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Competitive outcome between the rotifer *Brachionus calyciflorus* and the cladoceran *Moina macrocopa* depends on algal density but not temperature

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Abstract – The rotifer *Brachionus calyciflorus* often occurs simultaneously with the cladoceran *Moina macrocopa* in tropical water bodies. We studied the effects of temperature (20, 25 and 30 °C) and algal density (0.5, 1.0 and 3.0×10^6 cells.mL^{-1} *Scenedesmus obliquus*) on the outcome of competition and duration of coexistence between *B. calyciflorus* and *M. macrocopa* using population growth experiments. The results showed that regardless of temperature, *M. macrocopa* outcompeted *B. calyciflorus* at the lowest algal density (0.5×10^6 cells.mL^{-1}), whereas *B. calyciflorus* outcompeted *M. macrocopa* at the higher algal densities (1.0 and 3.0×10^6 cells.mL^{-1}). The duration of coexistence shortened with increasing temperature when *M. macrocopa* outcompeted *B. calyciflorus*, and those with increasing temperature and algal density when *B. calyciflorus* outcompeted *M. macrocopa*. Our results suggested that the competitive outcome between the rotifer *B. calyciflorus* and the cladoceran *M. macrocopa* was dependent on algal density but not temperature, the duration of coexistence between them was dependent on algal density and temperature, and the exploitative competition of *M. macrocopa* over *B. calyciflorus* may be more important than the interference competition.

Key words: Competitive outcome / coexistent duration / algal density / temperature / *Brachionus calyciflorus* / *Moina macrocopa*

Introduction

It is well known that competition and predation are the two major biotic interactions that regulate zooplankton population dynamics and community structure (*e.g.*, Rothhaupt, 1990; Arndt, 1993; Lampert and Sommer, 1997; Chase *et al.*, 2002; Dodson, 2005), and competition becomes crucial when predation pressure is low in some environments (Dodson, 1974). Competition, as defined by Birch (1957), includes exploitative competition for food and interference competition for space. Competitive outcome between two competitors is exclusion or coexistence. Competitive exclusion of one competitor is when two species compete for the same limiting resource and the inferior competitor is excluded (Tilman *et al.*, 1981). Coexistence is mediated if intraspecific competition is stronger than the interspecific competition (Begon *et al.*, 1996).

Rotifers and cladocerans are important constituents and dominant groups of freshwater zooplankton communities (Hutchinson, 1967). They are to compete for food resources due to resemblance in their life-history strategies (Allan, 1976) and overlap in their feeding habits (Downing and Rigler, 1984; Sterner, 1989; Walz, 1995). Generally, larger cladocerans ($\geq$1200 mm) suppress rotifers through exploitative and mechanical interference competition (Dodson, 1974; Gilbert, 1988a, 1988b), but exploitative competition is more common (Pollard *et al.*, 1998), due to higher filter feeding rates and larger body sizes of cladocerans (de Bernardi *et al.*, 1987; Yang and Huang, 2000). Smaller cladocerans ($\leq$1200 mm) are less likely than larger cladocerans to competitively suppress rotifers and often co-occur with them at high densities in natural communities in the absence of large *Daphnia* because smaller cladocerans: (1) generally do not mechanically interfere with rotifers; (2) are less likely to deplete food resources; (3) are themselves more likely to be suppressed by exploitative competition with rotifers; and (4) usually are more susceptible to invertebrate predation (Gilbert, 1988a).

In tropical waterbodies, several species of rotifers such as the genera *Brachionus* and smaller cladocerans such as

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*Corresponding author: `ylxi1965@126.com` the genera *Moina* occur simultaneously (Nogrady *et al.*, 1993; Dumont *et al.*, 1994; Lampert and Sommer, 1997). Many researchers have found that food density and temperature are two of the most important factors affecting the survival and reproduction of *Brachionus calyciflorus* (*e.g.*, Lucía-Pavón *et al.*, 2001; Dong *et al.*, 2004; Xi *et al.*, 2005a; Nandini *et al.*, 2007a; Kauler and Enesco, 2011) and *Moina macrocopa* (*e.g.*, Burak, 1997; Yoon *et al.*, 2000; Benider *et al.*, 2002; Nandini and Sarma, 2003; Xi *et al.*, 2005b; Nandini *et al.*, 2007b). The most conformable temperature for *B. calyciflorus* and *M. macrocopa* was from 25 to 30 °C (He, 1983; Xi *et al.*, 2000, 2005b). 3.0–6.0 × 10^6 cells.mL^{-1} of *Scenedesmus obliquus* densities and 0.5–2.0 × 10^6 cells.mL^{-1} of *Chlorella vulgaris* were the most favorable for *B. calyciflorus* and *M. macrocopa*, respectively (Xi *et al.*, 2000, 2005b). However, the body size of *C. vulgaris* was much smaller than that of *S. obliquus* (Song, 1962). So, the most favorable algal density for *B. calyciflorus* was much higher than that of *M. macrocopa*. Hence, we can infer that *M. macrocopa* has competitive superiority over *B. calyciflorus* under lower algal density and *B. calyciflorus* has competitive superiority over *M. macrocopa* under higher algal density and temperature may not alter competitive superiority of *B. calyciflorus* or *M. macrocopa* over each other. Meanwhile, the two factors may also have some effects on the competitive outcome between *B. calyciflorus* and *M. macrocopa*. For example, Xi and Hagiwara (2007) have showed that *M. macrocopa* rapidly excluded *B. calyciflorus* in polycultures but was itself unaffected by the presence of *B. calyciflorus*, regardless of the *C. vulgaris* density. However, they did not consider the effect of temperature on the competitive outcome between *M. macrocopa* and *B. calyciflorus*. Moreover, Espinosa-Rodríguez *et al.* (2012) suggested that the competitive outcome between cladocerans and rotifers was dependent on diet type. Hence, it is possible that the competitive outcome between *B. calyciflorus* and *M. macrocopa* may be different at different temperature and *S. obliquus* density.

Interaction strengths such as competitive strength estimate the magnitude of the effect of one species on another (Laska and Wootton, 1998). Temperature may affect a species by changing the strength of its competitive interaction with coexisting species (Rall *et al.*, 2010). By modifying interaction strength temperature may not only directly affect population densities, but it may also indirectly affect the population size of coexisting species (Berlow *et al.*, 2009). Field and laboratory experiments revealed that the strength of competition varied greatly along the food resource and temperature gradient, interspecific competition was more intense when food resource was more scarce (*e.g.*, Holbrook and Schmitt, 1989; Xi and Hagiwara, 2007; Sarma *et al.*, 2008) and temperature was higher (*e.g.*, Feniova and Zilitinkevich, 2012). Hence, competitive strength might be negatively related to duration of coexistence.

In the present study, the effects of temperature and *S. obliquus* density on the competitive outcome and duration of coexistence between *B. calyciflorus* and *M. macrocopa* were examined using population growth experiment to test the following hypothesis: (1) *M. macrocopa* strongly suppresses *B. calyciflorus* under low algal densities and *B. calyciflorus* strongly suppresses *M. macrocopa* under high algal densities; (2) temperature does not alter the competitive outcome between *M. macrocopa* and *B. calyciflorus*; (3) the intensity of the suppression is inversely related to algal density, but directly related to temperature.

Materials and methods

Experimental organisms

Brachionus calyciflorus and *M. macrocopa* were used in this study. *B. calyciflorus* was isolated from Lake Jiuliantang (31°33'N, 118°37'E, Wuhu city, China), and *M. macrocopa* was supplied by Laboratory of Aquaculture Biology, Nagasaki University of Japan. Both species were clonally cultured from one amictic female for more than 1 year at 25 ± 1 °C, on natural illumination in an illumination incubator, using EPA (pH 7.4–7.8; prepared by dissolving 96 mg $NaHCO_3$, 60 mg $CaSO_4$, 60 mg $MgSO_4$, and 4 mg KCl in 1 L distilled water) medium (USEPA, 1985) and *S. obliquus* at 1.0–2.0 × 10^6 cells.mL^{-1} as the exclusive food. Before the experiments commenced, the two zooplanktons were fed on 0.5, 1.0 and 3.0 × 10^6 cells.mL^{-1} *S. obliquus* at 20 ± 1, 25 ± 1 and 30 ± 1 °C for more than 1 week, respectively. During the period, the two zooplankton populations were kept in log-phase growth. *S. obliquus* were grown in a semi-continuous culture using HB-4 medium (Li *et al.*, 1959) and refreshed daily at 40%. Algae in exponential growth were centrifuged at 3000 rpm for 5 min and resuspended in the EPA medium and then stored at 4 °C. Stock algae density was determined using a haemocytometer, and diluted to the desired experimental algal density.

Competition experiments

Population growth experiments were conducted in 25 mL glass beakers containing 20 mL EPA medium. We all used three replicates for *B. calyciflorus* and *M. macrocopa* separated as controls and mixed at three food densities and temperatures mentioned above. Thus, a total of 81 glass beakers (three temperatures × three algae densities × three treats × three replicates) were used during the experiments. The initial density of *M. macrocopa* (<24 h) and *B. calyciflorus* (randomly picking from the exponential growth population) was 0.2 and 3.0 ind.mL^{-1}, respectively. Following inoculation, every day we estimated the density of *M. macrocopa* and *B. calyciflorus* using either total count or three aliquots of 1–5 mL each. We confirmed randomly that the rotifer densities estimated through aliquot sampling were not significantly different from whole counts. The test separated and mixed zooplanktons were then transferred

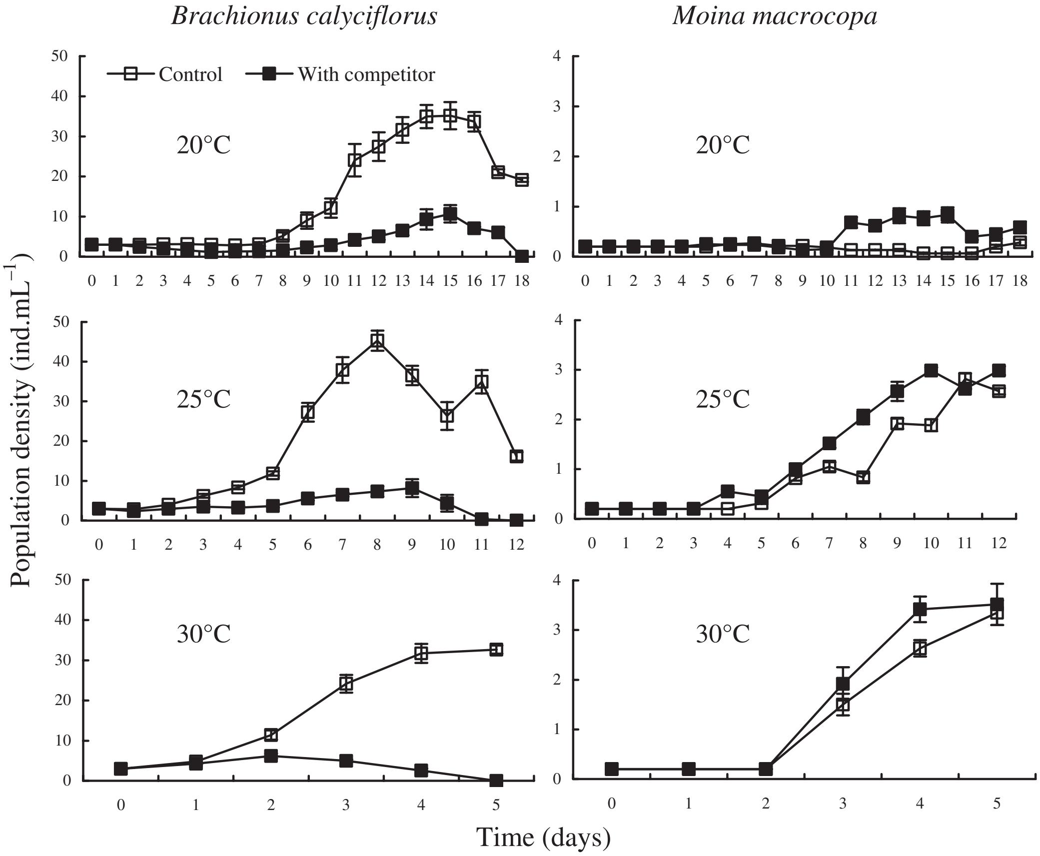

Fig. 1. Population growth of *Brachionus calyciflorus* and *Moina macrocopa* in control and mixed cultures at 0.5 × 10^6 cells.mL^{-1} *S. obliquus* and three temperatures (mean ± SE).

to fresh beakers containing the appropriate algal density under each temperature. The experiments were discontinued until one of the two species went to extinction. Based on the data collected, we derived the population growth rate (r) per day using the exponential equation: $r = (\ln N_t - \ln N_0)/t$, where N_0 and N_t are the initial and final population densities, respectively, and t is the time in days (Krebs, 1985). The varying data points along the growth curve were selected to calculate the mean growth rate per replicate. Generally, we took 4–6 data points during the exponential phase of the population growth for each replicate, following Dumont *et al.* (1995).

Statistical analysis

Analysis-of-variance (ANOVA) and multiple comparison tests were performed by SPSS 16.0 to quantify the differences in the population growth rates, maximal population densities and durations of coexistence of zooplankton, respectively.

Results

The population dynamics of *B. calyciflorus* and *M. macrocopa* in controls and mixed cultures at three *S. obliquus* densities (0.5, 1.0 and 3.0 × 10^6 cells.mL^{-1}) and three temperatures (20, 25 and 30 °C) are presented in Figures 1–3. In general, the densities of *B. calyciflorus* and *M. macrocopa* in controls and mixed cultures increased with increasing temperature and algal density except the groups that presented negative growth in the combination of the lowest temperature (20 °C) and highest algal density (3.0 × 10^6 cells.mL^{-1}). Regardless of the temperature and algal density, *B. calyciflorus* and *M. macrocopa* grown in the presence of competitor had lower population densities than that in the controls, but *M. macrocopa* presented the reverse trends at the lowest algal density. At each temperature, *M. macrocopa* outcompeted *B. calyciflorus* at low algal density (0.5 × 10^6 cells.mL^{-1}), reversely *B. calyciflorus* excluded *M. macrocopa* at higher algal density (1.0 and 3.0 × 10^6 cells.mL^{-1}).

Generally, at any *S. obliquus* densities, the population growth rates of *B. calyciflorus* and *M. macrocopa* cultured alone increased with increasing temperature. At the lowest algal density (0.5 × 10^6 cells.mL^{-1}), regardless of the temperature, the population growth rates of *B. calyciflorus* cultured with *M. macrocopa* were lower than that in controls, whereas the population growth rates of *M. macrocopa* cultured with *B. calyciflorus* were higher than that in controls and in *B. calyciflorus* cultured with *M. macrocopa* (Fig. 4). Statistically the population growth rate of *B. calyciflorus* was significantly affected by

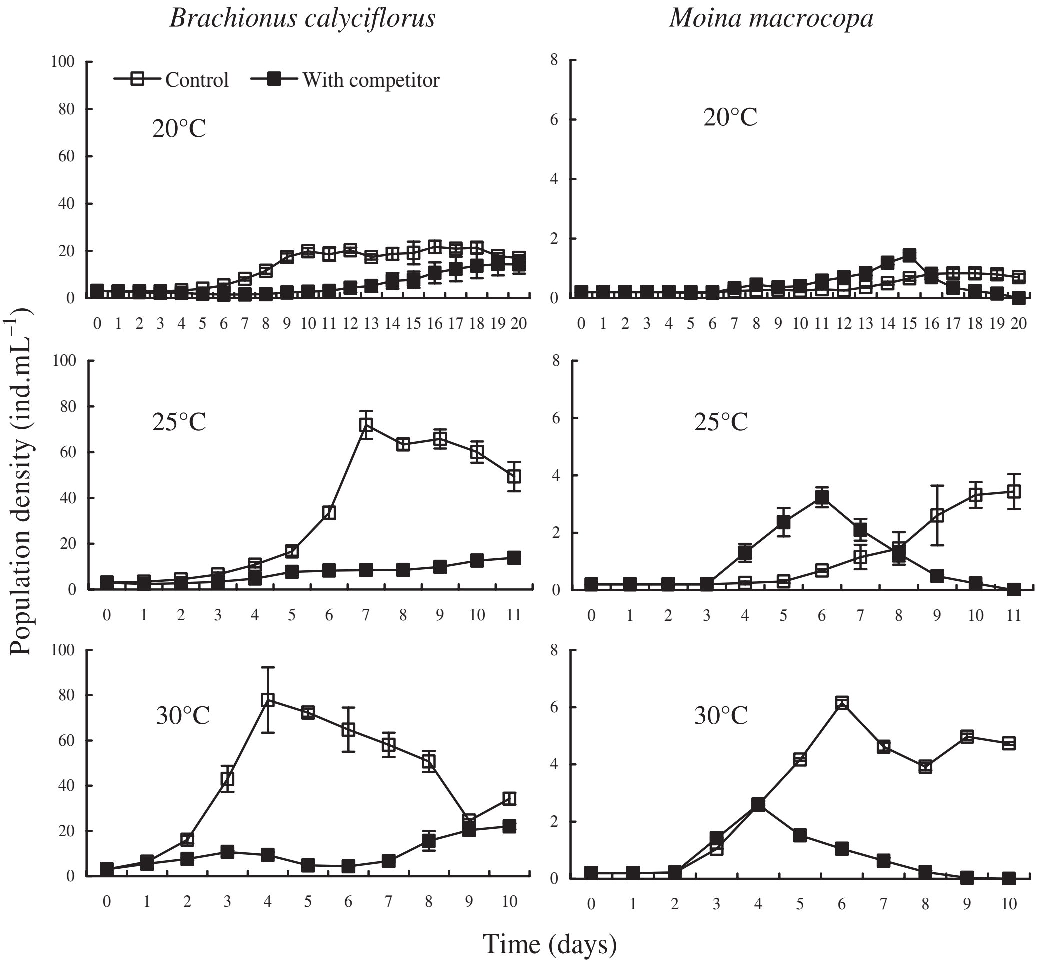

Fig. 2. Population growth of *Brachionus calyciflorus* and *Moina macrocopa* in control and mixed cultures at 1.0×10^6 cells.mL^{-1} *S. obliquus* and three temperatures (mean ± SE).

temperature, algal density, the presence of *M. macrocopa* and their interactions ($P < 0.05$). For *M. macrocopa*, the population growth rate was significantly affected by the temperature, interactions of temperature × algal density and temperature × competition of *B. calyciflorus* ($P < 0.001$) (Table 1).

At higher temperatures (25 and 30 °C), the peak population densities of *B. calyciflorus* cultured alone and with *M. macrocopa* increased with increasing *S. obliquus* density. At any temperatures and *S. obliquus* densities, the peak population densities of *B. calyciflorus* cultured with *M. macrocopa* were lower than that in controls. For *M. macrocopa*, at any algal densities, the peak population densities in controls increased with increasing temperature. At any temperatures, the peak population densities of *M. macrocopa* cultured with *B. calyciflorus* decreased with increasing algal density, and they were higher than that in controls (Fig. 5). Statistically the peak population density of *B. calyciflorus* was significantly affected by temperature, algal density, the presence of *M. macrocopa* and their interactions ($P < 0.05$). For *M. macrocopa*, temperature, the presence of *B. calyciflorus*, but not algal density, and their interactions significantly influenced the peak population density of *M. macrocopa* ($P < 0.01$) (Table 1).

The results of the duration of coexistence between *B. calyciflorus* and *M. macrocopa* grown at three temperatures and three algal densities are presented in Figure 6. The duration of coexistence shortened (competitive strength intensified) with increasing temperature when *M. macrocopa* outcompeted *B. calyciflorus* at the lowest algal density. Also, the duration of coexistence shortened (competitive strength intensified) with increasing temperature and algal density when *B. calyciflorus* outcompeted *M. macrocopa* at the higher algal densities. Statistically the duration of coexistence between *B. calyciflorus* and *M. macrocopa* was significantly affected by temperature, algal density and their interaction ($P < 0.01$) (Table 2).

Discussion

In natural water ecosystems, several environmental factors interact to regulate the development of zooplankton populations. Temperature and food density are two important ecological factors affecting the population

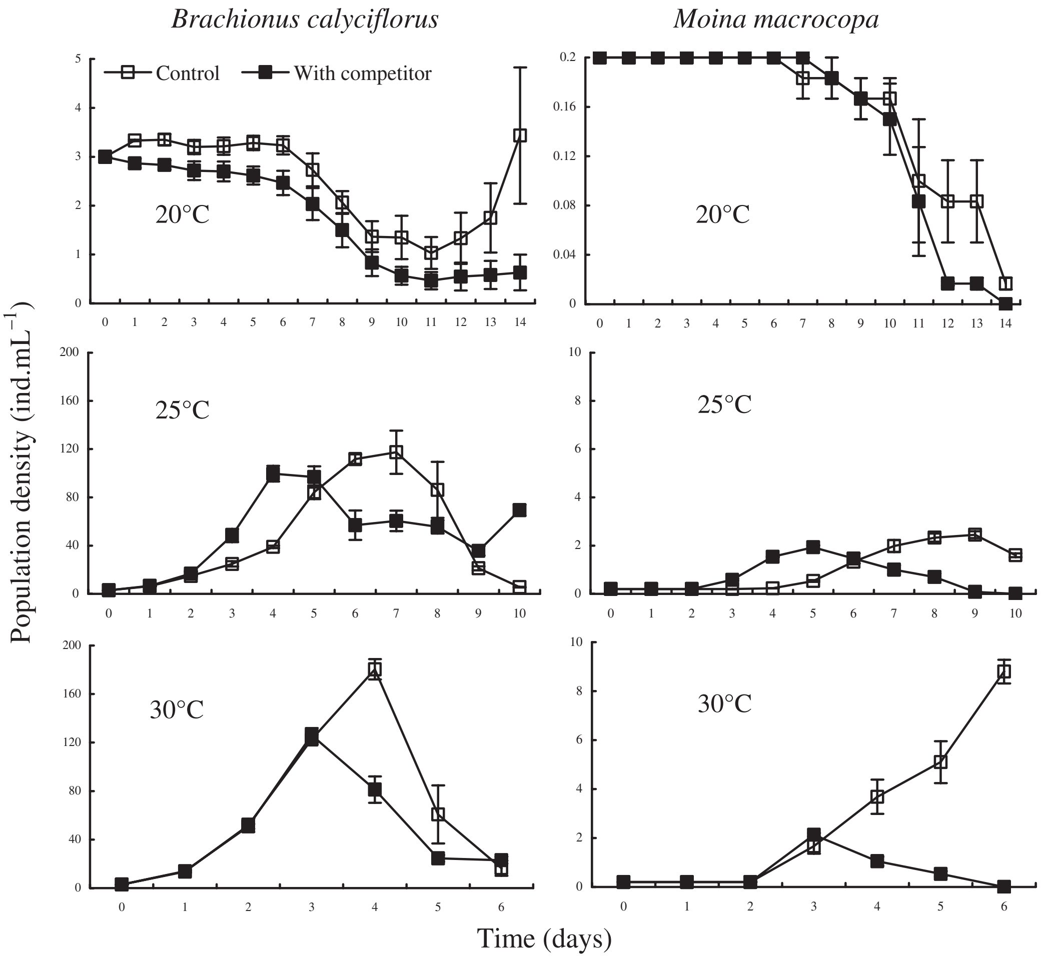

Fig. 3. Population growth of *Brachionus calyciflorus* and *Moina macrocopa* in control and mixed cultures at 3.0×10^6 cells.mL^{-1} *S. obliquus* and three temperatures (mean ± SE).

growth of rotifers and cladocerans. In general, increases in temperature and food density have stimulatory effect on the population growth rates of rotifers and cladocerans (*e.g.*, Burak, 1997; Yoon *et al.*, 2000; Lucía-Pavón *et al.*, 2001; Benider *et al.*, 2002; Nandini and Sarma, 2003; Xi *et al.*, 2005a, 2005b; Nandini *et al.*, 2007a, 2007b; Kauler and Enesco, 2011). However, the lower temperature and higher food density or higher temperature and lower food density may have adverse influence on the population growth of rotifers (Sarma and Rao, 1990). In the present study, population densities also increased with increasing temperature and algal density except the combination of the lowest temperature (20 °C) and highest algal density (3.0×10^6 cells.mL^{-1} *S. obliquus*), which presented negative growth. Excessively high algal density caused decreased population densities in *B. calyciflorus* and *M. macrocopa* at low temperature, which is probably caused by an increased effort in algae gathering and reduced net energy assimilation (Xi *et al.*, 2005b).

Although large *Daphnia* (≥ 1200 μm) can suppress rotifers by both through exploitative competition for shared, limiting food resources and through mechanical interference, rotifers seem to be much less inhibited by small cladocerans (≤ 1200 μm) and often co-occur with them at high densities in natural communities in the absence of large *Daphnia* (Gilbert, 1988a). *M. macrocopa* body size is about 1286 μm (Hurtado-Bocanegra *et al.*, 2002), which seems belong to medium cladoceran. So the competitive outcome between *M. macrocopa* and rotifers may be partly different from the conclusions of Gilbert (1988a). For example, Hurtado-Bocanegra *et al.* (2002) have showed that both the maximal population density and the population growth rate of *M. macrocopa* were negatively affected by *Brachionus patulus*, especially the combined effects of low food level (0.5×10^6 cells.mL^{-1} *C. vulgaris*) and high initial density of *B. patulus* (5 ind.mL^{-1}) resulted in a 50% reduction in the peak population density of *M. macrocopa*, although the population growth of *B. patulus* was also negatively influenced by the presence of *M. macrocopa*. However, Xi and Hagiwara (2007) have showed that *M. macrocopa* rapidly excluded *B. calyciflorus* from mixed-species cultures but was itself unaffected by the presence of *B. calyciflorus*, regardless of the algal density (*C. vulgaris*) or initial *B. calyciflorus* population density. In the present study, regardless of temperature, *M. macrocopa*

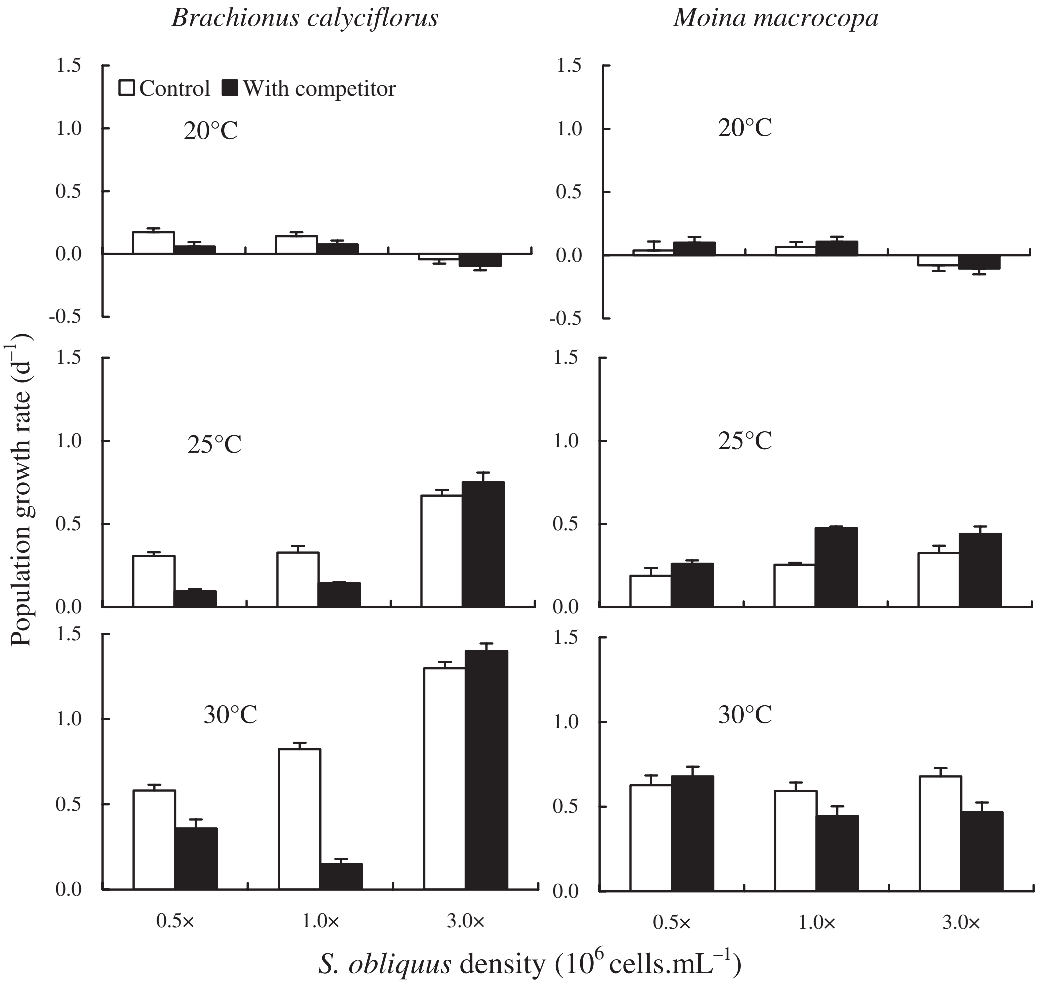

Fig. 4. Population growth rate per day of *Brachionus calyciflorus* and *Moina macrocopa* in control and mixed cultures at three densities of *S. obliquus* and three temperatures (mean ± SE).

outcompeted *B. calyciflorus* at limiting food resource (0.5×10^6 cells.mL^{-1} *S. obliquus*), reversely *B. calyciflorus* outcompeted *M. macrocopa* at relative abundant food resource (1.0×10^6 and 3.0×10^6 cells.mL^{-1} *S. obliquus*). It is obvious that competitive outcome between *M. macrocopa* and *B. calyciflorus* was dependent on algal density not on temperaturein our study. In addition, the competitive outcome between *M. macrocopa* and *B. calyciflorus* was also affected by heavy metals and exposure time (Gama-Flores *et al.*, 2006; Ahmed, 2011). The results above mentioned showed that the outcomes of competition between *M. macrocopa* and rotifers may be dependent on their relative initial population density, rotifers species and body size, food type and density, and toxicant concentrations and exposure time.

Various mechanisms such as the size efficiency hypothesis (Lampert and Sommer, 1997), the threshold food hypothesis (Stemberger and Gilbert, 1985; Lampert and Sommer, 1997), the resistance to starvation (Kirk, 1997; Chen *et al.*, 2004), the population growth rate (Romanovsky, 1984), the relative rates and efficiencies of filtration, consumption and assimilation, embryonic developmental time, lower age at first reproduction, and epizoic or evasive behavior of some rotifers (DeMott, 1989; Iyer and Rao, 1993; Kak and Rao, 1998) have been proposed for the suppression of rotifers by cladocerans. In the present study, *M. macrocopa* excluded *B. calyciflorus* at lower *S. obliquus* density possibly due to larger body size, higher efficiency of filtration (de Bernardi *et al.*, 1987; Yang and Huang, 2000) and higher population rate of *M. macrocopa* (Fig. 4). However, *B. calyciflorus* excluded *M. macrocopa* at higher *S. obliquus* density possibly due tohigher population abundanceof *B. calyciflorus* (Fig. 5) and *M. macrocopa* was suppressed by exploitative competition with rotifers. Positive relationship exists between threshold food concentration and body size for rotifers (Stemberger and Gilbert, 1987). Conversely, negative relationship exists between threshold food concentration and body size for cladocerans (Gliwicz, 1990). In addition, the relatively strong capacity of *Brachionus plicatilis* in tolerating starvation may be one of the important reasons for it wins the competition against *Moina mongolica* (Chen *et al.*, 2004). In our study, it is need to further study that *M. macrocopa* excluded *B. calyciflorus* at lower *S. obliquus* density whether due to lower threshold food concentration or stronger capacity in tolerating

Table 1. Results of the three-way analysis of variance performed on the population growth rates per day and peak population densities of *Brachionus calyciflorus* and *Moina macrocopa* grown at three temperatures, three algal densities and with and without the competitor.

Source of variation	DF	SS	MS	*F*
Population growth rate				
B. calyciflorus				
Temperature	2	6.69	3.35	579.90***
Algal density	2	3.07	1.53	265.96***
Competition	1	0.39	0.39	67.30***
Temperature × algal density	4	3.54	0.88	153.15***
Temperature × competition	2	0.15	0.08	13.02***
Algal density × competition	2	0.56	0.28	48.94***
Temperature × algal density × competition	4	0.41	0.10	17.65***
Error	73	0.42	0.01	
M. macrocopa				
Temperature	2	3.50	1.75	176.36***
Algal density	2	0.02	0.018	1.22 ns
Competition	1	0.01	0.018	1.01 ns
Temperature × algal density	4	0.30	0.08	7.65***
Temperature × competition	2	0.17	0.09	8.58***
Algal density × competition	2	0.02	0.01	1.21 ns
Temperature × algal density × competition	4	0.07	0.02	1.77 ns
Error	57	0.57	0.01	
Peak population density				
B. calyciflorus				
Temperature	2	35 294.75	17 647.37	217.77***
Algal density	2	43 816.09	21 908.05	270.35***
Competition	1	15 834.63	15 834.63	195.40***
Temperature × algal density	4	41 216.29	10 304.07	127.15***
Temperature × competition	2	3200.94	1600.47	19.75***
Algal density × competition	2	813.57	406.78	5.02*
Temperature × algal density × competition	4	1905.36	476.34	5.88***
Error	36	2917.32	81.04	
M. macrocopa				
Temperature	2	129.94	64.97	90.59***
Algal density	2	3.94	1.97	2.75 ns
Competition	1	16.12	16.12	22.47***
Temperature × algal density	4	13.98	3.49	4.87**
Temperature × competition	2	34.98	17.49	24.39***
Algal density × competition	2	16.48	8.24	11.49***
Temperature × algal density × competition	4	19.97	4.99	6.96***
Error	36	25.82	0.72	

DF, degrees of freedom; SS, sum of squares; MS, mean square; *F*, *F*-ratio.
* Significant ($P < 0.05$).
** Highly significant ($P < 0.01$).
*** Very highly significant ($P < 0.001$).
ns, non-significant ($P > 0.05$).

starvation of *M. macrocopa*. It appears that a single hypothesis or theory cannot be universally applied to understand the outcomes of competition among freshwater zooplankton.

Rotifer suppression by exploitative competition from large cladoceran has been clearly demonstrated (MacIsaac and Gilbert, 1991). Interference competition has also been proposed as a possible mechanism influencing interactions between large cladocerans and rotifers (Gilbert, 1985; Gilbert, 1988a; MacIsaac and Gilbert, 1990; Lampert and Rothhaupt, 1991). Some studies suggest exploitative competition to be the main mechanism through which cladocerans constrain rotifer populations (Fussmann, 1996; Pollard *et al.*, 1998; Conde-Porcuna, 2000; Yoshida *et al.*, 2003). However, *M. macrocopa* rapidly excluded *B. calyciflorus* (both zooplanktons are Japan strain) from mixed-species cultures at both low and high *C. vulgaris* density under both low and high initial *B. calyciflorus* population density and adult *M. macrocopa* imposed significant negative effects on the instantaneous reproductive rates, egg ratios and survivorship of newborn individuals of *B. calyciflorus* (Xi and Hagiwara, 2007). It is suggested that *M. macrocopa* induced interference competition may be more important than exploitative competition through which *M. macrocopa* suppressed *B. calyciflorus* population (Xi and Hagiwara, 2007). In the present study, *M. macrocopa* (Japan strain) outcompeted *B. calyciflorus* (China strain) at low *S. obliquus* density,

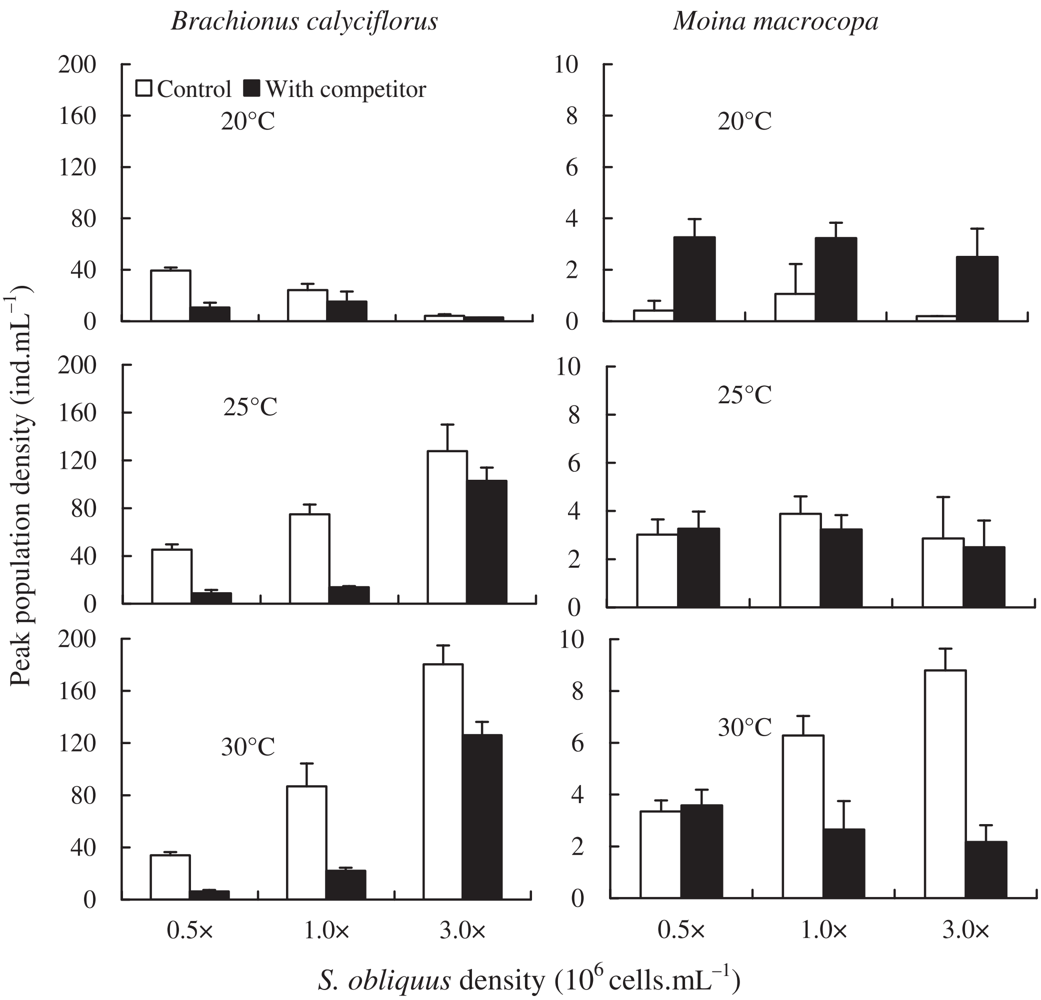

Fig. 5. Peak population density of *Brachionus calyciflorus* and *Moina macrocopa* in controls and mixed cultures at three densities of *S. obliquus* and three temperatures (mean ± SE).

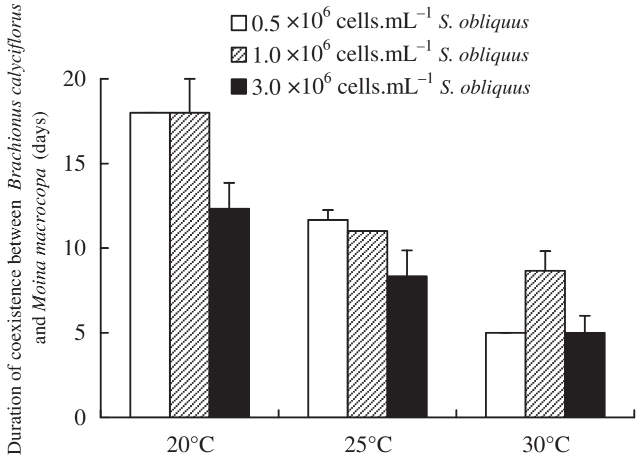

Fig. 6. Duration of coexistence between *Brachionus calyciflorus* and *Moina macrocopa* at three densities of *S. obliquus* and three temperatures (mean ± SE).

Table 2. Results of the two-way analysis of variance performed on the duration of coexistence between *Brachionus calyciflorus* and *Moina macrocopa* grown at three temperatures and three algal densities.

Source of variation	DF	SS	MS	*F*
Temperature	2	444.22	222.12	176.38^{***}
Algal density	2	78	39	30.97^{***}
Temperature × algal density	4	31.78	7.95	6.31^{**}
Error	18	22.67	1.26	

DF, degrees of freedom; SS, sum of squares; MS, mean square; *F*, *F* ratio.

** Highly significant ($P < 0.01$).

*** Very highly significant ($P < 0.001$).

ns, non-significant ($P > 0.05$).

but *B. calyciflorus* outcompeted *M. macrocopa* at high *S. obliquus* density. Our results suggested that exploitative competition of *M. macrocopa* over *B. calyciflorus* may be more important than interference competition. The differences between results of the present study and Xi and Hagiwara (2007) may be due to the differences between zooplankton strains or algal food types.

Competitive strength among zooplankton becomes more intense when food resources were scarce (Holbrook and Schmitt, 1989; Fernández-Araiza *et al*., 2005; Xi and Hagiwara, 2007; Sarma *et al*., 2008). However, the results of Nandini and Sarma (2002) showed that *Euchlanis dilatata* and *B. patulus* coexisted in more or less equal densities when *C. vulgaris* was offered in low concentration, but *E. dilatata* totally eliminated *B. patulus* when the algal level was enhanced. This means that competitive strength intensified with increasing food density. In our study, we got a similar result that competitive strength intensified with increasing food density when *B. calyciflorus* excluded *M. macrocopa*. There are possible two reasons. One is higher population abundance of *B. calyciflorus* under higher food density induced strong exploitative competition over *M. macrocopa*. The other is that interference competition of *M. macrocopa* over *B. calyciflorus* was weak or not existent. However, true reasons need to further research.

Fernández-Araiza *et al*. (2005) found that *Brachionus havanaensis* could coexist with other three brachionid species at 22 °C, while at 28 °C it was completely eliminated under low food density. For cladocerans, Feniova *et al*. (2011) observed the coexistence of *Ceriodaphnia reticulata* with other three cladoceran species at 25 °C, while it was completely excluded at 18 °C under the food deficit. These results above mentioned showed that the outcomes of interspecific competition at different temperatures were clearly different due to different responses of the different species to temperature change under low food density. However, some other results showed that outcomes of interspecific competition at different temperature were not apparent different. For example, the results of Stelzer (2006) showed that *B. calyciflorus* displaced *Synchaeta pectinata* at 12 and 20 °C. For cladocerans, *Daphnia magna* had a competitive advantage over *Simocephalus vetulus* at 20 and 25 °C, and its competitive strength was more intense at higher temperature (Deng *et al*., 2009). In the present study, a rising temperature also did not change the competitive outcome between *M. macrocopa* and *B. calyciflorus*, but competitive strength was intensifying with temperature. Hence, outcomes of interspecific competition at different temperature may be dependent on competitive ability and sensitivity to temperature change of competitors.

Conclusion

Regardless of the temperature and algal density, *B. calyciflorus* grown in the presence of *M. macrocopa* had lower population abundance than that in the control, but the population abundance of *M. macrocopa* was reverse at the lowest algal density (0.5×10^6 cells.mL^{-1} *S. obliquus*). Regardless of temperature, *M. macrocopa* outcompeted *B. calyciflorus* at the lowest algal density (0.5×10^6 cells.mL^{-1} *S. obliquus*), reversely *B. calyciflorus* outcompeted *M. macrocopa* at higher algal densities (1.0 and 3.0×10^6 cells.mL^{-1} *S. obliquus*). The duration of coexistence shortened with increasing temperature when *M. macrocopa* outcompeted *B. calyciflorus*, and those with increasing temperature and algal density when *B. calyciflorus* outcompeted *M. macrocopa*. Our results suggested that the competitive outcome between the rotifer *B. calyciflorus* and the cladoceran *M. macrocopa* was dependent on algal density but not temperature, the duration of coexistence between them was dependent on algal density and temperature, and the exploitative competition of *M. macrocopa* over *B. calyciflorus* may be more important than the interference competition.

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