Hidrobiológica 2008, 18 (1 Suplemento): 123-132

Effect of algal food (*Chlorella vulgaris*) concentration and inoculation density on the competition among three planktonic Brachionidae (Rotifera: Monogononta)

Efecto de la concentración de algas (*Chlorella vulgaris*) y la densidad de inoculación sobre la competencia entre tres Brachionidae (Rotifera: Monogononta) planctónicos

S.S.S. Sarma[1],
José Luis Franco-Téllez[1]
& S. Nandini[2]

[1]Laboratory of Aquatic Zoology, UMF, Division of Research and Postgraduate Studies, National Autonomous University of Mexico, Campus Iztacala, Av. de Los Barrios No. 1, Los Reyes, Iztacala, A.P. 314, C.P. 54090, Tlalnepantla, State of Mexico, Mexico. E-mail: sarma@servidor.unam.mx
[2]UIICSE, Division of Research and Postgraduate Studies, National Autonomous University of Mexico, Campus Iztacala, Av. de Los Barrios No. 1, Los Reyes, Iztacala, A.P. 314, C.P. 54090, Tlalnepantla, State of Mexico, Mexico.

Sarma S.S.S. , J. L. Franco-Téllez & S. Nandini. 2008. Effect of algal food (*Chlorella vulgaris*) concentration and inoculation density on the competition among three planktonic Brachionidae (Rotifera: Monogononta). *Hidrobiológica 18* (1 Suplemento): 123-132.

ABSTRACT

Competitive outcomes among three rotifer species (*Anuraeopsis fissa*, *Brachionus havanaensis* and *B. angularis*) were quantified with different inoculation densities of two competing species at a time (0, 25, 50, 75 and100%) and using different algal (*Chlorella vulgaris*) densities (0.2×10^6, 0.4×10^6 and 0.8×10^6 cells ml^{-1}). In control cultures, when each species was grown alone, the population growth of rotifers increased with increasing food availability in the medium, but in mixed cultures, decreased with increasing proportion of the competing species. At low food level, compared to *B. havanaensis*, *B. angularis* had stronger negative impact on *A. fissa*. However, with increasing algal density, both species of *Brachionus* had similar but reduced impact on *A. fissa*. Population growth of *B. havanaensis* was more adversely affected by *A. fissa* than *B. angularis* at low and intermediate concentrations. At high food level, the impact of either *A. fissa* or *B. angularis* on the growth of *B. havanaensis* was similar. When grown alone, for a given food density, *A. fissa* was more numerically (4 to 6 times) abundant than the other two species. The rate of population increase (*r*) of rotifers increased with increasing food levels. Depending on the rotifer species and the test conditions, the *r* varied from -0.001 to 0.34 d^{-1}. Results showed that the competitive outcome in the tested rotifers depended on the initial inoculation density of the competing species, the offered food concentration as well as the interaction of these two factors.

Key words: Competition, resource density, zooplankton, inoculation density

RESUMEN

Se evaluaron los resultados de la competencia entre tres especies de rotíferos (*Anuraeopsis fissa*, *Brachionus havanaensis* y *B. angularis*) usando dos especies a la vez con diferentes densidades de inóculo (0, 25, 50, 75 y 100%) y diferentes niveles de alga (*Chlorella vulgaris*; 0.2×10^6, 0.4×10^6 y 0.8×10^6 células ml^{-1}). En cultivos monoespecíficos, utilizados como control, el crecimiento poblacional de rotíferos aumentó con el aumento de disponibilidad del alimento en el medio, pero en los cultivos mixtos, disminuyeron con el aumento de la proporción de la especie competidora. En el nivel bajo de alimento, *B. havanaensis* tuvo un mayor impacto negativo sobre *A. fissa* en comparación con *B. angularis.*

Sin embargo, al aumentar la densidad del alga, ambas especies de *Brachionus* tuvieron un impacto reducido, pero similar. Por otro lado, el crecimiento poblacional de *B. havanaensis* fue afectado más por *A. fissa* que por *B. angularis* en las concentraciones bajas e intermedias de alimento. Con altas concentraciones del alga, el impacto de *A. fissa* o *B. angularis* sobre el crecimiento de *B. havanaensis* fue semejante. Cuando fue cultivado solo, para una densidad dada de alimento, *A. fissa* alcanzó una mayor abundancia (4 a 6 veces) que las otras dos especies. La tasa de crecimiento poblacional (*r*) de los rotíferos se incrementó con la disponibilidad del alga. Dependiendo de la especie de rotíferos y de las condiciones del experimento, la *r* varió entre -0.001 a 0.34 d^{-1}. Se concluye que el resultado de la competencia entre las especies de estudio depende de la densidad inicial de los competidores, de la concentración de alimento así como de la interacción de los dos factores.

Palabras claves: Competencia, densidad de recursos, densidad inicial, zooplancton.

INTRODUCTION

Limnetic rotifers play an important role in the zooplankton productivity (Wetzel, 1981). Compared to crustaceans, rotifers, due to their rapid maturation, faster development rates and higher reproductive output in relatively shorter time, may account for 10 to 40% of the total zooplankton production (Herzig, 1987). Rotifers rapidly occupy all available niches in ponds and lakes and thus help in transferring energy with high efficiency from primary producers (alga and bacteria) to secondary consumers (such as larval insects and fish; Wallace *et al.*, 2006).

The competition and predation are the important forces structuring the zooplankton communities in any aquatic ecosystem (DeMott, 1989; Dumont *et al.*, 1990). In newly formed ponds and lakes competition becomes more important for the initial colonization of zooplankton species (DeMeester *et al.*, 2002). Competition studies in zooplankton under experimental conditions have mainly revealed the existence of two common types of interactions: 1) exploitative competition where a larger species usually rapidly depletes limited food conditions and 2) the interference competition, where larger zooplankton species cause mechanical hindrance or damage to the smaller competing ones (Romanovsky & Feniova, 1985; Gilbert, 1988a, 1988b). Under limiting food conditions, the body size of the competing rotifer species is important in the maintenance of a population (Stemberger & Gilbert 1985; Nandini *et al.*, 2007). Since the amount of energy needed to swim diminishes with increasing body size of zooplankton (Gerristen & Kou, 1985), larger species are expected to have higher capacity to filter greater quantities of food from the medium. Larger species have as an additional advantage their higher ability to resist pulsed periods of starvation longer than smaller zooplankton (Threlkeld, 1976).

Competition among zooplankton is influenced by several factors such as food concentration, the nutritional quality of the diet and the relative initial densities of the competing species and temperature (Rothhaupt, 1988, 1990; DeMott, 1989; Sarma *et al.*, 1996, 1999; Fernández-Araiza *et al.*, 2005). The rate of population growth (*r*) is considered as one of the important determining factors in the competitive superiority of zooplankton species even though it has not received unequivocal support from literature (Lynch, 1978; Sarma *et al.*, 1996). In rotifers the *r* appears to be body size-dependent, i.e., under optimal culture conditions, larger species generally have higher growth rates than the smaller zooplankton. The minimum quantity of food needed to maintain a population, the zero population growth rate or $r = 0$, known as the threshold food concentration, is lower for smaller zooplankton than for the larger species (Stemberger & Gilbert, 1985). Hence smaller zooplankton species would maintain a population at a lower food concentration lower than larger species, as the phytoplankton densities diminish in waterbodies. Therefore the competitive edge of both smaller and larger species depends on the availability of food concentration in natural ponds which varies seasonally (Kirk, 1997; Grover, 1997). Since it is difficult to quantify the available phytoplankton in the field, its impact has been largely ignored (Tessier & Goulden, 1982).

Most works on competition among rotifers have been focused on relatively large species like *Brachionus patulus* (Müller, 1786), *B. calyciflorus* Pallas, 1766, *B. rotundiformis* Tschugunoff, 1921, *Euchlanis dilatata* Ehrenberg, 1832 (Nandini & Sarma, 2002; Sarma *et al.*, 2002). Nevertheless, in natural water bodies from Mexico a great variety of small rotifers, including *Brachionus havanaensis* Roussselet, 1911, *Brachionus angularis* (Gosse, 1851) and *Anuraeropsis fissa* (Gosse, 1851) are frequently encountered (Nandini *et al.*, 2005). Competition studies among them are either rare or at best fragmentary (Fernández-Araiza *et al.,* 2005).

Therefore, the aim of this study was to quantify the competitive interactions among three small rotifer species (*B. angularis*, *B. havanaensis* and *A. fissa*) under different algal concentrations and initial densities.

MATERIAL AND METHODS

For competition experiments, we used three rotifer species (mean ± standard error of the body length, µm, spines excluded): *B. havanaensis*, (120 ± 5), *B. angularis* (100 ± 5) and *A. fissa* (70 ±

5). All of them were isolated from the Lake Xochimilco Channels (Mexico City) and cultured separately on reconstituted moderately hardwater (EPA medium) for at least 2 years before carrying out the experiments. EPA medium was prepared by dissolving 96 mg $NaHCO_3$, 60 mg $CaSO_4$, 60 mg $MgSO_4$ and 4 mg KCl in one liter of distilled water (Weber, 1993). Rotifer mass cultures were raised on the single-celled green alga *Chlorella vulgaris* Beijerinck, 1890 as the exclusive diet. Using Bold's basal medium enriched every 3rd d with 0.5 g l^{-1} of sodium bicarbonate, batch-cultures of *C. vulgaris* were established in 2 L transparent bottles under continuous fluorescent illumination (Borowitzka & Borowitzka, 1988). Log phase alga was harvested, centrifuged at 4000 rpm for 5 min, rinsed and resuspended in distilled water. Stock algal density was estimated using Neubauer haemocytometer. From the algal stock, the desired algal levels (0.2×10^6, 0.4×10^6 and 0.8×10^6 cells ml^{-1}) were obtained by serial dilution using fresh EPA medium.

Rotifer competition experiments were conducted in 50 ml transparent glass jars containing 20 ml EPA medium with one of the selected algal densities. The general test conditions were: pH 7.0-7.5, temperature 28 ± 1 °C and continuous but diffuse illumination. The initial density of rotifers (alone or in mixed cultures) was 1 ind. ml^{-1}. For competitive interactions, we used two rotifer species at a time and five combinations of their initial densities (e. g., *A. fissa* (*A.f.*) vs. *B. angularis* (*B.a.*): 100 % *A.f.* + 0 % *B.a.*, 75 % A.f. + 25 % *B.a.*, 50 % *A.f.* + 50 % *B.a.*, 25% *A.f.* + 75 % *B.a.*, 0% *A.f.* + 100% *B.a.*). For each rotifer species we used 45 test jars (3 food levels × 5 combinations × 3 replicates). For initiation of growth experiments, the chosen rotifer species were individually introduced into each test jar using Pasteur pipette under stereomicroscope at 20× (Nikon SMZ645).

Following initiation of the experiments, we daily counted (total count or two aliquot samples of 1 to 2 ml each) the number of live rotifers in each jar. Following the estimation of the density, rotifer populations in each jar were transferred to fresh medium containing appropriate food concentration. The experiments were terminated on day 20, when the test populations in most replicates began to show declined growth.

From the data collected, we derived the rate of population increase (*r*) using the equation: $r = (ln\ N_t - ln\ N_0)/t$, where, N_0 = initial population density, N_t = density of population after time t (days) (Krebs, 1985). The *r* was obtained from a mean of 3-5 values during the exponential phase of the population growth from each replicate. For a given rotifer species, the differences in the growth rates in the presence and in the absence of a competitor and under different algal food concentrations were quantified using two-way analysis of variance (ANOVA; Sokal & Rohlf, 2000). For multiple comparisons of the growth rates, we further subjected the data to post hoc analysis (Tukey test) using the statistical software Statistica ver. 6 (StatSoft, Tulsa, OK, USA).

RESULTS

When grown alone, *A. fissa* increased with increasing food density. Regardless algal food concentration and inoculation density of the competing species, in the presence of *B. angularis* or *B. havanaensis*, population growth of *A. fissa* was reduced. At low food level, *B. angularis* had stronger negative impact on *A. fissa* than *B. havanaensis* and with increase in algal density, both *Brachionus* species had similar but reduced impact on *A. fissa* (Fig. 1). Population growth curves of *B. angularis* in relation to different concentrations of algal diet and in the presence and absence of *A. fissa* or *B. havanaensis* are presented in Figure 2. When cultured alone, an increase in the concentration of *Chlorella* resulted in increased population density of *B. angularis*. The presence of the competing species, however, reduced its growth. In general, higher algal level and higher initial density of competing species had more adverse effect on *B. angularis*. Population growth of *B. havanaensis* was more adversely affected by *A. fissa* at low and intermediate concentrations than *B. angularis*. At high food level, the impact of *A. fissa* or *B. angularis* on the growth of *B. havanaensis* was similar (Fig. 3).

At a given food density, the peak densities of the tested rotifers when grown alone were different. The peak population densities of *A. fissa* were 156 ± 3, 425 ± 14 and 698 ± 55 ind. ml^{-1}, when cultured on *Chlorella* of 0.2×10^6, 0.4×10^6 and 0.8×10^6 cells ml^{-1} respectively. The corresponding values for *B. angularis* and *B. havanaensis* were much lower (38 to 170 ind. ml^{-1} and 41 to 91 ind. ml^{-1} respectively. Thus, *A. fissa* was numerically more abundant than the other two species. Peak population densities of all tested rotifer species increased with an increase in food density, as well as the rate of population increase (*r*). For a given rotifer species the rate of population increase was significantly influenced by the food concentration and inoculation density of the competing species (two-way ANOVAs, $p<0.05$; Table 1). However, for *A. fissa* in the presence of *B. havanaensis*, the inoculation density was not significant ($p>0.05$). Except for two cases (*B. angularis* vs. *B. havanaensis* and *B. havanaensis* vs. A. *fissa*), the interaction of food level x inoculation density was also significant for the tested rotifer species ($p<0.05$). Depending on the rotifer species and the test conditions, the *r* varied from -0.001 to 0.34 d^{-1}. Post hoc tests revealed further the differences in the growth rates of each rotifer species grown alone and together with a competitor (Table 2).

DISCUSSION

The theoretical foundations of zooplankton competition have been mainly quantified on two modalities; mechanical interference and exploitative competition (Romanovsky & Feniova, 1985; Gilbert, 1988a; Ciros-Pérez *et al.*, 2001), and both are focused on large-bodied species or those with great differences in the body sizes. Gilbert (1985) has observed that *Daphnia* caused a significant mortality to eggs and the neonates of rotifers in the laboratory competition experiments. In later studies, Gilbert (1988 a, 1988b) showed that mechanical competition is of great importance in regulating the zooplankton community structure of natural waters. Of the three species selected in this study, two species (*A. fissa* and *B. angularis*) do not have posterior or posterolateral spines. Although *B. havanaensis* has long posterior spines, they are much reduced in the absence of predators (Pavón-Meza *et al*., 2007). Because of this reason, we consider the role of mechanical interference by such spines as probably insignificant. In exploitative competition, larger rotifer species apparently consume food with a greater rate than the smaller species and thus eliminate the smaller ones. Some works have confirmed this tendency under field and under laboratory conditions (Ooms-Wilms *et al*., 1999). Here we did not observe this consistently. For example, *B. havanaensis* which is relatively larger, was strongly reduced (including negative growth rates) in the presence of *A. fissa* at low and intermediate algal densities. Then, an important conclusion derived from this work is that in addition to body size, factors such as food level and the inoculation density of the competing species play a decisive role. Other studies such as Matveev (1985) and Sarma *et al.* (1996) also showed that the competitive advantage of a zooplankton species over the other depends on its initial population densities. Our results also demonstrated that the initial densities of the competing species and the food concentrations interacted to decide which species would prevail under competition pressure. Competitively inferior species may also show higher incidence of sexual reproduction (Ciros-Pérez *et al*., 2002). We have not quantified the male production in our study.

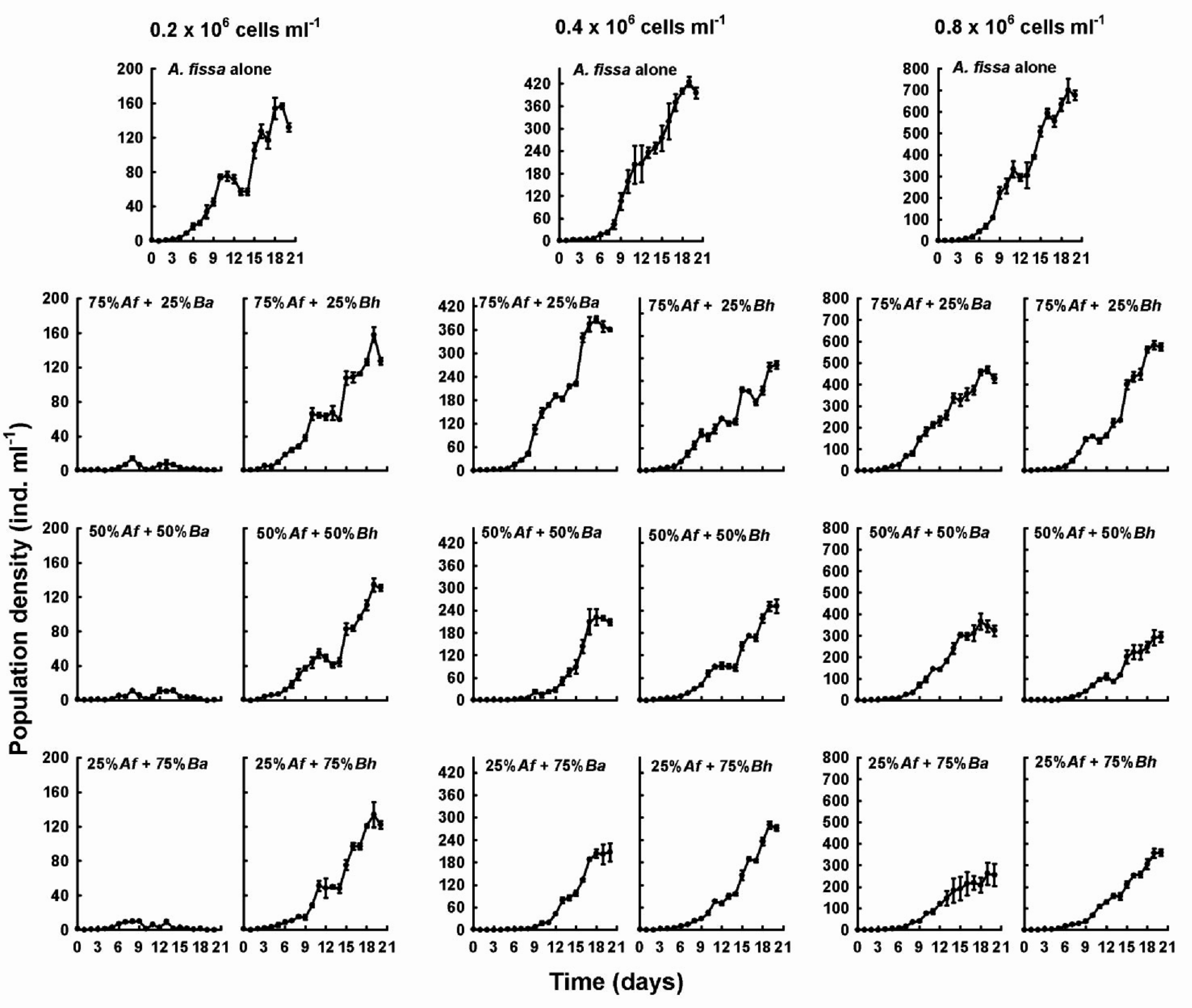

Figure 1. Population growth curves of *A. fissa* grown alone or in the presence of competition and at different concentrations (0.2 × 10^6, 0.4 × 10^6 and 0.8 × 10^6 cells ml^{-1}) of *Chlorella*. Af: *A. fissa;* Ba and Bh: *B. havanaensis*. Shown are mean ± standard error based on three replicates. Note the differences on the Y-axis scaling.

Table 1. Results of the two-way analysis of variance (ANOVA) performed on the rate of population increase of *A. fissa, B. angularis* and *B. havanaensis* grown separately or together with a competitor under different food concentrations and inoculation densities. DF = degrees of freedom, SS = sum of squares, MS = mean square, F-ratio(Fischer's F), *** = *p* <0.001; ** = *p* <0.01; * = *p* <0.05, ns = non-significant (*p* >0.05).

Source of variation	**DF**	**SS**	**MS**	**F-ratio**
Anuraeopsis fissa				
with *B. angularis*				
Food level (A)	2	0.337	0.168	457.16***
Initial density (B)	3	0.068	0.022	61.32***
Interaction of A X B	6	0.012	0.002	5.78***
Error	24	0.008	0.0003	
with *B. havanaensis*				
Food level (A)	2	0.055	0.027	15.71***
Initial density (B)	3	0.006	0.001	1.071^{ns}
Interaction of A X B	6	0.034	0.005	3.289^{*}
Error	24	0.042	0.001	
Brachionus angularis				
with *A. fissa*				
Food level (A)	2	0.017	0.008	12.71***
Initial density (B)	3	0.162	0.054	80.41***
Interaction of A X B	6	0.063	0.010	15.52***
Error	24	0.016	0.001	
with *B. havanaensis*				
Food level (A)	2	0.063	0.037	48.29***
Initial density (B)	3	0.241	0.080	122.45*
Interaction of A X B	6	0.008	0.001	2.04^{ns}
Error	24	0.016	0.001	
Brachionus havanaensis				
with *A. fissa*				
Food level (A)	2	0.151	0.076	51.47***
Initial density (B)	3	0.112	0.037	25.48***
Interaction of A X B	6	0.014	0.002	1.54^{ns}
Error	24	0.058	0.00	
with *B. angularis*				
Food level (A)	2	0.053	0.027	36.60***
Initial density (B)	3	0.061	0.020	28.12***
Interaction of A X B	6	0.020	0.003	4.56**
Error	24	0.016	0.00	

When two or more different species compete for the same resources under stable environmental conditions, one of them is eliminated of the competition, in agreement with the principle of competitive exclusion (Gause, 1934). In the lake Xochimilco a natural shallow waterbody in Mexico City (Mexico), Nandini *et al.* (2005) observed the co-existence of as many as 5 species of *Brachionus* at any sampling station. Further laboratory tests indicated that variable food density and temperature permitted this coexistence (Fernández-Araiza *et al.*, 2005). In a related study on the competition between two species of cladocerans of similar

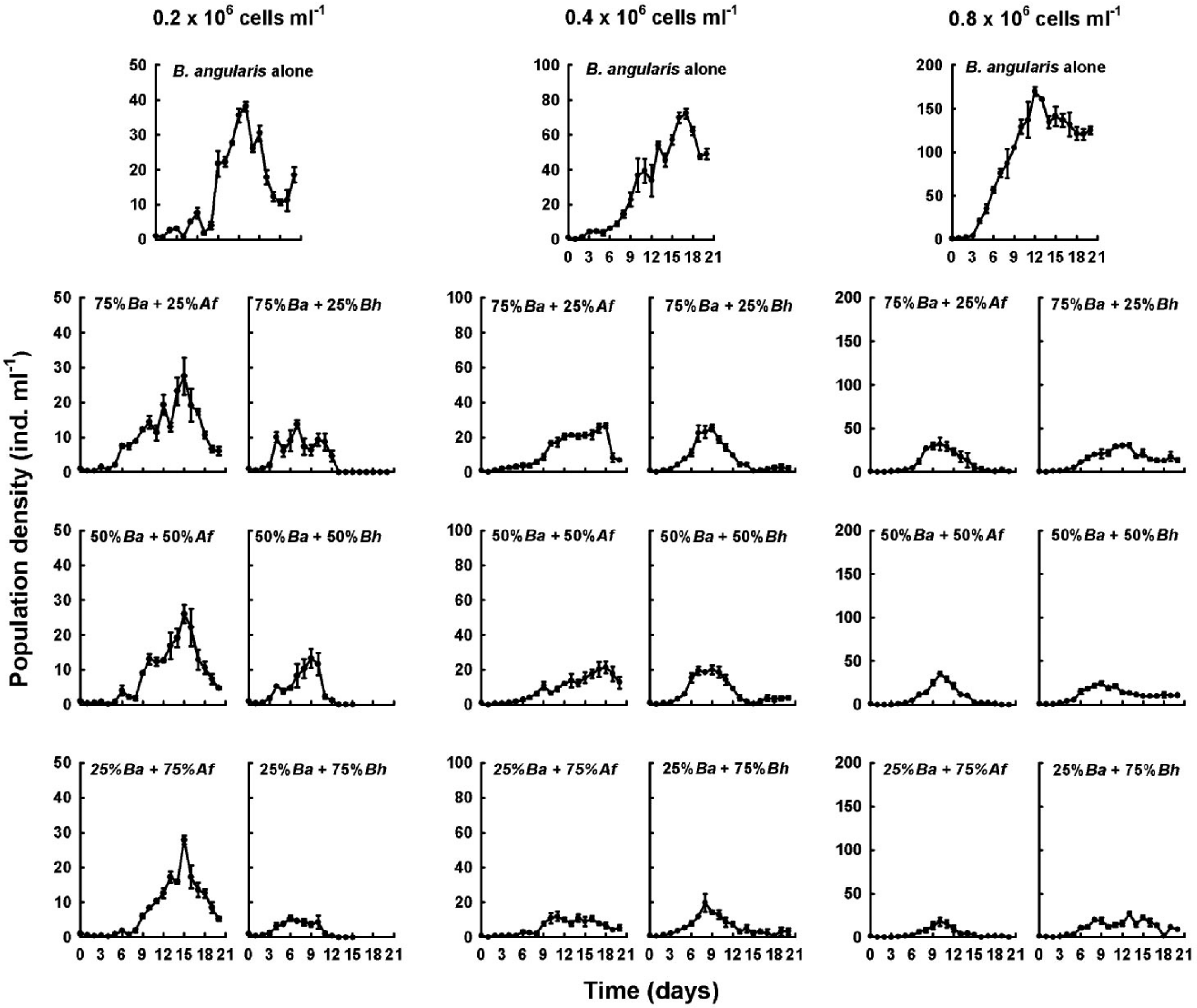

Figure 2. Curves of population growth of *B. angularis*, grown alone or in the presence of competition and under at different concentrations (0.2×10^6, 0.4×10^6 and 0.8×10^6 cells ml^{-1}) of *Chlorella*. Shown are mean ± standard error based on three replicates. Note the differences on the Y-axis scaling.

size, Sarma *et al.*, (2002) have also observed that under some combination of food level and initial density, the competing species were able to coexist together for some time. In the present study in most treatments coexistence of two rotifer species (with different densities) was noticed. The size difference among the rotifer species used here was probably not enough so as to exclude one of the two species from the competition. Similar situation has been observed between *A. fissa* and *B. calyciflorus* (Sarma *et al.*, 1996), where in low food concentrations the latter was suppressed but at high concentration the former was adversely affected, but in either case complete elimination was not observed.

In competition studies peak population abundance and the rate of population increase are sensitive variables (Sarma *et al.*, 1996). Independently of the food level, *A. fissa* was able to reduce the peak population abundance and growth rates of *B. havanaensis* more severely than *B. angularis*. It should be noted that peak abundances and the *r* of *A. fissa* were also affected by the presence of a competitor. At a given algal density, the smaller zooplankton species have higher peak abundances due to lower quantity of food required for maintenance and reproduction i.e., threshold food concentration (Nandini *et al.*, 2007). In the present study this tendency was also visible. Within the selected species, at any given food level, *A. fissa* being the smallest, had higher peak abundances than the other two species. The peak densities of the three species in general agree with the range reported in literature (*A. fissa*: ~2000 ind. ml^{-1} by Dumont *et al.*, 1995); *B. havanaensis*: 50-500 ind. ml^{-1} (Pavón-Meza *et al.*, 2004). Stemberger & Gilbert (1985) found that larger rotifer species have higher growth rates than smaller ones under comparable

Table 2. Rate of population increase (r, d^{-1}) of *A. fissa* (*A.f.*), *B. angularis* (*B.a.*) and *B. havanaensis* (*B.h.*) grown alone or in mixed cultures and under different algal concentrations (cells ml-1) and inoculation densities (%). Shown are mean ± standard error based on 3 replicates. For each species in competition data carrying a similar alphabet are not statistically significant ($p > 0.05$, Tukey test).

Species	**Treatment**	**Food level (× 10^6 cells ml^{-1})**		
		0.2	0.4	0.8
A. fissa	Alone	0.15 ± 0.02^{a}	$0.29 \pm 0.01^{d,f}$	0.34 ± 0.01^{f}
	With 25% *B. a*	0.02 ± 0.01^{b}	0.28 ± 0.01^{d}	$0.27 \pm 0.01^{d,i}$
	With 50% *B. a.*	0.02 ± 0.00^{b}	$0.21 \pm 0.02^{e,g,h,i}$	$0.26 \pm 0.00^{d,g}$
	with 75% *B. a.*	0.03 ± 0.00^{b}	$0.20 \pm 0.00^{a,h}$	$0.22 \pm 0.02^{e,g,h,i}$
	Alone	0.15 ± 0.02^{a}	$0.29 \pm 0.01^{b,d,e,g}$	$0.34 \pm 0.01^{b,h,i}$
	with 25% *B. h.*	0.23 ± 0.01^{a}	$0.25 \pm 0.00^{a,g,h}$	$0.34 \pm 0.01^{b,c,f,j}$
	with 50% *B. h.*	$0.22 \pm 0.01^{a,c,e}$	$0.24 \pm 0.01^{a,g,h}$	$0.24 \pm 0.03^{a,g,i,j}$
	with 75% *B. h.*	$0.22 \pm 0.00^{a,d,f}$	$0.23 \pm 0.00^{a,g,h}$	$0.25 \pm 0.02^{a,g,i,j}$
B. angularis	Alone	$0.21 \pm 0.00^{a,b}$	$0.24 \pm 0.00^{b,g}$	0.34 ± 0.02^{e}
	with 25% *A. f.*	$0.17 \pm 0.01^{a,g,h,i}$	$0.12 \pm 0.01^{c,h,j,k,l}$	$0.07 \pm 0.01^{d,l,m}$
	with 50% *A. f.*	$0.17 \pm 0.02^{a,g,h}$	$0.10 \pm 0.01^{c,i,k,m}$	$0.08 \pm 0.03^{d,l,m}$
	with 75% *A. f.*	$0.16 \pm 0.01^{a,j,k}$	$0.08 \pm 0.01^{d,k,n}$	$0.03 \pm 0.01^{f,m,n}$
	Alone	$0.21 \pm 0.00^{a,g}$	0.24 ± 0.00^{a}	0.34 ± 0.02^{d}
	with 25% *B. h.*	$0.08 \pm 0.01^{b,h,i}$	$0.04 \pm 0.01^{c,h,k,o}$	$0.13 \pm 0.02^{e,i,l}$
	with 50% *B. h.*	$0.06 \pm 0.02^{b,j,k,l}$	$0.03 \pm 0.01^{c,h,k}$	$0.11 \pm 0.00^{f,i,l,m,o}$
	with 75% *B. h.*	$0.04 \pm 0.03^{c,h,j,m}$	$0.03 \pm 0.02^{c,h,k}$	$0.14 \pm 0.02^{g,i}$
B. havanaensis	Alone	$0.08 \pm 0.02^{a,e,f}$	$0.19 \pm 0.01^{b,f,g,h,i}$	$0.25 \pm 0.01^{c,h,n}$
	with 25% *A. f.*	$0.00 \pm 0.03^{b,d}$	$0.09 \pm 0.00^{a,g,j,k}$	$0.19 \pm 0.02^{e,i,j,n}$
	with 50% *A. f.*	-0.00 ± 0.01^{a}	$0.07 \pm 0.01^{a,l,m}$	$0.17 \pm 0.03^{e,i,j,l,n}$
	with 75% *A. f.*	-0.01 ± 0.05^{a}	-0.01 ± 0.01^{a}	$0.08 \pm 0.01^{a,d,k,m}$
	Alone	$0.08 \pm 0.02^{a,k}$	$0.19 \pm 0.01^{b,d,e}$	$0.25 \pm 0.01^{c,e}$
	with 25% *B. a.*	0.04 ± 0.01^{a}	$0.13 \pm 0.01^{b,f,g}$	$0.13 \pm 0.01^{b,h,i,l}$
	with 50% *B. a.*	0.04 ± 0.01^{a}	$0.11 \pm 0.02^{a,d,h}$	$0.09 \pm 0.03^{a,g,l}$
	with 75% *B. a.*	0.04 ± 0.00^{a}	$0.09 \pm 0.02^{a,f,i,j}$	$0.07 \pm 0.01^{g,k,l}$

conditions. However, this does not seem to be a general trend (see Sarma *et al.*, 2001). In the present work, we also did not find a positive relation between body size and the *r*. This may be due to the food concentrations selected here. We have not tested a wide range of food concentrations to derive growth rates. It is however known that *r* increases with increasing food levels (Nandini *et al.*, 2007), as also observed here. Regardless of the rotifer species and the food concentration, the *r*-values observed here are within the range reported for *Anuraeopsis* and *Brachionus* (0.1-2.0 d^{-1}; Sarma *et al.*, 2001).

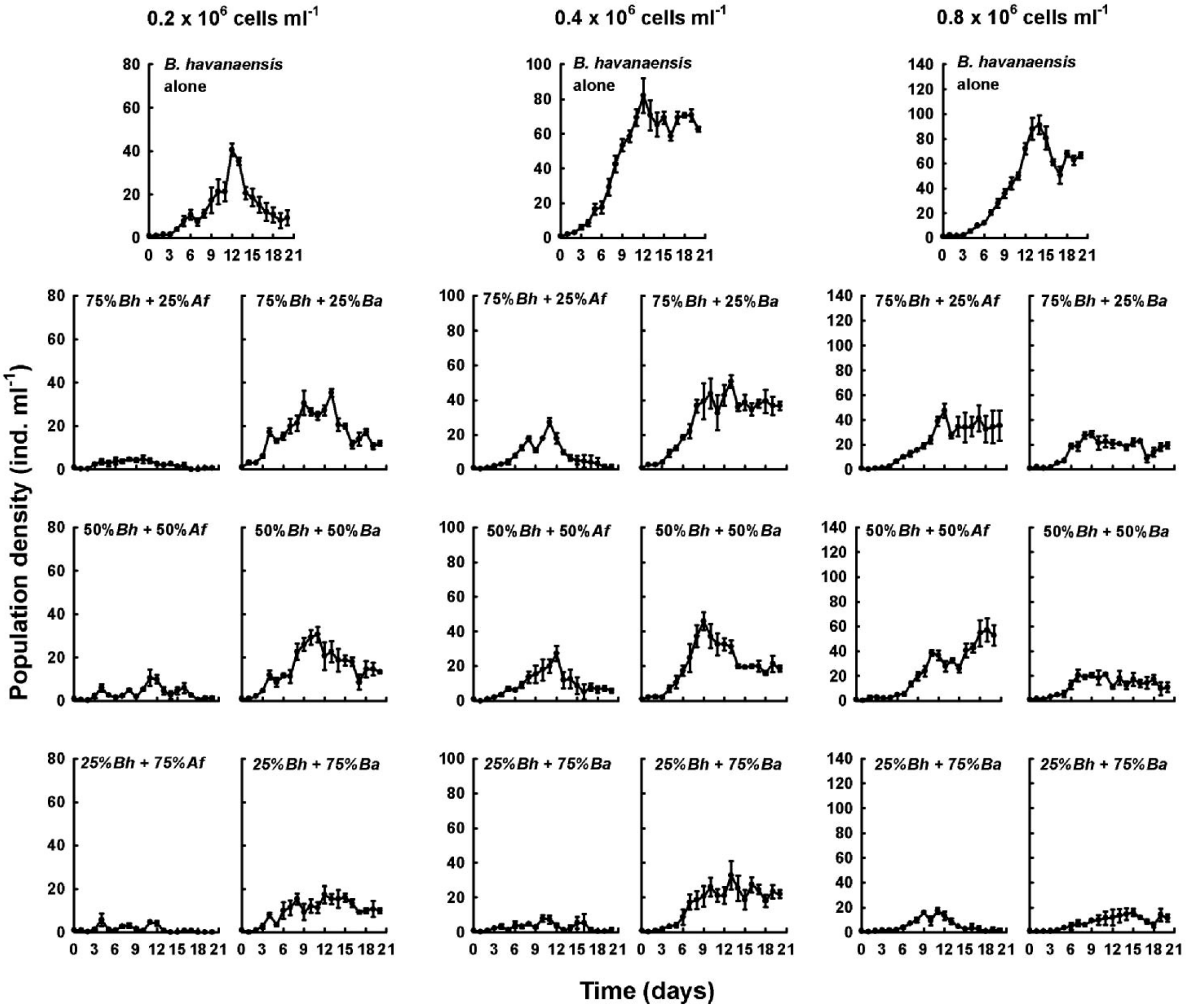

Figure 3. Curves of population growth of *B. havanaensis*, grown alone or in the presence of competition and under at different concentrations (0.2×10^6, 0.4×10^6 and 0.8×10^6 cells ml^{-1}) of *Chlorella*. Shown are mean ± standard error based on three replicates. Note the differences on the Y-axis scaling.

This study showed that the competitive outcome in the tested rotifers depended on the initial inoculation density of the competing species, the offered food concentration as well as the interaction of these two factors. While all the three species were adversely affected by the presence of competitor, *A. fissa* was strongly suppressed by *B. angularis* at low food level. Competition between these brachionid rotifers showed that *B. angularis* was affected by the presence of *B. havanaensis*, especially at higher food level. The body size-related traits of rotifers were evident in the peak abundances where large-bodied taxa had lower peak population density, *A. fissa* being the smallest species had highest abundance while under similar conditions, both *Brachionus* species had lower densities. The rate of population growth increased with increasing food concentrations.

ACKNOWLEDGMENTS

We thank three anonymous reviewers for critically evaluating our presentation. SSSS and SN thank PAPIIT IN201907 and PAPIME PE201406 for financial support.

REFERENCES

Borowitzka, M. A. & L. J. Borowitzka. 1998. *Micro-algal biotechnology*. Cambridge University Press, London. 477 p.

Ciros-Pérez, J., M. J. Carmona & M. Serra. 2001. Resource competition between sympatric sibling rotifer species *Limnology and Oceanography* 46: 1511-1523.

Ciros-Pérez, J., M. J. Carmona & M. Serra. 2002. Resource competition and patterns of sexual reproduction in sympatric sibling rotifer species. *Oecologia* 131: 35-42.

De Meester, L., A. Gómez, B. Okamura & K. Schwenk. 2002. The monopolization hypothesis and the dispersal–gene flow paradox in aquatic organisms. *Acta Oecologia* 23: 121-135.

DeMott, W. R. 1989. The role of competition in zooplankton success. *In*: U. Sommer (Ed.). *Plankton ecology: succession in plankton communities*. Springer- Verlag. Berlin, pp. 195-252.

Dumont, H. J. 1994. Ancient lakes have simplified pelagic food webs. *Archive* für *Hydrobiologie Beihaft* 44: 223-234.

Dumont, H. J., J. G. Tundisi & K. Roche (Eds.). 1990. *Intrazooplankton predation.* Developments in Hydrobiology No. 60. Kluwer Academic Publishers, Dordrecht, The Netherlands. 256 p.

Dumont, H. J. & S. S. S. Sarma. 1995. Demography and population growth of *Asplanchna girodi* (Rotifera) as a function of prey (*Anuraeopsis fissa*) density. *Hydrobiologia* 306: 97-107.

Dumont, H. J., S. S. S. Sarma & A. J. Ali. 1995. Laboratory studies on the population dynamics of *Anuraeopsis fissa* (Rotifera) in relation to food density. *Freshwater Biology* 33: 39-46.

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

Gause, G. J. 1934. *The Struggle for Existence*. Williams and Wilkins. Baltimore. 167 p.

Gerritsen, J. & J. Kou. 1985. Food limitation and body size. *Archive für Hydrobiologie Beihaft* 21:173-184.

Gilbert, J. J. 1985. Competition between rotifers and *Daphnia*. *Ecology* 66: 1943-1950.

Gilbert, J. J. 1988a. Susceptibilities of ten rotifer species to interference from *Daphnia pulex*. *Ecology* 69: 1826-1838.

Gilbert, J. J. 1988b. Suppression of rotifer populations by *Daphnia*: A review of the evidence, the mechanisms, and the effects on zooplankton community structure. *Limnology and Oceanography* 33: 1286-1303.

Grover, J. P. 1997. *Resource competition*. Chapman & Hall, New York. 375 p.

Herzig, A.1987. The analysis of planktonic population: a plea for long term investigation. *Hydrobiologia* 147:163-180.

Kirk, K. L. 1997. Life-history responses to variable environments: Starvation and reproduction in planktonic rotifers. *Ecology* 78: 434-441

Krebs, C. J., 1985. *Ecology: the experimental analysis of distribution and abundance*. 3rd ed. Harper & Row, New York. 800 p.

Lynch, M. 1978. Complex interactions between natural co-exploiters-*Daphnia* and *Ceriodaphnia*. *Ecology* 59: 552-564.

Matveev, V. 1985. Delayed density dependence and competitive ability in two cladocerans. *Archive für Hydrobiologie Beihaft* 21: 453-459.

Nandini, S. & S. S. S. Sarma. 2002. Competition between the rotifers *Brachionus patulus* and *Euchlanis dilatata*: Effect of algal food level and relative initial densities of competing species. *Russian Journal of Ecology* 33: 291-295.

Nandini, S., P. Ramírez-García & S. S. S. Sarma. 2005 Seasonal variations in the species diversity of planktonic rotifers in Lake Xochimilco, Mexico. *Journal of Freshwater Ecology* 20: 287-294.

Nandini, S., S. S. S. Sarma, R. J. Amador-López & S. Bolaños-Muñoz. 2007. Population growth and body size in five rotifer species in response to variable food concentration. *Journal of Freshwater Ecology* 22: 1-10.

Ooms-Wilms, A. L., Postema, G., Gulati, R.D. 1999. Population dynamics of planktonic rotifers in Lake Loosdrecht, the Netherlands, in relation to their potential food and predators. *Freshwater Biology* 42: 77-97

Pavón-Meza, E. L., S. S. S. Sarma & S. Nandini. 2004. Combined effects of food (*Chlorella vulgaris*) concentration and temperature on the population growth of *Brachionus havanaensis* (Rotifera: Brachionidae). *Journal of Freshwater Ecology* 19: 521-530.

Pavón-Meza, E. L., S. S. S. Sarma & S. Nandini. 2007. Combined effects of temperature, food (*Chlorella vulgaris*) concentration and predation (*Asplanchna girodi*) on the morphology of *Brachionus havanaensis* (Rotifera). *Hydrobiologia* 593: 95-101.

Romanovsky, Y. & I. Y. Feniova. 1985. Competition among Cladocera: effect of different levels of food supply. *Oikos* 44: 243-252

Rothhaupt, K. O. 1988. Mechanistic resource competition theory applied to laboratory experiments with zooplankton. *Nature* 333: 660-662.

Rothhaupt K. O. 1990. Resource competition of herbivorous zooplankton: A review of approaches and perspectives. *Archiv für Hydrobiologie* 118: 1-29.

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

Sarma, S. S. S., M. A. Fernández-Araiza & S. Nandini. 1999. Competition between *Brachionus calyciflorus* Pallas and *Brachionus patulus* (Muller) (Rotifera) in relation to algal food concentration and initial population density. *Aquatic Ecology* 33: 339-345.

Sarma, S. S. S., N. Iyer & H. J. Dumont. 1996. Competitive interactions between herbivorous rotifers: importance of food concentration and initial population density. *Hydrobiologia* 331: 1-7.

SARMA, S. S. S., P. S. LARIOS-JURADO & S. NANDINI. 2001. Effect of three food types on the population growth of *Brachionus calyciflorus* and *Brachionus patulus* (Rotifera: Brachionidae). *Revista de Biología Tropical* 49:75-82.

SOKAL, R. R. & F. J. ROHLF. 2000. *Biometry*. W. H. Freeman and Company, San Francisco. 887 p.

STEMBERGER, R. S. & J. J. GILBERT. 1985. Assessment of threshold food levels and populations growth in planktonic rotifers. *Ecology* 66: 1151-1159.

TESSIER, A. J. & C. E. GOULDEN. 1982. Estimating food limitation in cladoceran populations. *Limnology and Oceanography* 27: 707-717.

THRELKELD, S. T. 1976. Starvation and the size structure of zooplankton communities. *Freshwater Biology* 6: 489-496.

WALLACE, R. L., T. W. SNELL, C. RICCI & T. NOGRADY. 2006. *Rotifera Part 1: Biology, Ecology and Systematics. Guides to the identification of the microinvertebrates of the continental waters of the world.* Kenobi Productions Gent / Backhuys, The Netherlands. 299 p.

WEBER, C. I. 1993 *Methods for measuring the acute toxicity of effluents and receiving waters to freshwater and marine organisms.* 4th ed. United States Environmental Protection Agency, Cincinnati, Ohio, EPA/600/4-90/027F. 293 p.

WETZEL, G. R., 1981. *Limnología*. Ed. Omega, Barcelona. 679 p.

Recibido: 28 de agosto de 2006

Aceptado: 7 de septiembre 2007