

The relative importance of physicochemical factors and crustacean zooplankton as determinants of rotifer density and species distribution in lakes adjacent to the Yangtze River, China

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ABSTRACT

The planktonic community of freshwater Rotifera in 27 subtropical lakes was studied to assess the relative importance of physicochemical factors and crustacean zooplankton as determinants of rotifer density and species distribution. Factor analysis and multiple linear regressions showed that 21.9% and 29.9% of the variance in rotifer density was explained by physicochemical factors and crustaceans, respectively. Larger rotifer density was possible in shallower lakes with higher concentration of inorganic nitrogen and less herbivorous crustaceans such as *Sinocalanus dorrii* and *Daphnia*. Redundancy analysis showed that the variances of rotifer species distribution explained by crustaceans and physicochemical factors were 26.9% and 31.0%, respectively. Further analysis demonstrated that the variances explained by pure crustaceans and pure physicochemical factors were 12.5% and 16.6%, respectively. However, these two percentages were not statistically different. Rotifer species distribution was strongly associated with Chl *a* and *Moina micrura*. Their coexistence with crustaceans seemed to be determined by their defense against potential predators and competitors.

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Introduction

Rotifera is an important component of freshwater zooplankton. Its community dynamics is not only controlled by food availability (Devetter 1998), but also influenced by planktivorous fishes (Stenson 1982; Telesh 1993) and invertebrate predators and competitors (Fussmann 1996; Nagata and Hanazato 2006). Algae, heterotrophic nano-flagellates and bacteria are major food resources for rotifers, and are generally abundant in nutrient-rich environments (Auer et al. 2004; Yoshida et al. 2003). As most rotifers and cladocerans compete for the same food resources and some cyclopoid copepods are effective predators on rotifers (Brandl 2005; Williamson 1983), rotifers can be effectively depressed by crustacean zooplankton through exploitative competition and predation. Many studies have revealed the inverse relationship between the densities of crustaceans and rotifers in natural environments (e.g. Fussmann 1996; Gilbert 1985, 1989). Also, rotifers may suffer mortal damage when they are swept into the branchial chamber of large cladocerans (Gilbert 1988).

An increase in rotifer density with increasing trophic status is reported extensively (e.g. Bays and Crisman 1983; Pace 1986; Yoshida et al. 2003). The underlying forces shaping the regional rotifer species distribution are also suggested to be strongly associated with trophic status (Castro et al. 2005; Duggan et al. 2001, 2002; Yoshida et al. 2003). Moreover, other environmental factors such as pH (Bielanska-Grajner 2001), turbidity (Duggan et al. 2002), oxygen and temperature (Armengol et al. 1998; Miksch 1989) can also affect the rotifer abundance and species distribution. Although limnological literature provides a great variety of information on these impact factors, most of the studies concerned with natural rotifer communities are carried out in a single lake (e.g. Armengol et al. 1998; Devetter 1998; Poljar et al. 2005). Among the few comparative studies, more focus their attention on the impact of physicochemical factors (Castro et al. 2005; Duggan et al. 2001, 2002; Swadling et al. 2000), and less attention is paid on macrozooplankton (Yoshida et al. 2000, 2003). Since crustacean zooplankton and physicochemical factors can both affect the dynamics of the rotifer community, their control on rotifers may vary with lakes. Thus, determining the relative importance of these two forces may be of primary importance in ecological sciences. Up to now, no attempt is found at comparing whether the variance of rotifer density and species distribution explained by the sets of explanatory variables is statistically different.

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Although the middle and lower reaches of the Yangtze River are one of the central areas of freshwater shallow lakes in China, there has been very limited information on the interactions of rotifers with physicochemical factors and crustaceans (Geng et al. 2005; Qian et al. 2007; Shao et al. 2001). Worldwide, there are also relatively less data available on rotifer species distribution in subtropical lakes. The crustacean zooplankton species composition and distribution patterns have been discussed in a previous paper (Wang et al. 2007a). So in this study, we aimed to illuminate the relative importance of crustaceans and physicochemical factors in regulating the rotifer density and species distribution.

Material and methods

Sampling and Laboratory analyses

The 27 lakes selected for this study are shown in Fig. 1. Field sampling was carried out in 2003 and 2004. According to the heterogeneity of niche, 3–12 samples were collected within a single lake during each visit in spring (April–June) and summer (July–September). Among the 27 lakes, Lake Dongdong and Lake Shiji are connected to the Yangtze River. Lakes Dachahu, Banghu and Dahuchi, which are separate parts of Lake Poyang, the largest lake in China, are also affected by the river water level. Other lakes are either unconnected to or isolated from the river.

Crustacean zooplankton was collected by straining 10 or 20 L integrated water through a 64 µm plankton net and preserved with 5% formalin. Identification was done in the laboratory according to Chiang and Du (1979) and Shen (1979). Water sampled from 0.5 m below the water surface and 0.5 m above the lake bottom was combined and taken for measurement of chlorophyll *a* (Chl *a*), nutrient concentrations and rotifers. Chl *a* was measured using a spectrophotometer and the standard acetone extraction method. Total nitrogen (TN) was digested with alkaline potassium persulfate and absorbance measured at 220 nm. Total phosphorus (TP) was analyzed according to the ammonium molybdate method after oxidation with potassium persulfate under pressure. Ammonium-N (NH_4^+) was analyzed by colorimetry with Nessler's reagent. Nitrate (NO_3^-) was analyzed using the automated Korolev/cadmium reduction method and nitrite (NO_2^-) with the method of α -naphthylamine. 1 L water was fixed with Lugol's iodine solution and later concentrated to 30 mL after 48 h sedimentation. Three sub-samples of 1 mL were used for

rotifer counting with a compound microscope (at a magnification of $\times 100$). Rotifers were identified according to Koste (1978).

Statistical analyses

To illuminate the relationships of rotifer density to physicochemical factors and crustaceans, factor analysis (based on principal components analysis (PCA)) and stepwise multiple linear regressions were done using SPSS 10.0. Except for pH, the data were \log_{10} -transformed to guarantee variance homogeneity and subsequently all physicochemical factors were standardized to zero mean and unit variance before analysis to remove the influence of differing scales of measurement. In this study, each sample was assessed as a separate entity.

Canonical ordination, using the CANOCO 4.5 package (Ter Braak and Smilauer 2004), was performed to assess the association of rotifer species with environmental factors. The species data matrix was first analyzed by detrended correspondence analysis (DCA) to determine their distribution pattern (linear or unimodal). In the rotifer species data matrix, only those taxa were included, which occurred in at least 5% of the 347 samples. Thus, 21 of 56 enumerated taxa were met. To satisfy the assumption of normality of variance in data, the densities of rotifers and crustaceans were $\log(x+1)$ transformed. Using the software package Matlab, variation partitioning was performed according to Peres-Neto et al. (2006), which permits to single out the respective effects of physicochemical factors and crustaceans and to test if the amount of variance explained by explanatory variables is significantly different. In this study, two sets of explanatory variables were built: biotic (crustacean community) and abiotic (physicochemical factors). The abiotic matrix contained all measured physicochemical variables (including latitude, longitude, lake area, depth, transparency, temperature, pH, TN, NO_3^- , NH_4^+ , NO_2^- , TP, Chl *a*). These variables were also \log_{10} -transformed to approximate normal distributions and standardized to zero mean and unit variance. The final variables contained in the analysis were obtained by a forward selection.

Results

Limnological characteristics

The study lakes showed a wide range in trophic status and area, with Chl *a* ranging from 0.50 to 146 µg L⁻¹, TP 0.01 to

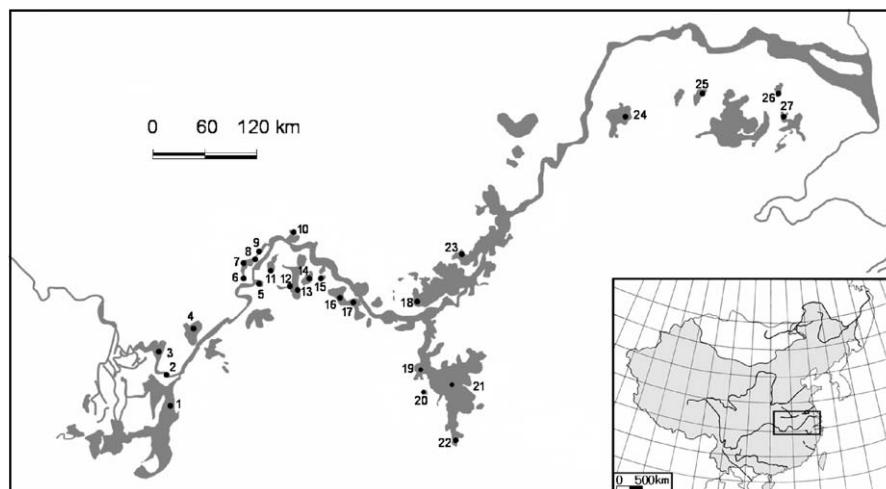


Fig. 1. Location of sampling lakes along the middle and lower reaches of the Yangtze River (1, Dongdong; 2, Laojiang; 3, Tianezhou; 4, Honghu; 5, Qingling; 6, Houguan; 7, Sanjiao; 8, Longyang; 9, Moshui; 10, Zhangdu; 11, Nanhu; 12, Niushan; 13, Baoan; 14, Qiaodun; 15, Huama; 16, Hongxing; 17, Sanliqi; 18, Longgan; 19, Banghu; 20, Dahuchi; 21, Dachahu; 22, Junshan; 23, Wuchang, 24, Shiji; 25, Gehu; 26, Yangcheng; 27, Dianshan).

1.45 mg L^{-1} , TN 0.11 to 12.7 mg L^{-1} , and area 100 to 34800 ha . They were typically shallow, with a mean depth of about 2.70 m . The water was generally alkaline, with pH ranging from 7.50 to 9.20 .

The average temperature was 24.8°C in spring and 28.2°C in summer, respectively (Table 1).

Table 1
Physicochemical variables and the dominant crustacean zooplankton found in the study lakes in spring and summer.

	Spring		Summer	
	Mean \pm SD	Range	Mean \pm SD	Range
Chl <i>a</i> ($\mu\text{g L}^{-1}$)	22.4 ± 35.8	0.50 – 141	33.6 ± 40.6	0.70 – 146
TN (mg L^{-1})	3.47 ± 4.17	0.11 – 12.7	2.02 ± 2.22	0.48 – 8.67
NO_3^- (mg L^{-1})	0.84 ± 0.70	0.21 – 3.13	0.67 ± 0.53	0.12 – 1.69
NO_2^- (mg L^{-1})	0.08 ± 0.15	0.00 – 0.75	0.10 ± 0.22	0.00 – 1.07
NH_4^+ (mg L^{-1})	1.61 ± 2.89	0.05 – 9.34	0.56 ± 0.94	0.02 – 3.73
TP (mg L^{-1})	0.20 ± 0.24	0.01 – 1.08	0.20 ± 0.32	0.01 – 1.45
pH	7.96 ± 0.30	7.50 – 9.20	7.98 ± 0.31	7.50 – 9.20
Transparency (cm)	113 ± 73.8	33 – 271	89.0 ± 77.6	23 – 391
Depth (m)	2.71 ± 1.51	0.90 – 7.60	2.70 ± 1.44	0.90 – 7.10
Area (ha)	7136 ± 9591	100 – 34800	7136 ± 9591	100 – 34800
Temperature ($^\circ\text{C}$)	24.8 ± 5.81	16 – 32	28.2 ± 2.81	22 – 33
Latitude ($^\circ$)	30.2 ± 0.73	28.6 – 31.6	30.2 ± 0.75	28.6 – 31.6
Longitude ($^\circ$)	115 ± 2.24	113 – 121	115 ± 2.28	113 – 121
Dap (ind L^{-1})	1.19 ± 3.20	0 – 16.1	0	0
Mmi (ind L^{-1})	0.11 ± 0.38	0 – 1.90	2.30 ± 4.72	0 – 20.6
Bos (ind L^{-1})	6.03 ± 18.9	0 – 98.1	14.0 ± 35.3	0 – 173
Sdo (ind L^{-1})	2.63 ± 7.79	0 – 40.0	0.08 ± 0.41	0 – 2.14
Mno (ind L^{-1})	2.08 ± 5.85	0 – 25.1	7.30 ± 11.2	0 – 40.3
Tta (ind L^{-1})	5.38 ± 16.1	0 – 67.7	9.13 ± 22.8	0 – 93.8
Cvi (ind L^{-1})	3.62 ± 9.94	0 – 43.2	0	0
Sfo (ind L^{-1})	0.23 ± 0.82	0 – 4.21	0.46 ± 1.99	0 – 10.2
Dbr (ind L^{-1})	0.77 ± 1.61	0 – 7.00	5.37 ± 7.67	0 – 37.7
Bde (ind L^{-1})	0.69 ± 1.83	0 – 7.22	0.22 ± 0.83	0 – 4.10
Cco (ind L^{-1})	0.42 ± 1.87	0 – 9.69	3.20 ± 7.45	0 – 30.5
Dia (ind L^{-1})	0.02 ± 0.07	0 – 0.33	1.33 ± 3.04	0 – 11.5
Chy (ind L^{-1})	0.08 ± 0.28	0 – 1.44	0.38 ± 1.86	0 – 9.67

Dap = *Daphnia*, Mmi = *Moina micrura*, Bos = *Bosmina*, Sdo = *Sinocalanus dorrii*, Mno = *Mesocyclops notius*, Tta = *Thermocyclops taihokuensis*, Cvi = *Cyclops vicinus*, Sfo = *Schmackeria forbesi*, Dbr = *Diaphanosoma brachyurum*, Bde = *Bosminopsis deitersi*, Cco = *Ceriodaphnia cornuta*, Dia = *Diaptomidae*, Chy = *Chydorus*.

Zooplankton density and dominant species

Zooplankton density varied greatly with respect to lakes and seasons. Crustaceans ranged from 0.19 to 43.6 and from 0.07 to 294 ind L^{-1} in spring and summer, respectively (Fig. 2). The densities of the most dominant crustaceans are shown in Table 1. *Cyclops vicinus* and *Daphnia* were found only in spring. *Bosmina*, *Thermocyclops taihokuensis* and *Mesocyclops notius* were more abundant in comparison with other species in the two seasons. Rotifers ranged from 10 to 7723 and 143 to 12156 ind L^{-1} in spring and summer, respectively (Fig. 2). A total of 56 rotifers were found in the 27 lakes (Table 2). *Polyarthra* spp. (mainly *Polyarthra dolichoptera* and *Polyarthra vulgaris*) were dominant species ($>10\%$ of total rotifer density) shared by the 27 lakes. *Keratella cochlearis* and *Trichocerca pusilla* both dominated 16 lakes. The following species were dominant in 3 – 9 lakes: *Filinia longisetosa*, *Brachionus angularis*, *Trichocerca similis*, *Brachionus calyciflorus*, *Keratella valga*, *Anuraeopsis fissa* and *Hexarthra mira* (Table 3).

Relationships between rotifer density and environmental variables

Factor analysis showed that 75.5% and 58.6% of the variance in physicochemical factors and crustaceans were explained by the first four axes, respectively. The matrix of factor loadings is shown in Table 4. NO_3^- and NO_2^- were significantly correlated with F1, depth with F2, temperature with F3 and pH with F4. With respect to crustaceans, *Chydorus* was significantly related to F1, *M. notius* and *Diaphanosoma brachyurum* to F2, *T. taihokuensis* to F3 and *Sinocalanus dorrii* and *Daphnia* to F4, respectively. The stepwise multiple linear regression revealed that rotifer density was significantly related to physicochemical factors (Rotifers = $2.58 + 0.193F_1 + 0.379F_2 + 0.134F_3$, $F_{3,343} = 32.0$, $P < 0.001$, $n = 347$) and crustaceans (Rotifers = $2.58 + 0.101F_2 - 0.511F_4$, $F_{2,344} = 73.5$, $P < 0.001$, $n = 347$), explaining 21.9% and 29.9% of the total

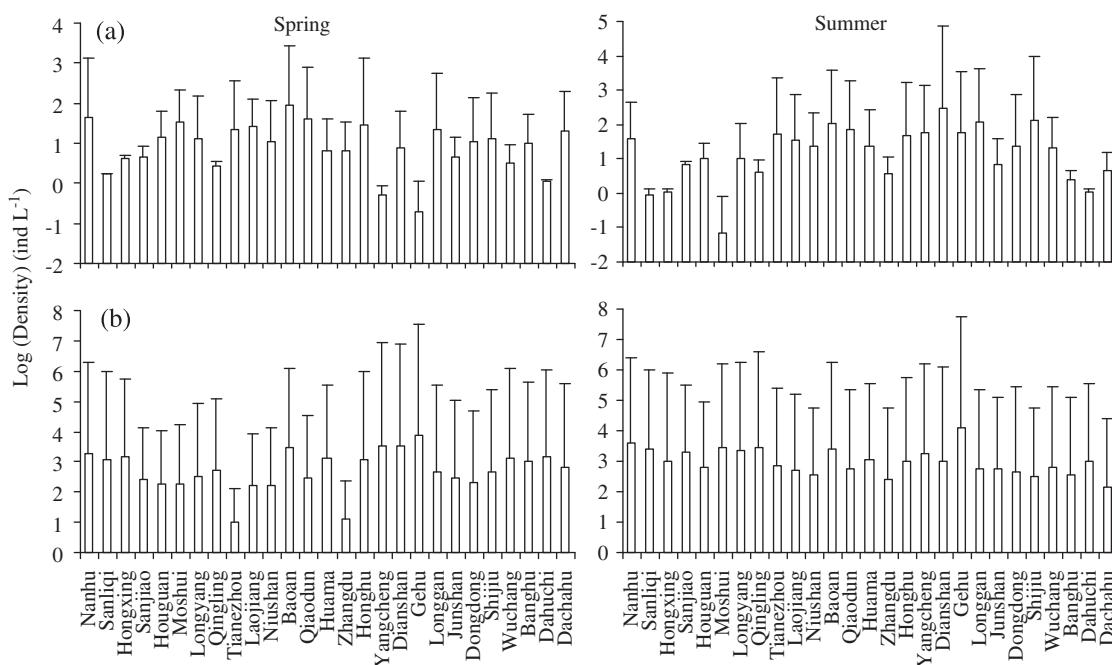


Fig. 2. Log-transformed density of crustaceans (a) and rotifers (b) in spring and summer in lakes along (see Fig. 1) the middle and lower reaches of the Yangtze River. Error bars represent standard deviation.

variance in rotifer density, respectively. The contribution of each factor to the model is demonstrated in Table 5. These results suggest that more rotifers were associated with lower lake depth, higher concentration of inorganic nitrogen and higher water temperature as well as less large herbivorous *S. dorrii* and *Daphnia*.

Table 2

Rotifer species composition observed in the study lakes and respective abbreviated names used in the text.

	Abbrev.		Abbrev.
<i>Anuraeopsis fissa</i>	Afi	<i>Lecane bulla</i>	
<i>Asplanchna girodi</i>	Asp	<i>L. curvicornis</i>	
<i>A. priodonta</i>		<i>L. halicysta</i>	
<i>Brachionus angularis</i>	Ban	<i>L. leontina</i>	
<i>B. budapestiensis</i>		<i>L. luna</i>	
<i>B. calyciflorus</i>	Bca	<i>L. stenroosi</i>	
<i>B. caudatus</i>	Bcau	<i>Lepadella</i> sp.	
<i>B. diversicornis</i>	Bdi	<i>Monostyla</i>	Mon
<i>B. falcatus</i>	Bfa	<i>Notholca labis labis</i>	
<i>B. forficula</i>	Bfo	<i>Polyarthra dolichoptera</i>	Pol
<i>B. leydigi</i>		<i>P. vulgaris</i>	
<i>B. quadridentatus</i>		<i>Platyias militaris</i>	
<i>B. urceolaris</i>		<i>P. quadricornis</i>	
<i>Colerella</i> sp.		<i>Ploesoma hudsoni</i>	
<i>Conochilus unicornis</i>	Cun	<i>Pompholyx sulcata</i>	
<i>Encentrum</i> sp.	Enc	<i>Scaridium</i> sp.	
<i>Euchlanis dilatata</i>		<i>Synchaeta oblonga</i>	
<i>Eudactylota eudactylota</i>		<i>Trichocerca capucina</i>	Tca
<i>Filinia brachiata</i>		<i>T. cylindrica</i>	Tcy
<i>F. cornuta</i>		<i>T. elongata</i>	
<i>F. longiseta</i>	Flo	<i>T. gracilis</i>	
<i>F. minuta</i>		<i>T. longiseta</i>	
<i>F. terminalis</i>		<i>T. lophoessa</i>	
<i>Gastropus hyptopus</i>	Ghy	<i>T. pusilla</i>	Tpu
<i>Hexarthra mira</i>	Hmi	<i>T. rousseleti</i>	
<i>Keratella cochlearis</i>	Kco	<i>T. similis</i>	Tsi
<i>K. quadrata</i>		<i>T. stylata</i>	
<i>K. valga</i>	Kva	<i>Trichotria tetractis</i>	

Rotifer species distribution in relation to environmental variables

The DCA result shows that the maximum length of gradient was 3.940 standard deviation (SD), suggesting the relationship between rotifers and environmental variables could be either linear or unimodal. Therefore, we performed both redundancy

Table 4

Factor loading matrix for rotifer-related variables after a varimax rotation.

	Factor 1	Factor 2	Factor 3	Factor 4
NO_3^-	0.92**	-0.02	0.11*	-0.05
NO_2^-	0.91**	-0.05	-0.02	-0.09
TN	0.78**	0.18**	-0.32**	-0.06
TP	0.73**	0.29**	-0.30**	0.02
NH_4^+	0.69**	0.31**	-0.26**	-0.05
Chl a	0.59**	0.48**	-0.34**	0.08
Latitude	0.30**	0.76**	0.09	0.24**
Longitude	0.01	0.70**	0.55**	-0.20**
Depth	-0.04	-0.88**	-0.02	0.02
Temperature	-0.09	0.09	0.82**	0.26**
pH	-0.13*	0.05	0.03	0.92**
Area	-0.40**	0.06	0.71**	-0.23**
Transparency	-0.53**	-0.43**	0.28**	0.29**
<i>Chydorus</i>	0.78**	-0.26**	0.10	-0.11*
Diaptomidae	0.71**	-0.02	-0.09	-0.15**
<i>C. cornuta</i>	0.69**	0.34**	0.03	0.10
<i>Bosmina</i>	0.57**	0.40**	0.35**	0.32**
<i>D. brachyurum</i>	0.36**	0.68**	0.23**	-0.25**
<i>T. taihokuensis</i>	0.23**	0.10	0.87**	-0.13*
<i>M. notius</i>	0.19**	0.68**	-0.46**	-0.08
<i>C. vicinus</i>	0.05	-0.58**	-0.18**	-0.25**
<i>M. micrura</i>	0.01	0.47**	0.09	-0.20**
<i>Daphnia</i>	-0.05	-0.31**	-0.14*	0.68**
<i>S. dorrii</i>	-0.06	-0.05	-0.04	0.89**
<i>S. forbesi</i>	-0.06	0.37**	-0.06	-0.13*
<i>B. deitersi</i>	-0.08	0.03	0.76**	-0.06

The asterisk indicates significant relationships between variables and factors (* $P < 0.05$, ** $P < 0.01$).

Table 3

Percentage composition of the most dominant rotifers in spring/summer.

	Kco	Ban	Bca	Flo	Kva	Pol	Tpu	Tsi	Afi	Hmi
Nanhu	16/2.7	39/7.8	5.2/9.2	19/11	0/4.8	21/11	0/47			
Sanliqi	5.6/0.2	26/3.1	11/24	15/7.0	0.7/0	38/41	0/4.1			
Hongxing	0.9/0	67/0.5	2.2/19	25/5.5		2.2/15	0/45			
Sanjiao	20/0	31/3.0	0/16	15/14	1.8/0	29/2.0	0/58			0/0.7
Houguan	9.6/0.8	6.3/0	5.9/0	14/15	5.0/0.8	35/20	10/40	3.4/2.0	2.5/1.6	1.4/0
Moshui		79/1.9	0/4.8	1.5/6.3		15/9.3	0/37			0/23
Longyang	5.3/0	11/12	4.3/25	62/22	1.1/0	2.1/24	0/2.9			0/10
Qingling	0.8/0		0.4/2.0	0.8/9.4		25/17	5.3/14			0/52
Tianzhenzhou	20/5.7	0/2.7	20/0	0/0.2	0/0.2	0/61	0/1.0			0/28
Laojiang	0/13	27/6.3		0/0.4		0/47	0/3.8	0/26		0/3.0
Niushan	43/67	0/1.4		1.2/0		52/17	2.4/1.7	0/1.0		
Baoan	52/6.3	1.4/0.6	0/0.4	2.3/2.1	0.2/2.1	31/8.3	0.9/3.9	0/55	4.7/4.7	
Qiaodun	0/22			2.5/0.6	10/35	76/10	1.3/0	0/3.8	0/17	
Huama	9.0/0	0.2/0	0/0.3	0.2/15		26/35	16/21	0.7/12		
Zhangdu	0/1.4	0/0.5		0/4.1		50/5.0	17/14	0/13		
Honghu	31/8.2	0.9/2.6		1.1/1.4	0.2/2.1	50/7.4	3.3/13	1.4/30	0/6.0	3.5/0
Yangcheng	23/13	6.3/2.9	3.7/1.1	4.2/7.6	7.7/3.1	53/26	0.1/20	0.9/13		0/2.1
Dianshan	2.8/6.2	8.4/12	18/6.2	26/6.8	6.2/2.1	33/42	0/1.1		0/1.6	0/1.4
Gehu	4.3/0	7.5/3.3	8.9/7.0	15/33	28/0	35/43	0/4.6		0/0.4	0/1.5
Longgan	9.7/31	4.4/2.4	0.4/0	0.9/5.5	1.3/0.8	78/25	3.5/14	1.3/11		
Junshan	1.5/53	0/2.9		1.5/0.3	0/1.6	82/15	1.5/10	0/5.2		
Dongdong	28/22	3.5/1.5	0/0.3	1.2/1.5	5.3/1.2	52/42	2.9/7.6	4.1/5.5		0.6/11
Shijiu	4.1/18	6.1/0.9		2.0/1.7	12/3.1	31/38	24/27	4.7/0.9		
Wuchang	38/7.4	0.9/4.6		0.3/5.7	6.9/0	1.2/49	32/27	19/0.1		
Banghu	21/14	1.7/0		0.6/0		56/67	2.9/13	1.5/0		11/5.8
Dahuchi	7.0/2.0	0.7/0			0.3/0	82.3/91.1	6.7/0	1.7/1.5		0/1.5
Dachahu	13/13	0.8/0		1.2/0	0.6/0	60/59	4.3/12	3.7/3.8		14/7.5

Table 5

Models for rotifer density are listed by the order of the factors involved. F1, F2, F3 and F4 refer to the first four factors extracted from the principal components analysis, see Table 4.

	Models	r^2
Physicochemicals	$y = 2.58 + 0.379F2$	0.158
	$y = 2.58 + 0.379F2 + 0.193F1$	0.199
	$y = 2.58 + 0.379F2 + 0.193F1 + 0.134F3$	0.219
Crustaceans	$y = 2.58 - 0.511F4$	0.288
	$y = 2.58 - 0.511F4 + 0.101F2$	0.299

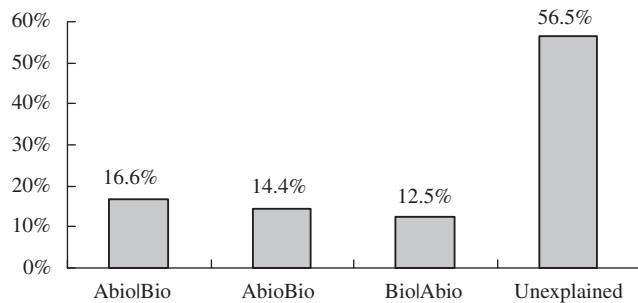


Fig. 3. The relative portion explained by pure physicochemical factors (Abio|Bio), pure crustaceans (Bio|Abio) and the interaction between the two explanatory data sets (AbioBio).

Table 6

Results of forward selection and Monte Carlo permutation tests from RDA.

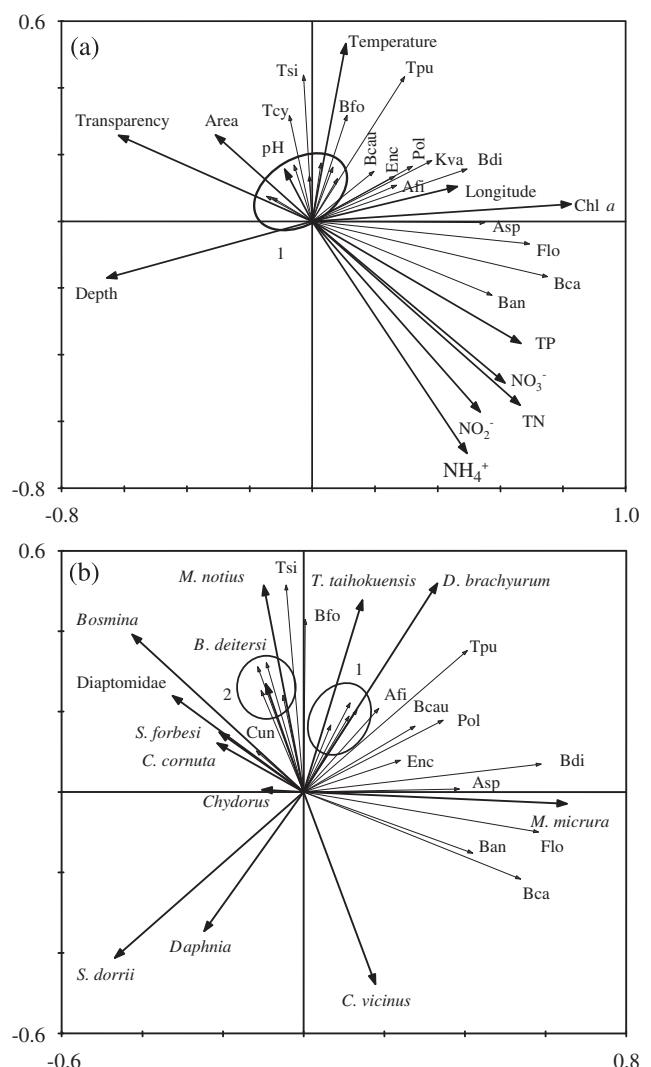
	$\lambda-1$	$\lambda-A$	P	F
Chl a	0.13	0.13	0.002	50.2
Longitude	0.05	0.04	0.002	18.9
NH ₄ ⁺	0.07	0.04	0.002	17.7
NO ₃ ⁻	0.08	0.02	0.002	9.48
TP	0.10	0.02	0.002	6.12
Area	0.04	0.01	0.002	5.13
Temperature	0.02	0.01	0.002	5.27
Transparency	0.08	0.01	0.002	5.47
Depth	0.08	0.01	0.002	4.20
NO ₂ ⁻	0.07	0.01	0.002	3.97
TN	0.10	0.00	0.004	2.91
pH	0.01	0.01	0.022	2.40
<i>M. micrura</i>	0.06	0.06	0.002	22.4
<i>Bosmina</i>	0.04	0.04	0.002	15.2
<i>S. dorrii</i>	0.04	0.03	0.002	13.5
<i>C. vicinus</i>	0.03	0.04	0.002	12.7
<i>D. brachyurum</i>	0.03	0.01	0.002	5.46
Diaptomidae	0.02	0.02	0.002	7.80
<i>S. forbesi</i>	0.01	0.01	0.002	6.18
<i>C. cornuta</i>	0.01	0.01	0.002	4.37
<i>B. deitersi</i>	0.02	0.01	0.002	3.82
<i>T. taihokuensis</i>	0.02	0.01	0.002	4.08
<i>M. notius</i>	0.02	0.02	0.002	7.30
<i>Chydorus</i>	0.01	0.00	0.002	3.78
<i>Daphnia</i>	0.02	0.01	0.016	2.25

analysis (RDA) and canonical correspondence analysis (CCA). Except for latitude, all environmental variables were retained in the forward selection procedure. Since the RDA explained more of the variance in rotifer species distribution than the CCA in the first four axes (RDA: 43.5%, CCA: 32.9%) we chose for the RDA. The results of the RDA applied to the two sets of explanatory variables indicate that both biotic and abiotic factors had significant influence on rotifer species distribution ($P < 0.05$; Monte Carlo permutation test, 499 unrestricted), explaining 26.9% and 31.0% of the total variance, respectively. The percentages contributed by

pure physicochemical factors and pure crustaceans were 16.6% and 12.5%, respectively (Fig. 3). However, these two percentages were marginally different (bootstrap test, $P = 0.052$).

The most discriminant physicochemical variables, e.g. Chl a and NH₄⁺, were strongly associated with Axis 1 and Axis 2, respectively (Table 6; Fig. 4a), indicating that these two axes were mainly related to trophic status. Along the gradient of trophic status, one distinct rotifer group was found at high trophic status. This group included *B. angularis*, *B. calyciflorus*, *F. longiseta*, *Brachionus diversicornis*, and *Asplanchna*. Other species were distributed at low or median trophic status. Several rotifer species were impacted by temperature to some extent; for example, *Trichocerca cylindrica*, *T. pusilla*, *T. similis* and *Brachionus forficula* were found at high temperature.

The coexistence of rotifer species with crustacean zooplankton seemed to be determined by their defense against potential competitors and predators (Fig. 4b). For example, *Moina micrura* is a small omnivorous species in eutrophic lakes. Rotifer species associated with it, e.g. *Brachionus*, *Asplanchna*, *Polyarthra*, *F. longiseta* and *T. pussila*, are also commonly found in eutrophic water. The small *Bosmina* had no strong negative effects on *K. cochlearis*, *T. cylindrica* and *Trichocerca capucina*. Notably, *T. similis* and *B. forficula* peaked with carnivorous *M. notius* and



T. taihokuensis, while no rotifer species was found peaking with large herbivorous *S. dorrii* and *Daphnia*.

Discussion

In the present study, water depth was the most important physicochemical variable in explaining the total variance of rotifer density. Beaver and Havens (1996) also found that at low lake level, the average lake-wide rotifer density was greater than during high water periods. In our study, the largest rotifer density was found in the shallowest Lake Gehu. When referring to Table 2 in Wang et al. (2007b), we could find that the shallower lakes were more eutrophic. Thus, the water depth may be regarded as a proxy of trophic status for the study lakes. Meanwhile, inorganic nitrogen such as NO_3^- and NO_2^- can help increase the rotifer density. Temperature only showed a little contribution to the model. Consequently, we concluded that trophic status is an important determinant of rotifer density in lakes. This trend is also reported for other zooplankton (Auer et al. 2004; Bays and Crisman 1983; Pace 1986; Yoshida et al. 2003).

The variance in rotifer density explained by crustaceans was mainly contributed by *S. dorrii* and *Daphnia*. Yoshida et al. (2003) attributed bottom-up forces being more important than crustaceans in regulating the rotifer density to the lack of large-sized *Daphnia*. The works of Fussmann (1996) and Conde-Porcuna (2000) also suggest exploitative competition to be the main mechanism through which cladocerans constrain rotifer populations. *S. dorrii* and *Daphnia* are generally filter-feeding species. Their higher filtering rates provide them the advantage to constrain rotifers. In Fig. 4b, no rotifer species was found peaking with them, suggesting that exploitative competition works between large crustaceans and rotifers.

Variation partitioning analysis showed that the variance of rotifer species distribution explained by pure physicochemical factors and pure crustaceans was not statistically different. The distribution of rotifer species was predominantly affected by Chl *a* and *M. micrura*. Although not all algae represented by Chl *a* can be consumed by rotifers, it may be a representative of edible algae or other food resources accompanied with it (Auer et al. 2004). *M. micrura* is a common species in eutrophic lakes (Wang et al. 2007a). As the rotifers associated with *M. micrura* are all indicators of eutrophic water (Sládeček 1983), it seems that Axis 1 in Fig. 4b was a reflection of trophic status. This may in turn explain why a relatively high contribution (14.4%) was shared by abiotic and biotic factors. The distribution of rotifer species along the gradient of trophic status has been suggested by Duggan et al. (2001, 2002). Our results also conform to this pattern. Their different preferences for trophic status are attributed to food type and density (Pejler 1983). For example, *B. angularis*, *B. calyciflorus*, *F. longiseta*, *B. diversicornis*, which are feeders of bacteria, appeared well adapted to living at high trophic status, while *Conochilus unicornis* and *Gastropus*, which are filtrators of minute algal particles, appeared well adapted to living at low trophic status.

In addition, some rotifers can protect themselves through particular morphological characteristics (Brandl 2005). For example, *T. similis* and *B. forficula*, which have rigid lorica, showed density peaks with predatory cyclopoids *M. notius* and *T. taihokuensis*. However, the soft-bodied species, e.g. *Asplanchna*, showed a trend to keep away from invertebrate predators.

The variance in rotifer density and species distribution unexplained by our data was relatively high, with a total of about 70% and 56.5% respectively. Pejler (1983) attributed species preferences along a trophic gradient to the size and nature of the particulate food present. In our study, the chemical variables were only indicators of potential food resources. No size-ranked

algae, heterotrophic nano-flagellates and bacteria were presented in the factor analysis and RDA. Another important undermined factor was planktivorous fish predation, a usual top-down force in subtropical lakes. In the present study, several lakes sampled were densely stocked with filter-feeding silver and bighead carp. Their direct prey on large crustaceans and rotifers may indirectly favor the development of small rotifers by releasing them from predators and competitors (Shao et al. 2001; Stenson 1982; Telesh 1993). The rotifer density was usually abundant in such lakes, such as Lakes Nanhу, Sanliqi, Hongxing and Gehu. Likewise, no other invertebrate predators, e.g. *Chaoborus* and *Leptodora kindtii*, were incorporated into the multivariate analysis (Devetter 1998; Hanazato 1991). Many other factors along the trophic gradient can also cause the variation of rotifer species distribution. Examples of these include toxic *Microcystis* (Liu et al. 2002), alkalinity (Devetter 1998) and the degree of oxygen (Berzins and Pejler 1989; Mikschi 1989). These factors will weigh in favor of the growth and survival of particular rotifer species.

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