relationships among and between species and the environment (ter Braak & Verdonschot, 1995). According to those preliminary CCA and RDA, we identified collinear variables and selected a subset on inspection of variance inflation factors (VIF < 20) (ter Braak & Smilauer, 2002). All the analyses included a forward selection procedure (ter Braak & Verdonschot, 1995) in order to include only significant explanatory variables in the model (Monte Carlo permutation test with 499 permutations, $\alpha = 0.05$). Partial RDA was used to separate and examine the relative importance for the species data of two sets of explanatory variables on the rotifer assemblage (Borcard et al., 1992)

Results

Environmental parameters

All the five lakes showed a relatively wide range in annual average value of the variables related to trophic status, with Chl-*a* ranging from 14.17 to 46.8 μg l^{-1}, TN 0.59–1.63 mg l^{-1}, TP 0.013–0.104 mg l^{-1}, and transparency 0.59–1.95 m (Fig. 2).

Marked differences existed in the annual average values of Chl-*a* concentration, transparency, TN, and TP among the five lakes (one-way ANOVA, $F_{\text{chl-}a\ (4,55)} = 17.65$, $P < 0.001$; $F_{\text{Transparency}\ (4,55)} = 260.81$, $P < 0.001$; $F_{\text{TN}\ (4,25)} = 37.31$, $P < 0.001$; $F_{\text{TP}\ (4,25)} = 60.95$, $P < 0.001$), but non-significant differences in TN, TP, as well as Chl-*a* concentration between Lake Jinghu and Lake Tingtang, and TN and Chl-*a* concentration between Lake Fengming and Lake Yinhu were found (LSD-test, $P > 0.05$) (Fig. 2).

The annual mean transparency of Lake Longwo was higher (approximation 2.0 m) than those of all the other lakes (<1.0 m), while TN, TP, and Chl-*a* concentration in Lake Fengming and Lake

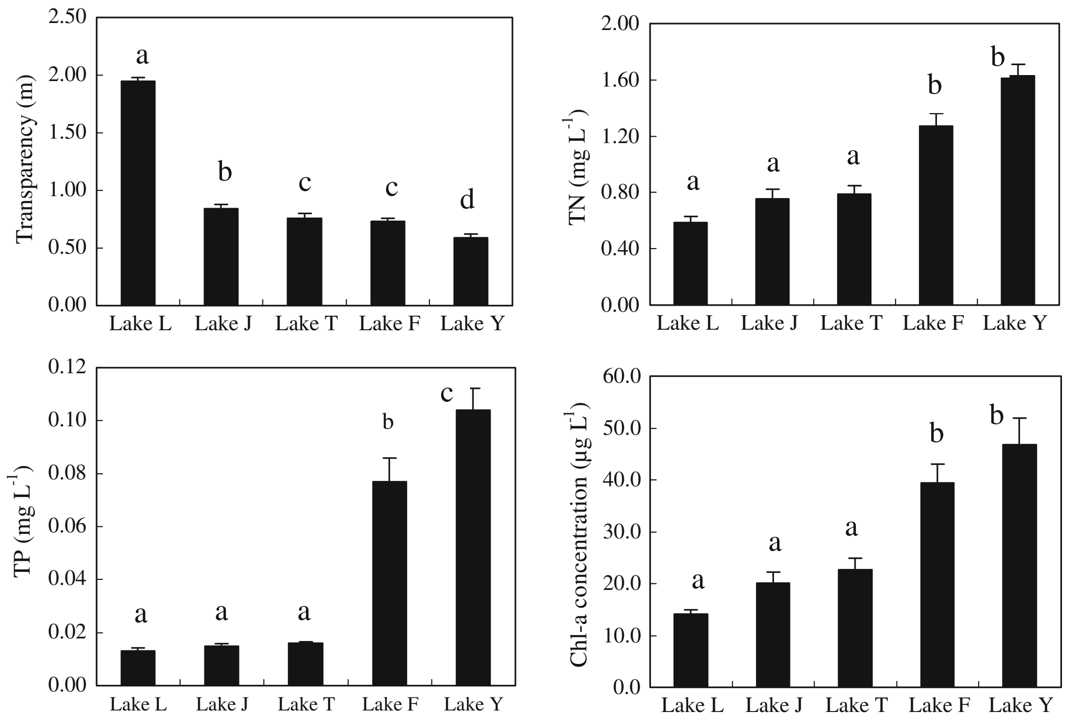

Fig. 2 The annual value of physicochemical variables including Chl-*a* concentration, transparency, TN, and TP in the five lakes. Differences were detected with LSD method, and *letters* indicate sample mean that are similar (*same letter*) or different (*different letter*) for each variable among lakes; *Lake L* Lake Longwo, *Lake J* Lake Jinghu, *Lake T* Lake Tingtang, *Lake F* Lake Fengming, *Lake Y* Lake Yinhu

Yinhu were all higher than those in Lake Longwo, Lake Jinghu, and Lake Tingtang.

Pearson correlation analysis revealed that TN showed a strong correlation with TP ($r = 0.88$, $P < 0.01$), and had the highest correlation coefficient with transparency ($r = -0.624$, $P < 0.01$) than the excluded variables of TP ($r = -0.51$, $P < 0.05$) and Chl-*a* concentration ($r = 0.61$, $P < 0.01$) in the multiple regressions model.

Species composition and dominance

A total of 82 rotifer species belonging to 20 families and 34 genera were observed in the five lakes (Qian et al., 2007), of which 35, 52, 50, 41, and 31 rotifer species were identified, and 28, 29, 30, 26, and 27 frequent rotifer species with the ratio higher than 0.1% of mean abundance to the total rotifer number occurred in Lake Longwo, Lake Jinghu, Lake Tingtang, Lake Fengming, and Lake Yinhu, respectively. The total species numbers of *Brachionus*, *Lecane*, and *Trichocerca*, accounting for nearly half of the frequent rotifer species, have shown higher species richness than the other rotifer taxa. Typically, several abundant rotifer species such as *L. aculeate*, *L. doryssa*, and *L. inermis* were observed only in Lake Yinhu (Table 1).

Lake Longwo showed a clear dominance of *Polyarthra dolichoptera* and *Keratella cochlearis*, followed by *Filinia longiseta* and *T. pusilla*, whereas Lake Jinghu and Lake Tingtang had more diversified community structure with the predominant species of *P. dolichoptera*, *K. cochlearis*, *A. fissa* and *F. longiseta*. In Lake Fengming and Lake Yinhu, the prevailing species were *K. cochlearis*, followed by *P. dolichoptera*, *A. fissa*, *F. longiseta*, and *T. pusilla*. In the five lakes, *Brachionus* also gave a large contribution to the total rotifer density (Fig. 3).

Keratella cochlearis abundance (*Y*) was significantly correlated with water temperature ($r = 0.384$, $P < 0.01$), Chl-*a* ($r = 0.504$, $P < 0.01$), TN ($r = 0.679$, $P < 0.01$), TP ($r = 0.593$, $P < 0.01$), and transparency ($r = -0.320$, $P < 0.05$), and TN gave the largest contribution to the abundance (multiple

Table 1 Dominance ranking of different taxa collected in the five lakes

Species	Symbol	Lake Longwo	Lake Jinghu	Lake Tingtang	Lake Fengming	Lake Yinhu
Brachionus angularis	Ban	2	2	2	2	2
B. diversicornis	Bdi	2	2	2	2	2
B. calyciflorus	Bcl	1	2	2	2	2
B. caudatus	Bca	1		2	1	1
B. forficula	Bfo	2	1	2	1	2
B. falcatus	Bfa	2				2
Keratella cochlearis	Kco	4	2	3	4	5
Anuraeopsis fissa	Afi	2	3	2	2	2
Polyarthra dolichoptera	Pdo	4	3	3	3	3
P. vulgaris	Pvu			2	2	
Synchaeta oblonga	Sob	2	2	1	1	1
S. tremula	Str	2	1	2	1	
S. stylata	Sst	1	2	2		1
Filinia longiseta	Flo	2	2	2	2	2
F. terminalis	Fte	1	2	2	2	
F. minuta	Fmi		2		2	
Trichocerca pusilla	Tpu	2	2	2	2	2
T. longiseta	Tlo	2	1		1	1
T. vargai	Tva	2		1	2	1
T. cylindrica	Tcy	2	1	1	1	2
T. rousseleti	Tro	2	2	2	1	1
T. gracilis	Tgr	1	2			
Asplanchna brightwelli	Abr	2	1	2	1	1
A. priodonta	Apr	2	1	1	1	1
A. girodi	Agi	2	2	2	1	2
Monostyla bulla	Mbu	1	1	1	2	2
M. lunaris	Mlu	2				2
Lecane aculeata	Lac					2
L. doryssa	Ldo					2
L. inermis	Lin					2
Pompholyx sulcata	Psu	2	2	2	2	2
Ascomorpha ecaudis	Aec		1	2		
A. ovalis	Aov			2		1
Cephalodella exigna	Cex	2	1	2	2	
Conochilus hippocrepis	Chi			2		
Conochiloides dossuarius	Cdo		1	2	1	
Rotaria rotatoria	Rta		2	2		
Rhinoglena frontalis	Rfi		2	2		
Hexarthra mira	Hmi	1	2			
Other occasional species (ratio of mean a less than 0.1% of total numbers)		7	23	20	15	4
Total numbers of species		35	52	50	41	31

Numbers in the table indicated the relative dominance, with 5, 4, 3, 2, 1 indicating the percentage of annual mean abundance >30%, 20–30%, 10–20%, 1–10%, and 0.1–1%, respectively

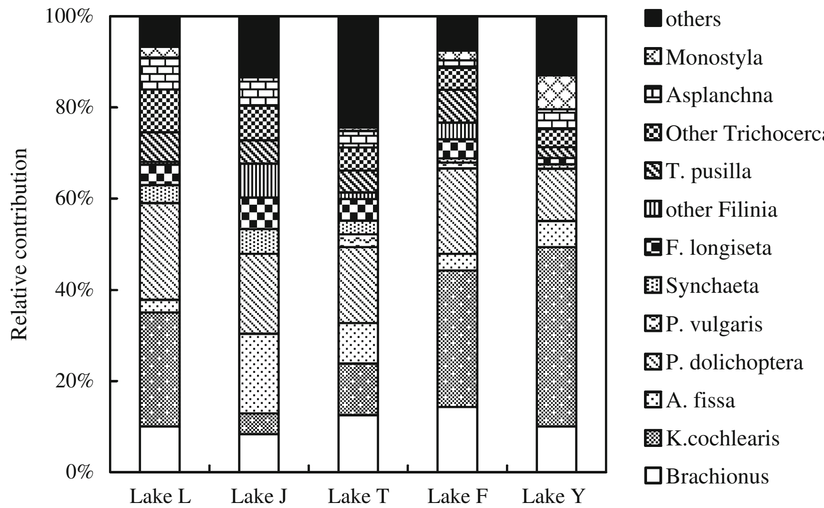

Fig. 3 Spatial variations of the relative contribution of the most representative rotifer taxa in five lakes (See Fig. 2 for sampling lakes)

regression analysis, $Y = 77.14\text{TN} + 1.67\text{Wt} - 0.89$ Chl-*a*, $R^2 = 0.617$, $P < 0.01$; standardized coefficients of $\beta_{\text{TN}} = 0.935$, $\beta_{\text{Wt}} = 0.481$, $\beta_{\text{Chl-}a} = -0.43$). Only water temperature was negatively associated with *P. dolichoptera* density ($r = -0.584$, $P < 0.01$) but positively correlated with *F. longiseta* abundance ($r = 0.512$, $P < 0.01$). No significant relationships between *A. fissa* abundance and any environmental factors were detected.

Index of community structure

Except for R, all the other five indices related to rotifer community structure differed among the five lakes ($F_{H'(4,55)} = 6.51$, $P < 0.001$; $F_{E(4,55)} = 2.22$, $P < 0.05$; $F_{N_{d(4,55)}} = 4.14$, $P < 0.01$; $F_{K\,(4,55)} = 5.54$, $P < 0.01$; $F_{N_{t(4,55)}} = 4.69$, $P < 0.01$; $F_{R\,(4,\,55)} = 1.39$, $P > 0.05$). The highest mean values of H' and E, and the lowest K were all observed in Lake Jinghu and Lake Tingtang. Generally, N_d and N_t of the rotifer community in Lake Jinghu, Lake Tingtang, Lake Fengming, and Lake Yinhu were both higher than those in Lake Longwo. The rotifer community indices of H', R, E, K, N_d, as well as N_t was similar between Lake Jinghu and Lake Tingtang (LSD-test, $P > 0.05$), which was also confirmed in Lake Fengming and Lake Yinhu (LSD-test, $P > 0.05$) except for N_d (LSD-test, $P < 0.05$) (Table 2).

The value of H' was negatively associated with Chl-*a*, TN, TP, and pH, while R showed a positive correlation with water temperature but a negative relationship with dissolved oxygen. E presented significantly negative relation with water temperature, Chl-*a* content, and pH, and K was related to TN, TP, and pH. N_d and N_t were both correlated with all the environmental variables except for DO content (Table 3).

Table 2 Annual mean value of rotifer community indices including Shannon–Wiener index (H'), species richness (R), evenness index (E), dominant species abundance (N_d), the dominance grade (K) and total abundance (N_t) of rotifers (mean ± SE) in the five lakes

Lake	H'	R	E	N_d	K	N_t
Longwo	2.08 ± 0.06^{ac}	11.3 ± 0.55^{a}	0.6 ± 0.022^{ac}	318 ± 71^{a}	0.26 ± 0.025^{ac}	1114.23 ± 163.35^{a}
Jinghu	2.37 ± 0.08^{b}	13.91 ± 1.23^{a}	0.64 ± 0.024^{a}	510 ± 168^{b}	0.19 ± 0.02^{c}	2272.5 ± 456.01^{ac}
Tingtang	2.23 ± 0.05^{ab}	13.00 ± 1.00^{a}	0.61 ± 0.01^{ac}	583 ± 130^{b}	0.24 ± 0.014^{c}	2413 ± 461.87^{ab}
Fengming	1.96 ± 0.08^{c}	11.41 ± 1.18^{a}	0.58 ± 0.026^{c}	906 ± 148^{b}	0.33 ± 0.03^{ab}	2980.75 ± 602.03^{bc}
Yinhu	1.94 ± 0.09^{c}	11.67 ± 0.69^{a}	0.55 ± 0.025^{c}	1517 ± 390^{c}	0.37 ± 0.036^{b}	3774.75 ± 589.16^{b}

Differences were detected with LSD method, and *letters* indicate sample mean that are similar (*same letter*) or different (*different letter*) for each variable among lakes

Table 3 Pearson correlation coefficients between rotifer community indices of H', R, E, N_d, K, and N_t versus seven physicochemical variables in the five lakes

Variable	H'	R	E	N_d	K	N_t
Wt	0.05	0.415*	−0.3*	0.478**	0.029	0.706**
Chl-*a*	−0.274*	−0.012	−0.291*	0.463**	0.296	0.558**
TN	−0.419*	−0.093	−0.353	0.549**	0.543**	0.510**
TP	−0.390*	−0.107	−0.327	0.493**	0.498**	0.481**
Transparency	0.018	−0.162	0.126	−0.386**	−0.182	0.510**
pH	−0.356*	0.148	−0.402*	0.363**	0.416**	0.258**
DO	−0.101	−0.444*	0.203	−0.194	0.09	−0.251

See Table 2 for abbreviations of community structure indices; * $P < 0.05$; ** $P < 0.01$

Table 4 Forward stepwise regression analyses between dependent variables (Y) of H', R, E, N_d, K, and N_t with independent variables of physicochemical factors

Index	Full model	R^2	P value	Standardized coefficient
H'	$Y = -0.297\text{TN} + 2.397$	0.176	<0.05	$\beta = -0.419$*
R	$Y = -0.81\text{DO} + 20.3$	0.197	<0.01	$\beta = -0.444$*
E	$Y = -0.141\text{pH} + 1.77$	0.162	<0.01	$\beta = -0.402$**
N_d	$Y = 2277\text{TN} - 0.35\text{DO} + 2137$	0.61	<0.01	$\beta_{TN} = 0.931$**; $\beta_{DO} = -0.693$*
K	$Y = 0.163\text{TN} + 0.122$	0.295	<0.01	$\beta = 0.543$*
N_t	$Y = 80\text{Wt} + 3406\text{TN} - 457\text{DO} + 2259$	0.775	<0.01	$\beta_{Wt} = 0.41$*; $\beta_{TN} = 0.732$**; $\beta_{DO} = -0.477$*

Only those independent variables with a significant F-value were selected in the regressions. When two or three variables were included in the regression, the standardized coefficient of each variable is shown. See Table 2 for abbreviations of community structure indices; * $P < 0.05$; ** $P < 0.01$

Stepwise multiple regression analyses demonstrated that environmental factors together accounted for 16.2–77.5% of the variance in rotifer communities structure indices (Table 4). TN explained 17.6 and 29.5% of the variance in H' and K, while Chl-*a*, TP, and pH were eliminated from the model (Table 4). DO and pH accounted for 19.7 and 16.2% of the variance in the index of R and E, respectively, but Wt, Chl-*a*, and DO were excluded in the model (Table 4). Wt, TN, and DO were correlated with N_t, while only TN and DO were related to N_d, and TN had the greatest effect on N_d and N_t according to the standardized coefficient (Table 4).

Multivariate analysis

Redundancy analysis (RDA) showed that the first two ordination axes explained 71.3% of species–environment variability in the ordination of physical and chemical factors (Fig. 4A). TN and TP were positively associated with axis 1, but transparency was strongly negative association with axis 1, indicating axis 1 was mainly related to lake trophic state. Temperature was strongly negatively with axis 2 which was likely to reflect warm- and cold-water assemblages caused by seasonal fluctuation. This diagram clearly showed a separation among the five lakes according to community structure, with Lake Jinghu and Lake Tingtang being somewhat more close to each other, which was also interestingly presented in Lake Fengming and Lake Yinhu, while Lake Longwo was noticeably apart. TN and TP were the main factor of variation between Lake Fengming and Lake Yinhu and the other three lakes, while transparency seemed to be the main source of variation between Lake Longwo and Lake Jinghu as well as Lake Tingtang. In addition, it showed spatial pattern of sampling months, with the top-left group of clusters relating to the winter assemblages (cold season), the bottom-right groups relating to the summer community (hot season), and the middle group relating to spring and autumn assemblages (warm season).

Thermophilous species were represented in the bottom-right quadrant of the biplot of Fig. 4B, such as *P. vulgaris*, *A. priodonta*, *A. ovalis*, *F. minuta*, *F. longiseta*, *B. diversicornis*, *B. forficula*, *B. angularis*, and *T. pusilla*, opposite to cold-water species including *P. dolichoptera* and *T. cylindrica*. Similarly, *B. calyciflorus*, *A. girodi*, *T. longiseta*, *B. falcatus*, *P. sulcata*, and *K. cochlearis* could tolerate high levels of TP, while *A. brightwelli*, *S. oblonga*, and *S. tremula* were related to low trophic status (e.g. high transparency and low TN and TP).

Discussion

The planktonic Rotifera are not all cosmopolitan in their geographical distribution, and there is a latitudinal variation in the assemblage of some planktonic species (Green, 1972). Subtropical floodplains are the world's richest habitats for rotifers (Segers et al., 1993; Segers, 2008), and approximately 150–160 species of rotifers are found in the temperate zone, while more than 210 species distribute in the tropical zone (Dumont & Segers, 1996), of which *Lecane*, *Brachionus*, and *Trichocerca* constitute the major component of the "tropical-centered" taxa (Green, 1972, 1994; Pejler, 1977; Segers, 2001), whereas *Notholca*, *Kellicottia*, and *Synchaeta* have most of their species in the cooler parts and the temperate zones in the world, with an occasional species in the tropics (Pejler, 1977; de Ridder, 1981; Green, 1994). Across 1 year, although most of the recorded species in the five subtropical lakes (Qian et al., 2007) are common and cosmopolitan, the relatively rich rotifer species observed was in accordance with the well-established concept that subtropical systems support a higher number of species than temperate systems. *Brachionus*, *Lecane*, and *Trichocera* dominated the rotifer species composition, but none or fewer species of *Notholca*, *Kellicottia*, and *Synchaeta* were observed in the five subtropical lakes (Wen et al., 2006; Qian et al., 2007), suggesting the latitudinal zonation of some rotifer species also existed in the subtropics, and was similar to that in the tropics.

Additionally, as the most abundant taxa in Lake Longwo, Lake Fengming, and Lake Yinhu, *K. cochlearis* should be investigated more because of the two

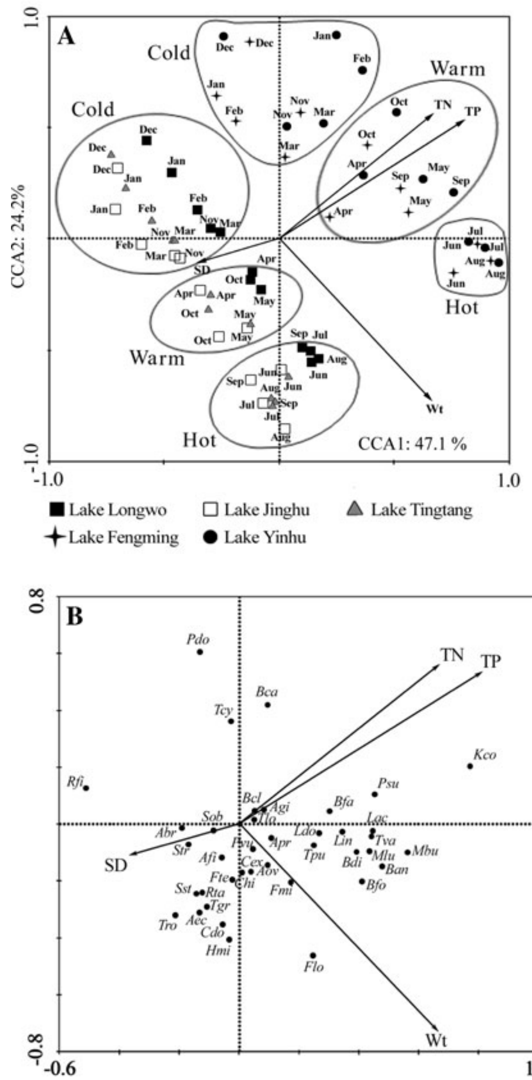

Fig. 4 Partial RDA ordination biplots of site scores (**A**), species scores (**B**) and selected environmental variables (represented by *arrows*) (See Table 1 for the symbols of rotifer species; *SD* transparency, *TN* total nitrogen, *TP* total phosphorus, *Wt* Water temperature)

morphological forms of *K. cochlearis cochlearis* and *K. cochlearis tecta*, the former is considered as oligotrophic and cold-water species (Hillbricht-Ilkowska, 1983), and the latter is influenced by the degree of eutrophication (Xi et al., 2002). Notably, *L. aculeate*, *L. doryssa*, and *L. inermis* were observed only in Lake Yinhu, which was likely to be related to the submerged macrophytes in this lake, because it has been shown that the genera *Lecane* inhabited in macrophyte-associated water body (Duggan et al., 2001b; Green, 2003; Kuczyńska-Kippen, 2009).

Species numbers (*R*) had non-significant seasonal variations and negative association with DO in the five lakes. This might attribute to water temperature and DO which are the main factors regulating the occurrence of rotifer species (Hofmann, 1977; Berzins & Pejler, 1989b). However, the total number of rotifer species varied among the studied five lakes, and more species were observed in Lake Jinghu and Lake Tingtang than in Lake Longwo, which is possibly due to more food resources available for rotifers in the slightly eutrophic environments (Hofmann, 1977). Algae, heterotrohic nano-flagellates, bacteria, and picoplankton are major food resources for rotifers and are generally abundant in nutrient-rich environments (Hwang & Heath, 1999; Yoshida et al., 2003; Auer et al., 2004). The lowest *K* found in Lake Jinghu and Lake Tingtang suggested a wider range of food niche partitioning for more rotifer species inhabiting the two lakes. In addition, the less species recorded in Lake Fengming and Lake Yinhu might be caused by some newly appeared species and increased eutrophication-tolerant species, but also some recently disappeared oligotrophic species (Shao et al., 2001).

Species diversity can increase without an increase in taxon number, if evenness increases (Hulbert, 1971). Hence, the highest H' observed in Lake Jinghu and Lake Tingtang might be attributed to the higher *E* value rather than the higher number of rotifer species occurring each month, because no distinctive differences in the occurrence of species numbers (*R*) per month were found among the five lakes, and evenness (*E*) was somewhat higher in Lake Fengming and Lake Yinhu than in the other three lakes. In contrast, the lowest H' of rotifers community was observed in both Lake Fengming and Lake Yinhu, as expected, which might be caused by the lower *E*. Obviously, relatively serious eutrophication decreased the evenness index and species diversity of the rotifer community.

It is well known that predation ("top–down" forces) and resource supply ("bottom–up" forces) are important factors regulating population dynamics and community structure in freshwater plankton (Sommer, 1989). During the 1-year cycle, rotifer abundance, Chl-*a* concentration, and nutrient loading were similar between Lake Jinghu and Lake Tingtang, and in Lake Fengming and Lake Yinhu. Moreover, the total abundance and the dominant species abundance were positively correlated with TN, and were higher in the four eutrophic lakes than those in mesotrophic Lake Longwo, demonstrating again that rotifer abundance is proportional to the trophic status (e.g. Huang et al., 1985; Balvay & Laurent, 1990; Karabin et al., 1997). Food availability to the rotifers generally increased with eutrophication. Chl-*a* may be a representative of edible algae or other food resources associated with it (Auer et al., 2004), and bacterial productivity may be positively correlated with nutrient loading and Chl-*a* concentration (Hwang & Heath, 1997). The rotifers of macro-filter-feeders such as *Trichocerca*, *Synchaeta*, *Polyarthra* feed mainly on edible algae, and micro-filter-feeders including *K. cochlearis*, *A. fissa*, *F. longiseta* are inclined to consume bacteria–detritus particles and nanoplankton (Špoljar et al., 2005). Hence, *P. dolichoptera*, *K. cochlearis*, *F. longiseta*, *T. pusilla*, and *A. fissa* were the dominant species in the five lakes, especially *K. cochlearis* which dominated in Lake Fengming and Lake Yinhu, implying that the rotifer dynamics were primarily controlled by food sources in those lakes.

Rotifers suffer predation by copepods, planktivorous fishes, macroinvertebrates such as *Chaoborus*, and competition (both interference and exploitative) from cladocerans (e.g. Williamson, 1983; Williamson & Butler, 1986; Gilbert, 1988; Yoshida et al., 2003). Thus, rotifer abundance can be reduced when mesozooplankton are abundant. *Chaoborus* was not recorded in this study because zooplankton samples were collected in nearly mid-day when invertebrate predators had likely migrated into sediments (Havens et al., 2007). In the present study, fish were not considered important predators to rotifers, because rotifers being small in size are not grazed by most open-water planktivores, although they may comprise an important part of the diet of larval fish (Bartsch et al., 2004). Moreover, the lower dominance of *A. priodonta* found in the five lakes suggests a minor effect of fish on the rotifer population dynamics, because a high *A. priodonta* density indicates an abundance of planktivorous fish (Alekseev & Potina, 1986; Telesh, 1993). However, the other groups such as copepods and cladocerans, which can depress the rotifers effectively through predation and competition, were more abundant in Lake Tingtang and Lake

Fengming than in Lake Jinghu and Lake Yinhu, respectively. Especially in Lake Jinghu, few crustacean zooplankters were observed throughout the year (unpublished data). Therefore, without considering the effect of *Chaoborus* on rotifer dynamics, the observations in this study were in agreement with Yoshida et al. (2003), who claimed that overall differences in rotifer abundance among lakes are mainly determined by "bottom–up" forces (resource supply) while temporal change in single lakes are shaped by "top–down" forces. Of course, further systematic benthic sampling for obtaining *Chaoborus* is still needed to confirm the conclusion mentioned above.

Eutrophication changes the species composition, and increases the abundance of rotifers (Stemberger & Gannon, 1977; Gannon & Stemberger, 1978; Huang et al., 1985; Zhuge & Huang, 1993; Karabin et al., 1997). Consequently, rotifer species composition and abundance can be used as biological indicators for water quality and eutrophication (Sládeček, 1983; Mäemets, 1983; Karabin et al., 1997; Duggan et al., 2001a; May & O'Hare, 2005; Wen et al., 2006). *A. fissa*, *Brachionus* spp., *Pompholyx sulcata*, and *T. cylindrica* are regarded as indicators of eutrophic conditions, *T. pusilla* and *F. longiseta* occur in meso- and eutrophic lakes, and *P. dolichoptera* is associated with low trophic state (Mäemets, 1983; Duggan et al., 2001a; Shao et al., 2001). However, *A. fissa*, *B. angularis*, *B. diversicornis*, *B. calyciflorus*, *B. forficula*, *P. sulcata*, *T. pusilla*, *F. longiseta*, and *P. dolichoptera* were all observed in the five study lakes, covering a nutrient gradient from mesotrophy to moderate eutrophy, suggesting that simple species composition of rotifers is limited in its ability to reflect trophic status of aquatic systems. In contrast, the annual mean abundances of both total rotifers and the dominant rotifers increased along the trophic gradient in the five lakes, suggesting that rotifer abundance might be a more sensitive indicator of trophic state than species composition, which was in accord with May & O'Hare (2005). Based on the similar calculation of trophic state of Lake Łuknajn and those five lakes (Karabin et al., 1997; Qian et al., 2007), and the combining results of Karabin et al. (1997) and this study, rotifer abundance in relation to lake trophy was roughly estimated, with 500–1000 ind. l^{-1} being characteristic of mesotrophic or meso-eutrophic lakes (i.e. highmesotrophy), 1000–2500 ind. l^{-1} eutrophic, and 3000–4000 ind. l^{-1} moderately eutrophic ones.

Comparative analyses of the six rotifer community indices and RDA revealed that the two slightly eutrophic lakes and the other two moderately eutrophic lakes exhibited a high degree similarity of community structure, indicating that the trophic state of a lake determined the rotifer community structure. Among the physicochemical parameters related to trophic state in this paper, SD was the main source of variation between Lake Longwo and the two slightly eutrophic lakes, and TN was related to indices of rotifer community structure in those three lakes, which might be due to the strongest relationship between SD and TN. However, TN showed greater effects on the indices of rotifer community structure in Lake Fengming and Lake Yinhu, and also was an important factor distinguishing rotifer assemblage of those two lakes from the other three lakes, inferring that TN played a more important role in determining the rotifer community structure in these two moderately eutrophic lakes. However, TP is most often shown to be the best indicator of trophic state (Vollenweider & Kerekes, 1982; Jeppesen et al., 1990b, 2000), and has a greater effect on rotifer community structure (Jeppesen et al., 2000; Kuczyńska-Kippen & Nagengast, 2006). Interestingly, in the other subtropical lakes with relatively serious eutrophication, nitrogen (N) played a more important role than phosphorus (P) in determining the community structure of zooplankton including rotifers. For example, a higher rotifer density is primarily related to a higher concentration of inorganic nitrogen during spring and summer in 27 subtropical lakes adjacent to Yangtze River (Wang et al. 2010), and the abundance of rotifers is significantly positively correlated with TN in Lake Taihu, a subtropical Chinese large lake (Yang et al., 2007). In addition, total zooplankton biomass is positively related to TN in subtropical Lake Okeechobee, FL, USA (Crisman et al., 1995).

Nitrogen (N) limitation is not only significantly more frequent in lakes of low ambient TN:TP (TN:TP mass ratio ≤ 14), but is also significantly more common in lakes with TP > 30 μg l^{-1} (Downing & McCauley, 1992). A total N:P ratio of 29:1 differentiates lakes with cyanobacteria dominance (TN:TP $<$29:1 by mass) and lakes without such dominance (TN:TP $>$29:1) (Smith, 1983; Havens et al., 2003). In some freshwater environments, particularly in the tropics and subtropics, N has been found to be the primary limiting nutrient for phytoplankton production, due in large part to excessive P and long growing seasons (e.g. Henry et al., 1985; Phlips et al., 1997; Phlips et al., 2002; Lin et al., 2008; James et al., 2009). In this study, the total N:P mass ratios of 16:1 and 15:1, and TP of 77 and 104 μg l^{-1} in Lake Fengming and Lake Yinhu suggested N-limitation and cyanobacteria dominance in phytoplankton communities might be possible. Because many rotifers cannot feed on cyanobacteria, food niche became narrow and species numbers and biodiversity decreased. Further increases in available N load to the lakes would be expected to greatly enhance algal blooms, and N load reduction was probably more critical for controlling algal boom in these water bodies.

The RDA biplot of species and months showed that rotifer assemblages followed a temperature gradient along axis 2, suggesting that temperature was the most important factor in determining seasonality, which might be related to the characteristic of distinctive seasons in subtropical zone.

In summary, in the five subtropical shallow lakes, *P. dolichoptera*, *K. cochlearis*, *F. longiseta*, *T. pusilla* and *A. fissa* were all the dominant species according to the annual mean abundance, whilst the rotifer abundance increased along the trophic gradients, which indicated that rotifer abundance might be a more sensitive indicator of trophic state than species composition. With the rising nutrient loading, the total abundance of rotifers, the dominant species abundance and the dominance grade increased significantly, and Shannon–Wiener index decreased remarkably. The trophic state determined the structure of the rotifer communities, with TN being the most important roles for shaping the rotifer community in the two moderately eutrophic lakes. Trophic state and water temperature was strongly associated with the rotifer species distribution, and water temperature was the most important factor in determining seasonality of rotifers.

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