Ann. Limnol. - Int. J. Lim. 2019, 55, 2
© EDP Sciences, 2019
https://doi.org/10.1051/limn/2019001

Available online at:
www.limnology-journal.org

RESEARCH ARTICLE

# Competition between *Brachionus calyciflorus* and *Brachionus angularis* (Rotifera) in relation to algal food level and initial population density

Kun Zhang[1], Quan Wan[1], and Yi-Long Xi[1,2,*]

[1] Provincial Key Laboratory for Conservation and Utilization of Important Biological Resource in Anhui, College of Life Sciences, Anhui Normal University, Wuhu 241000, Anhui Province, PR China
[2] Collaborative Innovation Center of Recovery and Reconstruction of Degraded Ecosystem in Wanjiang City Belt, Anhui Province, Anhui Normal University, Wuhu, 241000, Anhui Province, PR China

Received: 5 October 2018; Accepted: 21 January 2019

**Abstract –** Intensive interspecific competition for limited resource often can result in the exclusion of inferior competitors, decrease the species diversity and alter the structure of the zooplankton community. Competitive experiments between *Brachionus calyciflorus* and *Brachionus angularis* were conducted at three *Scenedesmus* densities ($0.5 \times 10^6$, $1.0 \times 10^6$ and $2.0 \times 10^6$ cells $ml^{-1}$) and four initial inoculation densities (numerically, 100% *B. calyciflorus*, 75% *B. calyciflorus* and 25% *B. angularis*, 50% each of the two species, 25% *B. calyciflorus* and 75% *B. angularis*, and 100% *B. angularis*). The results showed that at the low food level, *B. angularis* outcompeted *B. calyciflorus* and *vice versa* at the high food levels. At the intermediate food level, *B. angularis* was displaced by *B. calyciflorus* at nearly all the initial inoculation densities except for 75% *B. angularis,* at which both species coexisted until the termination of the experiment. When grown alone at $0.5 \times 10^6$, $1.0 \times 10^6$ and $2.0 \times 10^6$ cells $ml^{-1}$ of *Scenedesmus*, *B. calyciflorus* reached the peak abundance values of $34 \pm 4$, $69 \pm 5$ and $101 \pm 9$ individuals $ml^{-1}$ and had population growth rates of $0.608 \pm 0.032$, $0.654 \pm 0.033$ and $0.518 \pm 0.039$ $d^{-1}$, respectively. The corresponding values for *B. angularis* were $265 \pm 8$, $330 \pm 30$ and $802 \pm 87$ individuals $ml^{-1}$ and $0.623 \pm 0.020$, $0.770 \pm 0.036$ and $0.871 \pm 0.013$ $d^{-1}$. The results suggest that the outcome of competition depends not only on the size of the competing species and food availability but also on their colonizing density.

**Keywords:** rotifer / interspecific competition / food level / initial inoculation

## 1 Introduction

Intensive interspecific competition for limited resource can often result in the exclusion of inferior competitors, decrease of the species diversity and can alter the structure of the zooplankton community (Lynch, 1979; DeMott, 1989; Dumont, 1994; Bonsall and Hassell, 1997; Chase *et al.*, 2002), but fluctuating environmental conditions such as variability of available resources can promote coexistence of zooplankton competitors (DeMott, 1989; Rothhaupt, 1990; McCauley *et al.*, 1996; Kirk, 1997; Nisbet *et al.*, 1997).

Competition among rotifer species is influenced by various factors such as body size, feeding habits, food type and nutritional quality, temperature, salinity, food level, inoculation density and diapause (Rothhaupt, 1988, 1990; DeMott, 1989; Boraas *et al.*, 1990, Sarma *et al.*, 1999, 2002; Fernández-Araiza *et al.*, 2005; Montero-Pau and Serra, 2011; Divya *et al.*, 2012; Li and Niu, 2015; Rebolledo *et al.*, 2018). Body size is an important factor in determining competitive ability and controlling the outcome of competition in rotifers under different food levels (Sarma *et al.*, 1996, 1999; Ooms-Wilms, 1998; Ciros-Pérez *et al.*, 2001; Divya *et al.*, 2012). Field studies have revealed that under food-limited conditions, smaller rotifer species are able to reproduce and maintain a population, and thus outcompete the larger species (Sarma *et al.*, 1996, 1999), but larger rotifer species are unable to maintain a population because of differences in the available energy versus the maintenance costs (Downing and Rigler, 1984). On the other hand, at very high food levels, smaller species are unable to utilize food since their filtration systems get clogged, leading to poor population growth. However, at medium food levels, the outcome of competition in rotifers needs more investigation.

*Corresponding author: ylxi1965@126.com

Food levels may modify the outcome of competition between two rotifer species which differ widely in their growth rates. When two species of rotifers compete for limited food, normally the one with higher population growth rate may be expected to outcompete the other with lower growth rate (Rothhaupt, 1990). However, this does not appear to hold true for many species (Sarma *et al.*, 1996, 1999, 2007; Sarma and Nandini, 2002; Divya *et al.*, 2012). When two planktonic rotifers, *Brachionus angularis* and *B. calyciflorus,* compete for limited food resource, the relationship between the outcome of competition and their population growth rates remains unknown.

Initial inoculation density is also an important factor affecting the population growth rates and controlling the outcome of competition in rotifers. High food levels usually lead to smaller rotifer species poor population growth, but their sufficiently initial density may reverse this condition (Sarma *et al.*, 1996, 1997, 1999; Divya *et al.*, 2012). Similarly, a low *Chlorella* level leads to larger rotifer species *B. patulus* poor population growth, but a higher ratio of *B. patulus* to *Euchlanis dilatata* at the onset of the experiments permits both rotifer species to coexist until the end of the experiments (Nandini and Sarma, 2002). At different food levels, what is the initial inoculation density required by *B. angularis* and *B. calyciflorus* to coexist?

*B. angularis* and *B. calyciflorus* are two common herbivorous rotifer species in freshwater lakes and ponds. Compared to *B. calyciflorus*, *B. angularis* is smaller and has a lower threshold food level but a higher population growth rate (Stemberger and Gilbert, 1987; Pan *et al.*, 2017, 2018). The present study examined the combined effects of algal food level and initial inoculation density on the competitive interaction between the two herbivorous rotifer species, with the aim of testing the following two hypotheses: (i) at the low food level, *B. angularis* outcompeted *B. calyciflorus* and *vice versa* at the high food level, according to the available results (Sarma *et al.*, 1996, 1999; Ooms-Wilms, 1998; Divya *et al.*, 2012); and (ii) similar to the outcome of competition between the rotifers *E. dilatata* and *B. patulus* (Nandini and Sarma, 2002), a certain food level and inoculation density might permit the competition persistence between *B. calyciflorus* and *B. angularis*.

## 2 Materials and methods

### 2.1 Sample collection and culture

Individuals of *B. calyciflorus* Pallas and *B. angularis* Gosse, which were obtained by hatching the resting eggs in sediments from Lake Jinghu (31°36′11″ N, 118°38′23″ E) and identified morphologically under a microscope, were clonally cultured in rotifer culture medium (Gilbert, 1963). All clones were cultured in the laboratory for over 1 year, and one clone of each species was randomly selected for the experiments. The average lorica length (in μm, mean ± standard deviation, based on 100 individuals) of *B. calyciflorus* and *B. angularis* were 217 ± 4 and 99 ± 1, and the average lorica width were 167 ± 2 and 80 ± 3, respectively. Prior to the experiments, the two rotifer clones were mass-cultured. For clonal and mass cultures of the rotifers, an illumination incubator with a 16:8-h light: dark photoperiod at 130 lx at (23 ± 1)°C was used, and $1.5 \times 10^6$ cells $ml^{-1}$ of *Scenedesmus obliquus* (Turp.) Kütz was supplied as food. The algal cells were semicontinuously cultured in HB-4 medium (Li *et al.*, 1959), and those at the exponential phase of growth were harvested by centrifugation at 3,000 rpm for 5 min, resuspended in rotifer culture medium and stored at 4 °C. The density of algal cells was determined by counting using a haemocytometer.

### 2.2 Competitive experiments and parameter calculation

Competitive experiments between *B. calyciflorus* and *B. angularis* were conducted in 25 ml glass beakers each containing 20 ml rotifer culture medium with the chosen density of *S. obliquus*. Prior to the competitive experiments, the two rotifer clones were maintained at the designated food levels for more than 5 days to allow acclimation. For the competitive experiments, three *S. obliquus* densities ($0.5 \times 10^6$, $1.0 \times 10^6$ and $2.0 \times 10^6$ cells $ml^{-1}$) and four initial inoculation densities (numerically, 100% *B. calyciflorus*; 75% *B. calyciflorus* and 25% *B. angularis*; 50% each of the two species; 25% *B. calyciflorus* and 75% *B. angularis*, and 100% *B. angularis*) were chosen. In all, the starting density of rotifers (alone or combined) was five individuals $ml^{-1}$. Four replicates were set up for each treatment.

Following inoculation, every day three aliquot samples of 0.5–1 ml were taken from each of the beakers, and the number of the rotifers was counted. After counting, the three aliquot samples were returned to the original beaker, and the culture medium was changed using fresh culture medium with appropriate algal density. The experiment was terminated after 13 days when all populations nearly completed one cycle.

The population growth rate was obtained using the following exponential equation:

$$r = (\ln N_t - \ln N_0)/t,$$

where $N_0$ and $N_t$ are the initial and final population densities; $t$ is time in days. We used varying data points along the growth curve to calculate the mean per replicate. In general, we took four to six data points during the exponential phase of the population as documented in Dumont and Sarma (1995).

### 2.3 Statistical analyses

All statistical analyses were performed using SPSS 11.5. The Levene's test was performed to test the homogeneity of variances. One-way analysis of variance (ANOVA) was conducted to identify the significant effect of initial inoculation density and food level on each of the population growth variables of the rotifers cultured at each algal density and initial inoculation density, respectively. Two-way ANOVA was conducted to analyse the significant effects of initial inoculation density, food level and their interactions on each population growth variable. Multiple comparisons of the least significant difference were performed to determine which groups were significantly different among the four groups at each food level as well as the three groups at each initial inoculation density. Results with $P$ values of less than 0.05 were considered statistically significant.

## 3 Results

The population growth curves of *B. calyciflorus* and *B. angularis* showed increased abundance in relation to food level. When both species were introduced together, and at $0.5 \times 10^6$ cells ml$^{-1}$ of *S. obliquus*, *B. angularis* outcompeted *B. calyciflorus* regardless of initial inoculation density. This trend reversed as the food density offered increased to $2.0 \times 10^6$ cells ml$^{-1}$. At $1.0 \times 10^6$ cells ml$^{-1}$ of *S. obliquus*, and when the initial inoculation density of *B. angularis* was one-third and the same as that of *B. calyciflorus*, *B. angularis* was displaced by *B. calyciflorus*; but when the initial inoculation density of *B. angularis* was three times that of *B. calyciflorus*, both species coexisted until the termination of the experiment (Fig. 1).

Only when *S. obliquus* density was $2.0 \times 10^6$ cells ml$^{-1}$ was the time required to reach the maximum population density by *B. calyciflorus* significantly affected by inoculation density (One-way ANOVA, $P < 0.05$). The time required to reach the maximum population density by *B. calyciflorus* at the inoculation densities of 100, 75 and 25% were similar but were shorter than that at 50%. When the inoculation densities of *B. calyciflorus* were 100 and 50%, the time required to reach the maximum population density by *B. calyciflorus* was affected by food level (One-way ANOVA, $P < 0.01$). At both inoculation densities, the time required to reach the maximum population density at $0.5 \times 10^6$ and $1.0 \times 10^6$ cells ml$^{-1}$ of *S. obliquus* were similar but were shorter than that at $2.0 \times 10^6$ cells ml$^{-1}$ of *S. obliquus* (Fig. 1).

Only when *S. obliquus* density was $2.0 \times 10^6$ cells ml$^{-1}$ was the time required to reach the maximum population density by *B. angularis* significantly affected by inoculation density (One-way ANOVA, $P < 0.05$). The time required to reach the maximum population density by *B. angularis* at the inoculation densities of 100, 75 and 50% were similar but were longer than that at 25%. Similarly, only when the inoculation density of *B. angularis* was 25% was the time required to reach the maximum population density by *B. angularis* affected by food level (One-way ANOVA, $P < 0.05$). The time required to reach the maximum population density at $0.5 \times 10^6$ cells ml$^{-1}$ of *S. obliquus* was longer than that at $1.0 \times 10^6$ and $2.0 \times 10^6$ cells ml$^{-1}$ of *S. obliquus*, with the latter two being similar (Fig. 1).

Two-way ANOVA indicated that the time required to reach the maximum population density by both species was significantly affected only by food density (Tab. 1). In general, at $0.5 \times 10^6$ and $1.0 \times 10^6$ cells ml$^{-1}$ of *S. obliquus*, *B. calyciflorus* reached the peak population abundance earlier than *B. angularis* regardless of initial inoculation density; but at $2.0 \times 10^6$ cells ml$^{-1}$ of *S. obliquus*, this trend reversed. In the absence of competing species, *B. calyciflorus* reached the peak population abundance on days 3–4, 4–5 and 6–7 following inoculation at $0.5 \times 10^6$, $1.0 \times 10^6$ and $2.0 \times 10^6$ cells ml$^{-1}$ of *S. obliquus*, respectively. The corresponding values for *B. angularis* were days 6–7, 5–7 and 6 (Fig. 1; Tab. 1).

At all the three food levels, the maximum population density achieved by *B. calyciflorus* was not significantly affected by inoculation density (one-way ANOVA, $P > 0.05$). However, at each inoculation density, the maximum population density achieved by *B. calyciflorus* was markedly influenced by food level (one-way ANOVA, $P < 0.01$). When the inoculation densities of *B. calyciflorus* were 100, 75 and 50%, the maximum population density achieved by *B. calyciflorus* increased with increasing food level. When the inoculation density of *B. calyciflorus* was 25%, the maximum population densities at $0.5 \times 10^6$ and $1.0 \times 10^6$ cells ml$^{-1}$ of *S. obliquus* were similar, but were lower than that at $2.0 \times 10^6$ cells ml$^{-1}$ of *S. obliquus* (Fig. 2).

At all the three food levels, the maximum population density achieved by *B. angularis* was significantly affected by inoculation density (one-way ANOVA, $P < 0.01$). At $0.5 \times 10^6$ cells ml$^{-1}$ of *S. obliquus*, the maximum population density achieved by *B. angularis* was the highest at the inoculation density of 100% and the lowest at the inoculation densities of 50 and 25%. At $1.0 \times 10^6$ cells ml$^{-1}$ of *S. obliquus*, the maximum population density was the highest at the inoculation density of 100% and the lowest at the inoculation density of 25%. The maximum population density at the inoculation of 50% was similar to those at the inoculation densities of 75 and 25%. When the inoculation densities of *B. angularis* were 100 and 25%, the maximum population density achieved by *B. angularis* was markedly influenced by food level (one-way ANOVA, $P < 0.01$). The maximum population densities at $0.5 \times 10^6$ and $1.0 \times 10^6$ cells ml$^{-1}$ of *S. obliquus* were similar, but were lower than that at $2.0 \times 10^6$ cells ml$^{-1}$ of *S. obliquus* (Fig. 2).

Two-way ANOVA indicated that the maximum population densities achieved by *B. calyciflorus* and *B. angularis* were significantly affected by food level, inoculation density and their interaction (Tab. 1). In general, at any given food density, *B. angularis* was numerically more abundant than *B. calyciflorus*. When grown alone, *B. angularis* reached the peak abundance values of $265 \pm 8$ (mean $\pm$ standard error), $330 \pm 30$ and $802 \pm 87$ individuals ml$^{-1}$ at $0.5 \times 10^6$, $1.0 \times 10^6$ and $2.0 \times 10^6$ cells ml$^{-1}$ of *S. obliquus*, respectively. The corresponding values for *B. calyciflorus* were $34 \pm 4$, $69 \pm 5$ and $101 \pm 9$ individuals ml$^{-1}$ (Fig. 2).

At each food level, the population growth rate of *B. calyciflorus* was not significantly affected by inoculation density (One-way ANOVA, $P > 0.05$). Similarly, at each inoculation density, the population growth rate of *B. calyciflorus* was not influenced by food level (one-way ANOVA, $P > 0.05$). However, at $2.0 \times 10^6$ cells ml$^{-1}$ of *S. obliquus*, the population growth rate of *B. angularis* was significantly affected by inoculation density ($P < 0.01$). The population growth rate of *B. angularis* was the highest at the inoculation density of 25% and the lowest at the inoculation densities of 50 and 75%. At each inoculation density, the population growth rate of *B. angularis* was influenced by food level (One-way ANOVA, $P < 0.01$). When the inoculation density of *B. angularis* was 100 and 25%, the population growth rate increased with increasing food level. When the inoculation density of *B. angularis* was 50 and 75%, the population growth rates were similar at $1.0 \times 10^6$ and $2.0 \times 10^6$ cells ml$^{-1}$ of *S. obliquus* and were higher than at $0.5 \times 10^6$ cells ml$^{-1}$ of *S. obliquus* (Fig. 3).

Two-way ANOVA indicated that the population growth rate of *B. calyciflorus* was significantly affected only by food level but that of *B. angularis* was influenced by food level, inoculation density and their interaction (Tab. 1). In general, at

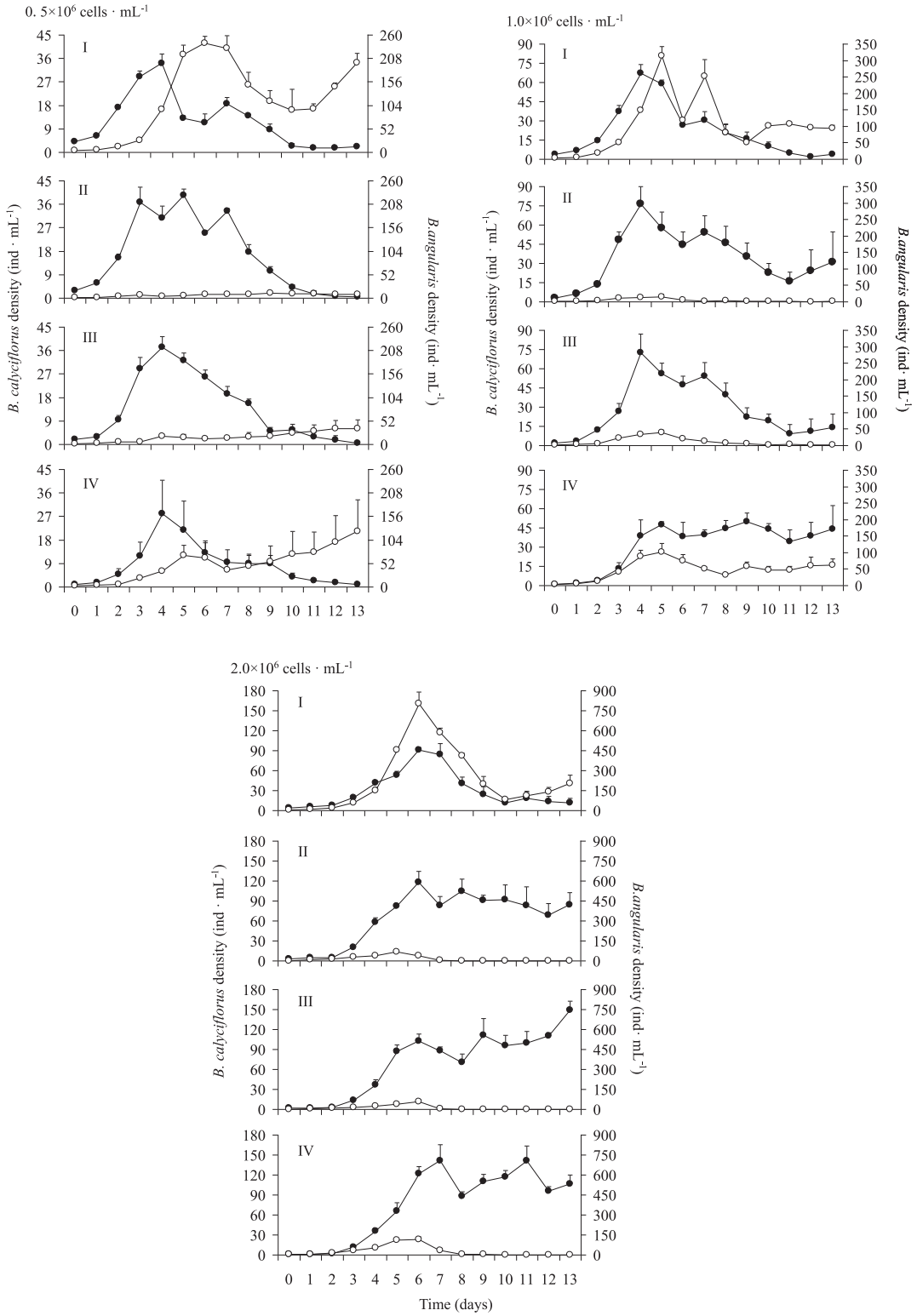


**Fig. 1.** Population growth curves of *B. calyciflorus* (filled circle) and *B. angularis* (unfilled circle) cultured at different *Scenedesmus obliquus* levels and inoculation densities. Series I: 100% *B. calyciflorus* or *B. angularis*; II: initial proportion of 75% *B. calyciflorus* + 25% *B. angularis*; III: 50% *B. calyciflorus* + 50% *B. angularis*; IV: 25% *B. calyciflorus* + 75% *B. angularis*. Shown are the mean + standard error values based on four replicate recordings.

**Table 1.** Effects of algal food level and initial population density on maximum population density, date at maximum density and population growth rate of *B. calyciflorus* and *B. angularis* (two-way ANOVA).

| Variation source | SS | df | MS | *F* | *P* |
|---|---|---|---|---|---|
| Date at maximum density | | | | | |
| *B. calyciflorus* | | | | | |
| Food density (A) | 104.06 | 2 | 52.03 | 13.10 | <0.01 |
| Inoculation density (B) | 30.44 | 3 | 10.15 | 2.56 | >0.05 |
| A × B | 43.72 | 6 | 7.29 | 1.83 | >0.05 |
| Error | 95.33 | 24 | 3.97 | | |
| *B. angularis* | | | | | |
| Food density (A) | 79.06 | 2 | 39.53 | 8.18 | <0.01 |
| Inoculation density (B) | 1.56 | 3 | 0.52 | 0.11 | >0.05 |
| A × B | 23.61 | 6 | 3.94 | 0.81 | >0.05 |
| Error | 116.00 | 24 | 4.83 | | |
| Maximum population density | | | | | |
| *B. calyciflorus* | | | | | |
| Food density (A) | 55500.31 | 2 | 27750.15 | 100.85 | <0.01 |
| Inoculation density (B) | 2732.34 | 3 | 910.78 | 3.31 | <0.05 |
| A × B | 4266.17 | 6 | 711.03 | 2.58 | <0.05 |
| Error | 6603.95 | 24 | 275.17 | | |
| *B. angularis* | | | | | |
| Food density (A) | 161052.71 | 2 | 80526.36 | 24.91 | <0.01 |
| Inoculation density (B) | 1106676.83 | 3 | 368892.28 | 114.09 | <0.01 |
| A × B | 361292.82 | 6 | 60215.47 | 18.62 | <0.01 |
| Error | 77598.59 | 24 | 3233.28 | | |
| Population growth rate | | | | | |
| *B. calyciflorus* | | | | | |
| Food density (A) | 0.17 | 2 | 0.09 | 4.86 | <0.05 |
| Inoculation density (B) | 0.11 | 3 | 0.04 | 2.00 | >0.05 |
| A × B | 0.03 | 6 | 0.01 | 0.29 | >0.05 |
| Error | 0.43 | 24 | 0.02 | | |
| *B. angularis* | | | | | |
| Food density (A) | 0.76 | 2 | 0.38 | 64.52 | <0.01 |
| Inoculation density (B) | 0.35 | 3 | 0.12 | 19.78 | <0.01 |
| A × B | 0.34 | 6 | 0.06 | 9.59 | <0.01 |
| Error | 0.14 | 24 | 0.01 | | |

$0.5 \times 10^6$ cells $ml^{-1}$ of *S. obliquus*, *B. calyciflorus* had a higher population growth rate than *B. angularis*; but at $2.0 \times 10^6$ cells $ml^{-1}$ of *S. obliquus*, the reverse was also true. At $1.0 \times 10^6$ cells $ml^{-1}$ of *S. obliquus*, their population growth rates were similar. When grown alone, *B. angularis* had population growth rates of $0.623 \pm 0.020$, $0.770 \pm 0.036$ and $0.871 \pm 0.013$ $d^{-1}$ at $0.5 \times 10^6$, $1.0 \times 10^6$ and $2.0 \times 10^6$ cells $ml^{-1}$ of *S. obliquus*, respectively. The corresponding values for *B. calyciflorus* were $0.608 \pm 0.032$, $0.654 \pm 0.033$ and $0.518 \pm 0.039$ $d^{-1}$ (Fig. 3).

## 4 Discussion

Classical population growth curves of rotifers in batch cultures with living algal cells as food show a lag phase, an exponential growth phase, a post-exponential growth phase and a final declining phase. The stationary phase, if it appears, is very short (Yuferal and Navarro, 1995). With the rotifer species *B. plicatilis* as test animals, Yoshinaga *et al.* (2001) observed a stationary phase instead of the decline phase. The present results showed that the population growth curves of both *B. calyciflorus* and *B. angularis* differed with food level and initial inoculation density.

It is well known that the increase in food availability results in increased population abundance and higher growth rates of rotifers (Sarma *et al.*, 1996, 1999; Ooms-Wilms, 1998; Divya *et al.*, 2012). The present study showed that in general the population abundance of both *B. calyciflorus* and *B. angularis* increased with increasing food availability. The population growth rate of *B. angularis* also increased with increasing food level but that of *B. calyciflorus* was the highest at $1.0 \times 10^6$ cells $ml^{-1}$ of *S. obliquus*. The diverse responses in population growth rate to increasing food level might be attributed to different rotifer species.

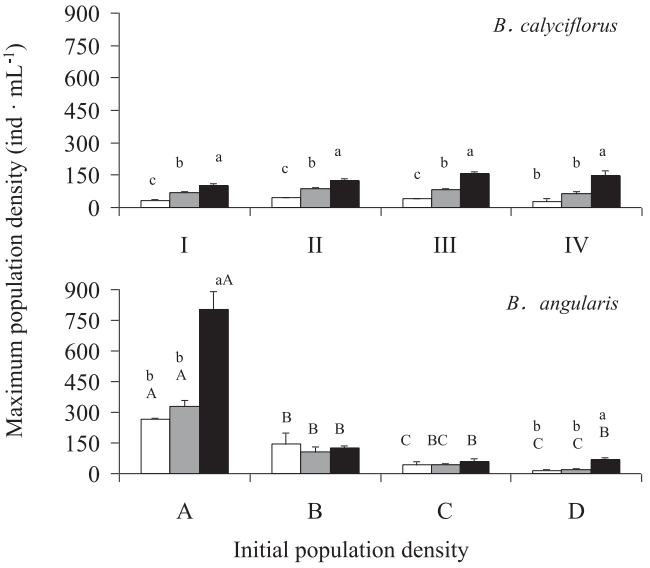


**Fig. 2.** The maximum population density (mean + standard error, based on three replicates) achieved by *B. calyciflorus* and *B. angularis* cultured at different *Scenedesmus obliquus* levels and inoculation densities. The inoculation densities used for *B. calyciflorus* are as follows: I – 100% *B. calyciflorus*; II – 75% *B. calyciflorus*; III – 50% *B. calyciflorus*; IV – 25% *B. calyciflorus*. For *B. angularis,* the inoculation densities A, B, C and D represent 100, 75, 50 and 25% *B. angularis*, respectively. Shown are the values mean + standard error based on four replicates. Small letters indicate means that are similar (same letter) or different (different letters) among three food levels when inoculated at each of four densities (LSD multiple comparison), and capital letters indicate means that are similar (same letter) or different (different letters) among four inoculation densities when fed $0.5 \times 10^6$ (white bars), $1.0 \times 10^6$ (grey bars) and $2.0 \times 10^6$ (black bars) cells $ml^{-1}$ of *S. obliquus*, respectively (LSD multiple comparison).

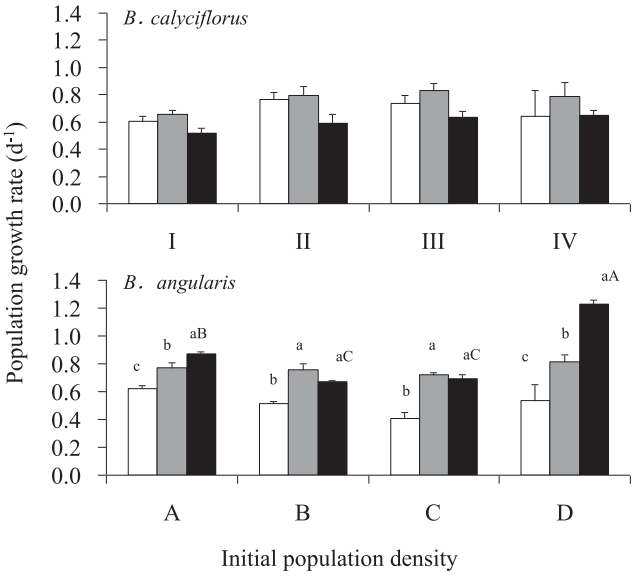


**Fig. 3.** The population growth rate (mean + standard error, based on three replicates) achieved by *B. calyciflorus* and *B. angularis* cultured at different *Scenedesmus obliquus* levels and inoculation densities. The inoculation densities used for *B. calyciflorus* are as follows: I – 100% *B. calyciflorus*; II – 75% *B. calyciflorus*; III – 50% *B. calyciflorus*; IV – 25% *B. calyciflorus*. For *B. angularis,* the inoculation densities A, B, C and D represent 100, 75, 50 and 25% *B. angularis*, respectively. Shown are the values mean + standard error based on four replicates. Small letters indicate means that are similar (same letter) or different (different letters) among three food levels when inoculated at each of four densities (LSD multiple comparison), and capital letters indicate means that are similar (same letter) or different (different letters) among four inoculation densities when fed $0.5 \times 10^6$ (white bars), $1.0 \times 10^6$ (grey bars) and $2.0 \times 10^6$ (black bars) cells $ml^{-1}$ of *S. obliquus*, respectively (LSD multiple comparison).

When two species of rotifers compete for limited food resource, normally the one with higher population growth rate may be expected to outcompete the other with lower growth rate (Rothhaupt, 1990). However, this does not appear to hold true for many species (Sarma *et al.*, 1996, 1999, 2007; Sarma and Nandini, 2002; Divya *et al.*, 2012). The present study showed that at $0.5 \times 10^6$ cells $ml^{-1}$ of *S. obliquus*, *B. calyciflorus* had a higher population growth rate than *B. angularis*, but the former was displaced by the latter. At $2.0 \times 10^6$ cells $ml^{-1}$ of *S. obliquus*, *B. calyciflorus* had a lower population growth rate than *B. angularis*, but the former outcompeted the latter. At $1.0 \times 10^6$ cells $ml^{-1}$ of *S. obliquus*, their population growth rates were similar but the outcome of competition between them differed with their initial inoculation densities.

Stemberger and Gilbert (1985a) defined the food threshold for rotifers as the concentration of food required to maintain a zero population growth rate. When competitors were continuously exposed to food depleting situations, species with an ability to maintain at least a zero population growth rate should persist over the others that could not do so. It is known that smaller rotifer species have lower threshold food levels than larger rotifer species (Stemberger and Gilbert 1985b), which implies that under food-limited conditions, smaller rotifer species should be able to reproduce and maintain a population and thus outcompete the larger species. Under food-limited conditions, both *A. fissa* and *B. patulus* with relatively smaller lorica sizes outcompeted the larger species *B. calyciflorus* (Sarma *et al.*, 1996, 1999), and *B. rotundiformis* with a smaller lorica length formed superior competitor than *B. plicatilis* with a larger lorica length (Divya *et al.*, 2012). Identical to these results, the present study showed that at $0.5 \times 10^6$ cells $ml^{-1}$ of *Scenedesmus*, smaller species *B. angularis* outcompeted larger species *B. calyciflorus*. At $2.0 \times 10^6$ cells $ml^{-1}$ of *Scenedesmus*, *B. angularis* initially increased its population but thereafter declined due to increased food limitation, not only from its own population but also from continuously growing *B. calyciflorus*, which was identical to the conclusion of DeMott (1989) that the higher growth rates of some zooplanktonic species would allow them to reach densities at which inter- and intraspecific competition would become important. The outcome of competition between *B. angularis* and *B. calyciflorus* at the low and high food levels supported the hypothesis that at the low food level, *B. angularis* outcompeted *B. calyciflorus* and *vice versa* at the high food level.

The inoculation density of two competing species is generally thought to play a decisive role in the competitive outcome, but the accumulating evidences showed that its impact was also related to food level and growth characteristics of the competing species. At higher food levels, higher inoculation densities of inferior competitors helped themselves coexist with superior ones (Sarma *et al.*, 1996; Nandini and Sarma, 2002; Divya *et al.*, 2012). Similarly, the present study showed that at $1.0 \times 10^6$ cells $ml^{-1}$ of *S. obliquus*, and when the initial inoculation density of *B. angularis* was three times that of *B. calyciflorus*, both species coexisted until the termination of the experiment, which supported the hypothesis that a certain food level and inoculation density might permit the competition persistence between *B. calyciflorus* and *B. angularis*.

In natural water bodies, zooplankton organisms are exposed to large-scale changes in their physical, chemical and biotic environments that may impact the demographic structure of populations. In consequence, many zooplankton species are often found during a restricted season (King and Serra, 1998). In Lake Jinghu, a subtropical shallow lake, *B. angularis* appeared during the period from the end of July to the end of October, 2008, and reached the peak population density of 0.075 individuals $ml^{-1}$ in early August (Wen *et al.*, 2011), much lower than those obtained in the present study. Similarly, *B. calyciflorus* appeared during the period from the end of December, 2008, to the beginning of April, 2009, and reached the peak density of 0.035 individuals $ml^{-1}$ in mid-February (Wen *et al.*, 2016), also much lower than those obtained in the present study. Because of seasonal distribution, interspecific competition between these two species might not occur.

## 5 Conclusion

The present study demonstrates that the outcome of competition between two differently sized herbivorous rotifer species is not only dependent on food density but also on relative initial population densities, and on the interaction of these two factors. In nature, it is likely that small *B. angularis* colonize oligotrophic water bodies more successfully than larger *B. calyciflorus*.

*Acknowledgements.* This work was funded by the Natural Science Foundation of China (31470015, 31170395) and the Foundation of Provincial Key Laboratory of Biotic Environment and Ecological Safety in Anhui Province.

## References

Bonsall MB, Hassell MP. 1997. Apparent competition structures ecological assemblages. *Nature* 388: 371–373.

Boraas ME, Seale DB, Horton JB. 1990. Resource competition between two rotifer species (*Brachionus rubens* and *B. calyciflorus*): an experimental test of mechanistic model. *J Plankton Res* 12: 77–87.

Chase JM, Abrams PA, Grover JP. 2002. The interaction between predation and competition: a review and synthesis. *Ecol Lett* 5: 302–315.

Ciros-Pérez J, Carmona MJ, Serra M. 2001. Resource competition between sympatric sibling rotifer species. *Limnol Oceanogr* 46: 1511–1523.

DeMott WR. 1989. The role of competition in zooplankton succession. In: Sommer U (ed.), Plankton ecology: succession in plankton communities. New York: Springer, pp. 195–252.

Divya SP, Kathiresan K, Asha P, Sekar V, Rajasekaran R. 2012. Experimental study of the interspecific competition between two sibling marine herbivorous rotifers in relation to food availability and initial population density. *Acta Oceanol Sin* 31: 113–126.

Downing JA, Rigler FH. 1984. A manual on the methods for the assessment of secondary productivity in fresh waters. IBP Handbook No. 17, 2nd ed. London: Blackwell Science Publications, p. 501.

Dumont HJ. 1994. Ancient lakes have simplified pelagic food webs. *Arch Hydrobiol Beih* 44: 223–234.

Dumont HJ, Sarma SSS. 1995. Demography and population growth of *Asplanchna girodi* (Rotifera) as a function of prey (*Anuraeopsis fissa*) density. *Hydrobiologia* 306: 97–107.

Fernández-Araiza MA, Sarma SSS, Nandini S. 2005. Combined effects of food concentration and temperature on competition among four species of *Brachionus* (Rotifera). *Hydrobiologia* 546: 519–534.

Gilbert JJ. 1963. Mictic female production in rotifer *Brachionus calyciflorus*. *J Exp Zool* 153: 113–124.

King CE, Serra M. 1998. Seasonal variation as a determinant of population structure in rotifers reproducing by cyclical parthenogenesis. *Hydrobiologia* 387/388: 361–372.

Kirk KL. 1997. Life-history responses to variable environments: starvation and reproduction in planktonic rotifers. *Ecology* 78: 434–441.

Li C, Niu C. 2015. Effects of sexual reproduction of the inferior competitor *Brachionus calyciflorus* on its fitness against *Brachionus angularis*. *Chin J Oceanol Limnol* 33: 356–363.

Li S-H, Zhu H, Xia Y-Z, Yu M-J, Liu K-S, Ye Z, Chen Y-Y. 1959. The mass culture of unicellular green algae. *Acta Hydrobiol Sin* 4: 462–472.

Lynch M. 1979. Predation, competition, and zooplankton community structure: an experimental study. *Limnol Oceanogr* 24: 253–272.

McCauley E, Nisbet RM, Deross AM. 1996. Structured population models of herbivorous zooplankton. *Ecol Monogr* 66: 479–501.

Montero-Pau J, Serra M. 2011. Life-cycle switching and coexistence of species with no niche differentiation. *PLoS One* 6: e20314.

Nandini S, Sarma SSS. 2002. Competition between the rotifers *Brachionus patulus* and *Euchlanis dilatata*: effect of algal food level and relative initial densities of competing species. *Russ J Ecol* 33: 291–295.

Nisbet RM, McCauley E, Gurney WSC. 1997. Simple representation of biomass dynamics in structured populations. In: Othmer HG, Adler FR, Lewis MA, *et al.* (eds.), Case studies in mathematical modeling: ecology, physiology, and cell biology. New Jersey: Prentice-Hall, pp. 61–79.

Ooms-Wilms A. 1998. On the food uptake and population dynamics of rotifers in a shallow eutrophic lake. The Netherlands: Universiteit van Amsterdam, pp. 153.

Pan L, Xi Y-L, Gu J, Jiang S, Zhu H, Zhang B-X. 2017. Interactive effects of algal level and predator density (*Asplanchna sieboldi*) on the life-history strategy and morphology of *Brachionus calyciflorus*. *J Exp Zool A Ecol Integr Physiol* 327: 523–531.

Pan L, Xi Y-L, Gu J, Jiang S, Zhu H, Zhang B-X. 2018. *Asplanchna*-kairomone induces life history shifts in *Brachionus angularis* (Rotifera). *Ann Limnol – Int J Lim* 54: 13.

Rebolledo AU, Nandini S, Sarma SSS, Reyes CRJ, de Oca ARMG. 2018. Demographic and competition studies on *Brachionus ibericus* and *Proales similis* in relation to salinity and algal (*Nannochloropsis oculata*) density. *Aquacult Int* 26: 629–644.

Rothhaupt KO. 1988. Mechanistic resource competition theory applied to laboratory experiments with zooplankton. *Nature* 333: 660–662.

Rothhaupt KO. 1990. Resource competition of herbivorous zooplankton: a review of approaches and perspectives. *Arch Hydrobiol* 118: 1–29.

Sarma SSS, Nandini S. 2002. Comparative life table demography and population growth of *Brachionus macracanthus* Daday, 1905 and *Platyias quadricornis* Ehrenberg, 1832 (Rotifera, Brachionidae) in relation to algal (*Chlorella vulgaris*) food density. *Acta Hydrochim Hydrobiol* 30: 128–140.

Sarma SSS, Iyer N, Dumont HJ. 1996. Competitive interactions between herbivorous rotifers: importance of food concentration and initial population density. *Hydrobiologia* 331: 1–7.

Sarma SSS, Araiza MAF, López RJA. 1997. Influence of food concentration and inoculation density on the population growth of *Brachionus calyciflorus* Pallas (Rotifera). *Environ Ecol* 15: 435–441.

Sarma SSS, Fernández MA, Nandini S. 1999. Competition between *Brachionus calyciflorus* Pallas and *Brachionus patulus* (Müller) (Rotifera) in relation to algal food concentration and initial population density. *Aquat Ecol* 33: 339–345.

Sarma SSS, Elguea-Sánchez B, Nandini S. 2002. Effect of salinity on competition between the rotifers *Brachionus rotundiformis* Tschugunoff and *Hexarthra jenkinae* (De Beauchamp) (Rotifera). *Hydrobiologia* 474: 183–188.

Sarma SSS, Rivera SA, Hinojosa FE. 2007. Combined influence of food level and inoculation density on competition between *Anuraeopsis fissa* and *Brachionus patulus* or *Brachionus macracanthus* (Rotifera: Brachionidae). *Russ J Ecol* 38: 353–362.

Stemberger RS, Gilbert JJ. 1985a. Assessment of threshold food levels and population growths in planktonic rotifers. *Arch Hydrobiol Beih* 21: 269–275.

Stemberger RS, Gilbert JJ. 1985b. Body size, food concentration and population growth in planktonic rotifers. *Ecology* 66: 1151–1159.

Stemberger RS, Gilbert JJ. 1987. Rotifer threshold food concentrations and the size efficiency hypothesis. *Ecology* 68: 181–187.

Wen X-L, Xi Y-L, Yang Y-F, Zhang X-A, Zhang G. 2011. Temperature is the key factor controlling population dynamics of *Brachionus angularis* in Lake Jinghu during summer and autumn. *J Freshw Ecol* 26: 277–286.

Wen X-L, Xi Y-L, Zhang G, Xue Y-H, Xiang X-L. 2016. Coexistence of cryptic *Brachionus calyciflorus* (Rotifera) species: roles of environmental variables. *J Plankton Res* 38: 478–489.

Yuferal M, Navarro N. 1995. Population growth dynamics of the rotifer *Brachionus plicatilis* cultured in non-limiting food condition. *Hydrobiologia* 313/314: 399–405.

Yoshinaga T, Hagiwara A, Tsukamoto K. 2001. Why do rotifer populations present a typical sigmoid growth curve? *Hydrobiologia* 446/447: 99–105.

**Cite this article as**: Zhang K, Wan Q, Xi Y-L. 2019. Competition between *Brachionus calyciflorus* and *Brachionus angularis* (Rotifera) in relation to algal food level and initial population density. *Ann. Limnol. - Int. J. Lim.* 55: 2