

Effects of salinity, food level, and the presence of microcrustacean zooplankters on the population dynamics of rotifer *Brachionus rotundiformis*

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Abstract We investigated the population dynamics of the rotifer *Brachionus rotundiformis* fed with the alga *Isochrysis galbana* at two food concentrations (3×10^4 and 40×10^4 cells ml^{-1}) and four salinity levels (5, 10, 20, and 30) in the presence and absence of two copepod species, *Pseudodiaptomus annandalei* and *Apocyclops royi* and one cladoceran, *Diaphanosoma aspinosum*. Both the density and population growth rate of *B. rotundiformis* increased at higher food concentration and at salinity levels of 10 and 20. Among the microcrustaceans, only *P. annandalei* had a significant negative effect on the growth rate of the rotifer population because of its efficient predation. In contrast, the presence of both *A. royi* and *D. aspinosum* did not affect the growth rates at any of the salinity and food levels.

Brachionus rotundiformis had significantly larger size during the log-phase, particularly if *P. annandalei* was present. Thus, *B. rotundiformis* grows better at higher food level and medium salinity levels. Unlike the larger calanoid, *P. annandalei*, *B. rotundiformis* can definitely coexist with relatively small cyclopoid copepods (*A. royi*) and cladocerans (*D. aspinosum*), because of the absence of interference.

Keywords Rotifers · Live food · Copepods · Cladocerans · Interference · Predation

Introduction

Rotifers are a group of organisms important in aquatic ecosystems, because they play an important role in providing live food for aquaculture (Lubzens, 1987; Yúfera, 2001). They are considered as ideal first feed for the development of early larval stages of fish in aquaculture. Moreover, they are mainly used because of their relatively higher intrinsic rates of increase and short population renewal time (Allan, 1976).

Abiotic and biotic factors regulate rotifer development by acting mainly on their diversity and population growth rate. Abiotic factors including instability of water temperature and salinity play an important role in rotifer development (Dumont et al., 1995; Rothhaupt, 1995; Haberman & Sudzuki, 1998).

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Many studies have reported interactions of rotifer population dynamics with temperature, salinity, and food level. Oltra & Todoli (1997) showed that in the marine rotifer *Synchaeta cecilia valentina*, the effect of temperature on fecundity depends on food level. *Brachionus plicatilis* was reported to grow and reproduce better at salinities between 5 and 10 at 18°C and a salinities of 10 and 15 at both 24 and 30°C (Yin & Zhao, 2008).

In natural settings, rotifers coexist with many others organisms (e.g., cladocerans, copepods) and constitute an important link in the food chain (Gilbert, 1988; Park & Marshall, 2000). They are the preferred prey of many copepods, insects, and fish (Kumar & Rao, 1999). Predators and/or competitors are important factors affecting growth of rotifer population (Kumar & Rao, 2001; Rao & Kumar, 2002). The rotifer *Asplanchna*, cyclopoid, and calanoid copepods are particularly known to be efficient predators of rotifers and often cause a seasonal decline in rotifer populations and replacement of species (Kumar & Rao, 2001; Brandl, 2005; Feike & Heerkloss, 2009). Diéguez & Gilbert (2002) reported predation to be more closely linked to rotifer suppression by copepods than exploitative resource competition. Several studies have reported negative effects of cladocerans on the rotifer population growth rate due to interference competition (Gilbert, 1988; Fussmann, 1996; Kak & Rao, 1998; Nandini et al., 2002). Mechanical interference for exploitative food competition can explain rotifer suppression by cladocerans (Burns & Gilbert, 1986). In response to predation by other rotifers (e.g., *Asplanchna*), other zooplankters (copepods), or interference by large cladocerans (e.g., *Daphnia* spp.), many rotifers have been reported to develop various behavioral and/or morphological adaptations (Gilbert, 1987; Kumar, 2003). Abiotic factors, such as temperature and salinity, may induce morphological variation in rotifers. For example, temperature induces morphological variation in *Keratella cochlearis* (Bielanska-Grajner, 1995; Diéguez et al., 1998).

There are several investigations on the combined effect of temperature and salinity on the population dynamics of rotifer species (Oltra & Todoli, 1997; Fernández-Araiza et al., 2005; Yin & Zhao, 2008). In nature, temperature and salinity act in concert with biotic factors (e.g., competition and predation) in shaping population structure of species. However,

only a few studies have focused on the combined effect of abiotic and biotic factors on rotifer population dynamics (Nandini et al., 2002; Rao & Kumar, 2002). The euryhaline rotifer *Brachionus rotundiformis* commonly coexists with copepods and cladocerans in brackish water ecosystems in tropical and subtropical regions, subjected to a wide range of temperature and salinity variations (Kak, 1999). Ciliates, e.g., *Euplotes* sp. have been reported to inhibit the growth of *B. rotundiformis* (Hagiwara et al., 1995; Cheng et al., 2004). However, no study reports the effect of microcrustaceans on population structure of this rotifer. Except *Diaphanosoma aspinosum*, both *Apocyclops royi* and *Pseudodiaptomus annandalei* are commonly used in aquaculture live food production in the Indo-Pacific region (James & Thompson, 1986; Liao et al., 2001; Chen et al., 2006).

The three microcrustaceans selected for this study often coexist in brackish water aquaculture or mariculture ponds, lagoons, and in back waters of estuaries in Indo-Pacific regions (Hwang et al., 2010). Their differential food threshold and tolerance to salinity fluctuations point to the importance of the combined effect of salinity and co-occurring microcrustaceans on the population dynamics of *B. rotundiformis*. However, very few studies attempted to investigate the combined effect of salinity and co-occurring microcrustaceans on the population dynamics of *B. rotundiformis* (Cheng et al., 2004). Moreover, Hagiwara et al. (1995) have reported the effect of other microcrustacean zooplankters (*Diaphanosoma celebensis* and *Tigriopus japonicus*) of on another congeneric euryhaline species, *B. plicatilis*. The aim of this study was to determine the effects of microcrustaceans: the calanoid copepod, *P. annandalei*, the cyclopoid copepod, *A. royi*, and the cladoceran, *D. aspinosum* on the population dynamics and body size of *B. rotundiformis* as a function of salinity and food levels.

Materials and methods

Algal culture

The unicellular alga, *Isochrysis galbana* (5–9 µm), from a lab culture was used as the food in all experiments. The alga was mass cultured in 5 l borosilicate glass bottles containing f/2 medium

(Guillard & Ryther, 1962). These bottles were exposed to fluorescent illumination at intensities from 146×10^{-6} to 2928×10^{-6} W cm $^{-2}$ (at 555 nm) in a 12 h light/12 h dark cycle. The cultures were maintained at 27–32°C at a salinity of >15. The alga were harvested in the exponential phase at $\sim 3 \times 10^7$ cells ml $^{-1}$ for the culture maintenance and experiments, and diluted to required concentrations with filtered seawater at the set salinity.

Zooplankton cultures

Animals were grown in cultures at least 3 months before starting the experiments. The starter cultures of *B. rotundiformis*, *Pseudodiaptomus annandalei* (total length ~ 1280 μ m for adults), and *Apocyclops royi* (total length ~ 1034 μ m for adults) were originally isolated from zooplankton samples collected from a coastal brackish water pond (salinity ~ 20) in Tungkang, Southern Taiwan. *Diaphanosoma aspinosum* (~ 1150 μ m) was collected from different brackish ponds by filtering water through a 100 μ m mesh size plankton net, and the animals were acclimatized to the laboratory culture conditions. The experimental animals were cultured in a mixture of filtered seawater and autoclaved tap water. Monocultures of all experimental animals were maintained in 2-l beakers containing a 1.5-L medium at 20–25 salinity and $28 \pm 1.5^\circ\text{C}$ temperature. *I. galbana* was provided as the exclusive food (6×10^4 – 10×10^4 cells ml $^{-1}$) for all animals in culture. Food was daily refreshed.

Population growth experiment

In one experiment, we examined the effects of low (*I. galbana*: 3×10^4 cells ml $^{-1}$) and high concentration of food (*I. galbana*: 40×10^4 cells ml $^{-1}$), four salinity levels (5, 10, 20, and 30), and three crustacean zooplankters (*P. annandalei*, *A. royi*, and *D. aspinosum*) on *B. rotundiformis* population growth. All zooplankters were acclimated at each experimental salinity level for at least 2 weeks prior to experiments. The experimental temperature was 28°C, i.e., same as in the cultures. We used three replicates for each salinity level, food concentration, and zooplankton combined taxa. Population growth rates of the zooplankters were measured in 150 ml

transparent beakers containing 50 ml medium at the chosen food concentration and salinity level.

The experiment used 96 test beakers (2 food concentrations [3×10^4 cells ml $^{-1}$ and 40×10^4 cells ml $^{-1}$] \times 4 salinities [5, 10, 20, 30] \times 4 treatments [control, *A. royi*, *P. annandalei*, *D. aspinosum*] \times 3 replicates). In each experiment, the rotifer *B. rotundiformis* was introduced in the log phase at an initial density of 2 ind. ml $^{-1}$ (100 ind./beaker) using a Pasteur pipette under a stereomicroscope. Two adults of each crustacean were added to the beakers containing 100 rotifers in 50 ml water in the beakers. Rotifer densities in the experimental beakers were counted daily under a stereomicroscope using 1–5 ml (depending on density) of the aliquot sample. After density counts, the rotifers, and crustaceans in the test beakers were transferred to fresh beakers containing the selected food and salinity at set levels. The populations of all three crustaceans were maintained at two adults per 50 ml in all experiments. Daily observations were continued until most of the rotifer densities became almost constant.

To avoid the effect of food limitation on the body, because of low food level, size of rotifers was measured only at high food levels. The rotifer body size was measured during their log-phase (i.e., at the time of rotifer introduction) and K-phase (when rotifer population started declining) in both controls and crustacean treatments. The lorica volumes were calculated using the following formula:

$$\text{Lorica volume} = 0.52 * L * W * H$$

where *L*, *W*, and *H* denote the length, width, and height, respectively, (Ruttner-Kolisko, 1977).

Data analyses

The population growth rate (*r*) for each replicate in control and treatment vessels was calculated from the exponential phase of the growth using the growth equation of Krebs (1985):

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

where *N*₀ and *N*_{*t*} represent the initial and final population density after a time duration *t* (*N*_{*t*}) compared with the initial density (*N*₀). The average *r* was calculated from the three replicates in each case (Dumont et al., 1995).

Using SPSS 13.0 for Windows, the significance of differences between experimental groups, including assessments of the effect of salinity, food level, and the presence of other zooplankters on the maximal density, population growth rate, and lorica volume, was determined by three-way analysis of variance (ANOVA). A posteriori (post hoc) multiple comparison among means was performed by the Scheffé test.

Results

The population growth rate curves of *B. rotundiformis* at four salinity levels (5, 10, 20, and 30), cultured with and without *P. annandalei*, *A. royi*, and *D. aspinosum* show that the densities of rotifers increased with high food level (Fig. 1). However, magnitude of the increase in density of rotifers at high food level varied with salinity level and mainly with the presence of crustaceans. At salinity 5, rotifer densities increased an average 3–4 (in control and in presence of *A. royi* and *D. aspinosum*) to 27 (in presence of *P. annandalei*) times. At salinity 10, rotifer densities increased an average 4–5 (in control and in presence of *A. royi* and *D. aspinosum*) to 95 (in presence of *P. annandalei*) times. At salinity 20, rotifer densities increased an average 4–5 (in control and in presence of *A. royi* and *D. aspinosum*) to 8 (in presence of *P. annandalei*) times. At salinity 30, rotifer densities increased an average 4–6 (in control and in presence of *A. royi* and *D. aspinosum*) to 51 (in presence of *P. annandalei*) times. Regardless of the food and salinity levels, the rotifer population growth was similar in both control and in the presence of crustaceans. However, the salinity increase did adversely affect the densities of *B. rotundiformis*. The highest densities were recorded at salinity 10. The rotifers had similar population curve trends in the presence and absence of *A. royi* and *D. aspinosum*, particularly at high food density. The lowest densities of *B. rotundiformis* (<20 ind. ml^{-1}) occurred at salinity levels of 20 and 30 at low food density, and in the presence of *P. annandalei*. Low food level and the presence of *P. annandalei* caused an increase in rotifer density only at salinity levels of 10 and 20. At high food density, a slight population increase was observed in the presence of *P. annandalei* after a lag phase of 2, 3, 4, and 5 days at salinity levels of 20, 10, 30, and 5, respectively (Fig. 1).

Fig. 1 Population growth curves of *Brachionus rotundiformis* grown alone (control) and in the presence of *Pseudodiaptomus annandalei*, *Apocyclops royi*, and *Diaphanosoma aspinosum* under low (3×10^4 cells ml^{-1}) and high (40×10^4 cells ml^{-1}) food levels, at four different salinity levels (5, 10, 20, and 30). Values are the mean \pm standard deviation of three experimental replicates. *Note*: the scales for y-axis for low food and high food levels differ by factor 4

The rates of population increase ($r \text{ d}^{-1}$) exhibited a similar trend to those of population growth (Fig. 2). The increase of food concentration enhanced the growth rate of *B. rotundiformis*. The highest values of r were reached at salinity 10 and 20 in the control, *A. royi* and *D. aspinosum* experiments. The lowest values of r were observed in the presence of *P. annandalei* and at low food concentration, which exhibited the lowest growth values.

Salinity, food density, and the presence of zooplankters demonstrated significant effect on the population peaks and growth rate of *B. rotundiformis* ($P < 0.001$, three-way ANOVA, Table 1). The interaction of these three factors was significant ($P < 0.001$) for population peaks and growth rate, as were the interactions of salinity–food concentration, salinity–presence of zooplankters, and food level–presence of zooplankters. Population peaks and growth rate of *B. rotundiformis* significantly differed for salinities 5, 10, 20, and 30 (post hoc tests, Scheffé; Table 2). The rotifer population growth rate significantly differed at the three salinity levels, 10, 20, and 30. Post hoc multiple comparisons of the population peaks showed significant differences between the control, *P. annandalei*, *A. royi*, and *D. aspinosum* treatments. However, rotifer growth rates did not differ significantly between the control, *A. royi*, and *D. aspinosum* treatments (post hoc tests, Scheffé; Table 2).

Lorica volumes of *B. rotundiformis* increased with increasing salinity level and were larger during the log phase and in the presence of *P. annandalei* (Fig. 3). Interactions of the salinity–presence of crustacean zooplankters–developmental phase, salinity–development phase, and salinity–presence of crustaceans had significant effects on the lorica volume for *B. rotundiformis* (Table 1). In contrast, the interaction of salinity–development phase did not have significant effect on the lorica volume. Post hoc tests (Scheffé) showed significant differences of the lorica volume between salinity 5, 10, 20, and 30,

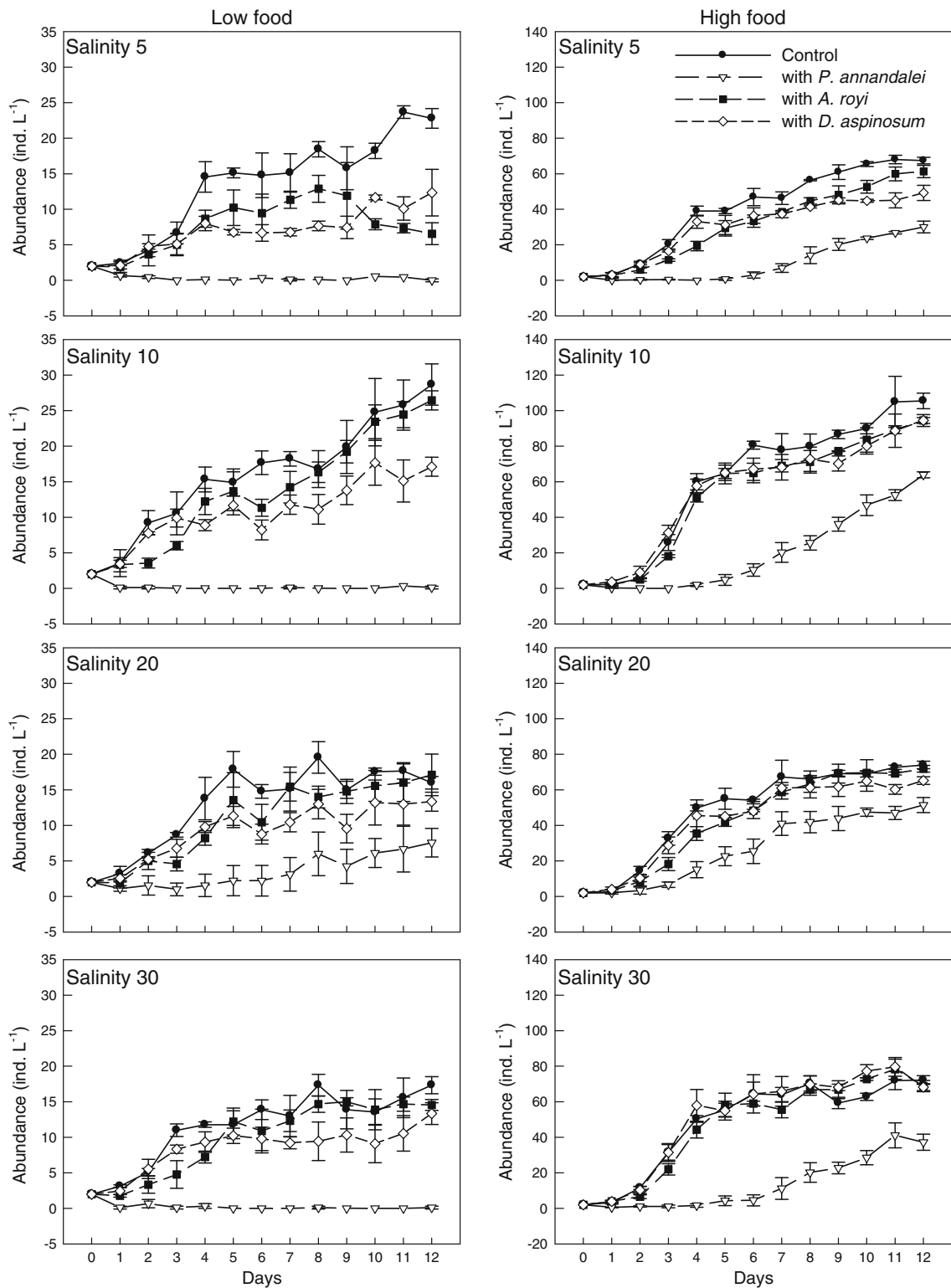
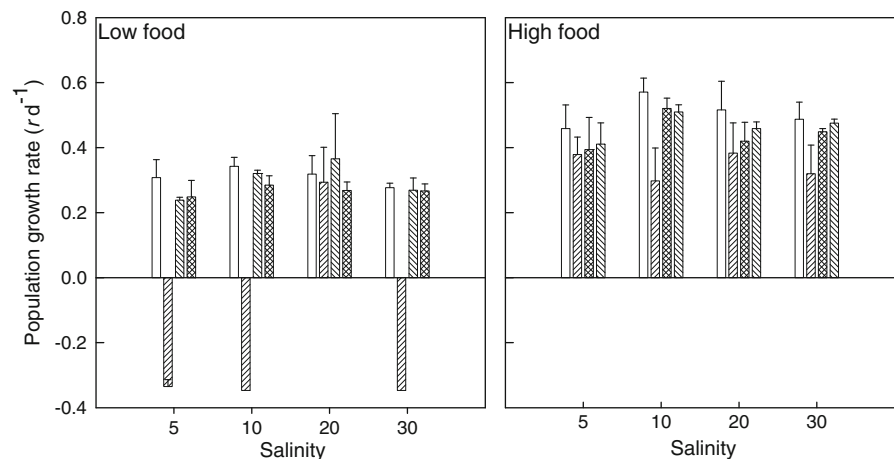


Fig. 2 Rate of population increase $r\ d^{-1}$ (mean \pm standard deviation) of *Brachionus rotundiformis* for the experiments illustrated in Fig. 1



whereas no significant difference exhibited between salinity 10 and 20 (Table 2). The presence of *P. annandalei* had significant effect on the lorica volume, but the presence of *A. royi* and *D. aspinosum* (post hoc tests) showed no such effect. However, the lorica volumes did not differ significantly among the control, *A. royi*, and *D. aspinosum* treatments.

Discussion

This study shows that food and salinity levels, and the presence of crustacean zooplankters, are important factors influencing the population dynamics of *B. rotundiformis*. The highest population densities and increased population growth rates of *B. rotundiformis* occur at high food levels, at salinity levels up to 20, and in the absence of other zooplankters. However, only *P. annandalei* has a significantly negative effect on the population dynamics of *B. rotundiformis*. In addition to salinity level, the presence of crustacean zooplankters and the developmental phase of the rotifer significantly affect the lorica volume of *B. rotundiformis*. An increase of the lorica volume was observed during the log phase, particularly in the presence of *P. annandalei*.

Impact of food and salinity levels on population growth rate of rotifers

Food level appears to be an important factor affecting rotifer development. The importance of the type of algal food (Rothhaupt, 1990; Suchar & Chigbu, 2006),

food quantity (Galindo et al., 1993; Dumont et al., 1995), algal size (Rothhaupt, 1990; Yin & Zhao, 2008), and essential biochemical constituents of the algae such as phosphates and PUFA (Rothhaupt, 1995; Gulati & DeMott, 1997) on the population dynamics of rotifers is well known. Food level has significant effect on all life parameters of rotifers (Galindo et al., 1993; Sarma & Nandini, 2001). While *B. rotundiformis* is regarded as tolerant to salinity (Haberman & Sudzuki, 1998; Hagiwara et al., 2001), this rotifer can reach its highest densities and growth rate at medium salinity levels (5–20) as shown by Sarma et al. (2002), Yin & Zhao (2008), and this study. These observations are consistent with other studies that report high salinity values to negatively affect rotifer populations by decreasing the production of mictic females, shortening lifespan, decreasing female fecundity, and decreasing the intrinsic growth rate and number of species (Lubzens et al., 1985; Oltra & Todoli 1997; Park & Marshall, 2000). Sarma et al. (2002) reported that salinity 0 had a negative effect on rotifers. However, the tolerance to salinity depends on strains of the euryhaline rotifer species (Mustahal et al., 1991).

Coexistence of small cladocerans and copepods with rotifers

The highest population growth rate and population peaks found in the control experiments in our study are caused by the absence of predation, competition, and interference. Nandini et al. (2002) and Fernández-Araiza et al. (2005) observed highest growth

Table 1 Results of three-way analysis of variance for peak population density, rate of population increase per day, and body size of the rotifer *Brachionus rotundiformis* grown at two food levels (3×10^4 cells ml^{-1} and 40×10^4 cells ml^{-1}), four salinity levels (5, 10, 20, and 30), and with and without the presence of *Pseudodiaptomus annandalei*, *Apocyclops royi*, and *Diaphanosoma aspinosum*

Variable/source	DF	SS	MS	F ratio
Population peaks				
Salinity (A)	3	5977.51	1992.50	212.32***
Food density (B)	1	72875.26	72875.26	7765.69***
Zooplankters (C)	3	10561.96	3520.65	375.17***
Interaction (A x B)	3	3180.94	1060.31	112.99***
Interaction (A x C)	9	1099.12	122.13	13.01***
Interaction (B x C)	3	978.40	326.13	34.75***
Interaction (A x B x C)	9	432.94	48.10	5.13***
Error	64	600.60	9.38	
Growth rate				
Salinity (A)	3	0.19	0.06	16.89***
Food density (B)	1	1.52	1.52	409.95***
Zooplankters (C)	3	1.22	0.41	109.33***
Interaction (A x B)	3	0.14	0.05	12.53***
Interaction (A x C)	9	0.35	0.04	10.43***
Interaction (B x C)	3	0.41	0.14	36.46***
Interaction (A x B x C)	8	0.26	0.03	7.67***
Error	60	0.22	0.00	
Lorica volume				
Salinity (A)	3	2.44E+12	8.14E+11	15.13***
Zooplankton (C)	3	1.33E+13	4.42E+12	82.12***
Phase (D)	1	3.10E+11	3.10E+11	5.76*
Interaction (A x C)	9	1.55E+12	1.72E+11	3.2**
Interaction (A x D)	3	5.27E+11	1.76E+11	3.27*
Interaction (B x D)	3	4.48E+10	1.49E+10	0.28ns
Interaction (A x C x D)	9	2.14E+12	2.38E+11	4.42***
Error	64	3.44E+12	5.38E+10	

DF degrees of freedom, SS sum of squares, MS mean square, F F-ratio. Levels of significance: $P < 0.001 = \text{***}$, $P < 0.01 = \text{**}$, $P < 0.05 = *$, and $P > 0.05 = \text{ns}$

rates at higher food levels rather than interference competition as reported in the literature (Gilbert, 1988). The presence of *A. royi* and *D. aspinosum* (post hoc test, non-significant difference) did not interfere with *B. rotundiformis*. Thus, in our study, both small cladocerans and cyclopoids do not seem to cause mechanical interference. The fact that rotifers

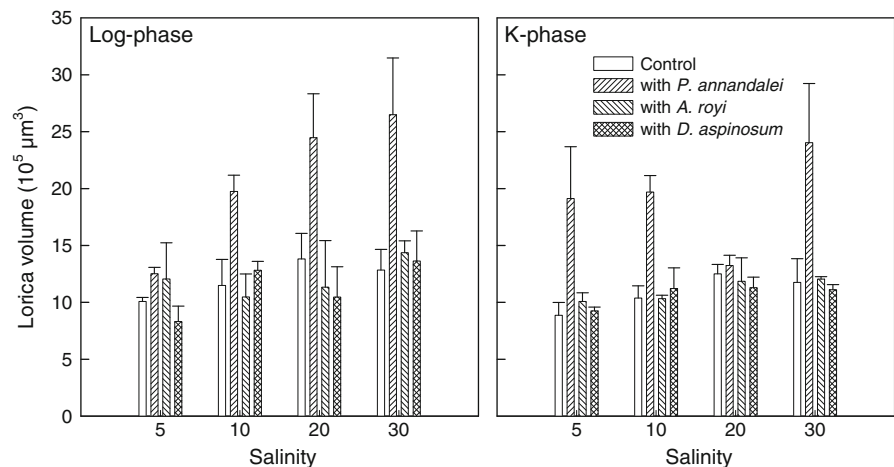
Table 2 Results of post-hoc tests (Scheffé) obtained after performing three-way analysis of variance on peak population density, rate of population increase per day, and body size of *Brachionus rotundiformis* grown at two food levels (3×10^4 cells ml^{-1} and 40×10^4 cells ml^{-1}), four salinity levels (5, 10, 20, and 30), and with and without the presence of *Pseudodiaptomus annandalei*, *Apocyclops royi*, and *Diaphanosoma aspinosum*

Variable (I)	Variable (J)	Sig.	Variable (I)	Variable (J)	Sig.
Population peaks					
5	10	***	Control	<i>A. royi</i>	***
	20	***		<i>D. aspinosum</i>	***
	30	***		<i>P. annandalei</i>	***
	20	***	<i>P. annandalei</i>	<i>A. royi</i>	***
	30	***		<i>D. aspinosum</i>	***
	20	ns	<i>A. royi</i>	<i>D. aspinosum</i>	**
Growth rate					
5	10	***	Control	<i>A. royi</i>	ns
	20	***		<i>D. aspinosum</i>	ns
	30	**		<i>P. annandalei</i>	***
10	20	ns	<i>P. annandalei</i>	<i>A. royi</i>	***
	30	ns		<i>D. aspinosum</i>	***
20	30	ns	<i>A. royi</i>	<i>D. aspinosum</i>	ns
Lorica volume					
5	10	*	Control	<i>A. royi</i>	ns
	20	*		<i>D. aspinosum</i>	ns
	30	***		<i>P. annandalei</i>	***
10	20	ns	<i>P. annandalei</i>	<i>A. royi</i>	***
	30	**		<i>D. aspinosum</i>	***
20	30	*	<i>A. royi</i>	<i>D. aspinosum</i>	ns

For details see Table 1 which also shows levels of significance

co-occur frequently in lakes at high densities with small cladocerans (Kâ et al., 2006; Garcia et al., 2009) corroborates with this observation but contrasts with several studies that report that small cladocerans, e.g., *Ceriodaphnia dubia*, *Moina macrocopa* can reduce rotifer populations (Iyer & Rao, 1993; Nandini et al., 2002). However, Kak & Rao (1998) reported that rotifer suppression depends on the species and food level. These studies report that in some rotifers, e.g., *B. calyciflorus* and *B. angularis*, suppression by *Daphnia similoides* and *Ceriodaphnia cornuta* occurs, regardless of the food level. Larger cladocerans negatively affect other rotifers by causing sublethal injuries or mortality and by detaching or/and ingesting rotifer eggs (Burns & Gilbert, 1986;

Fig. 3 Lorica volume (mean \pm standard deviation) of *Brachionus rotundiformis* grown alone (control) and in the presence of *Pseudodiaptomus annandalei*, *Apocyclops royi*, and *Diaphanosoma aspinosum* under high food levels ($40 \times$ cells ml^{-1}) at four different salinity levels (5, 10, 20, and 30)



Nandini et al., 2002). In our study, the intermediate sized cladoceran *D. aspinosum* did not have significant impact on rotifers.

Fussman (1996) postulated the existence of an exploitative competition for similar food resources between *Daphnia longispina* and rotifers, because *Daphnia* spp., by grazing generally on small-sized phytoplankton, deprive rotifers of their main food resource. The importance of this interference depends on the type of rotifer species, e.g., colonial rotifer *Conochilus unicornis* seems unaffected by crustacean plankton (Rothhaupt, 1988; Fussmann, 1996), and some epizotic rotifers, e.g., *B. rubens*, escape from the deleterious effects of mechanical interference by larger cladoceran, *Daphnia carinata* (Iyer & Rao, 1993). We did not find *A. royi* to negatively affect the population dynamics of *B. rotundiformis*. This finding contrasts with many studies that report that copepods predate on rotifers because of their small size and restricted mobility (Rao & Kumar 2002; Kumar, 2003; Brandl, 2005). The predation of cyclopoid copepods on rotifers depends on species (Brandl, 2005; Nagata & Hanazato, 2006), sex, and ontogenical development (Diéguez & Gilbert, 2002). Predation is known to only lightly affect loricate rotifers (Kumar, 2003; Brandl, 2005). For example, the small-size copepod, *Thermocyclops taihokuensis*, has a selective predation impact on rotifers, eliminating mainly the iloricata forms, but not the spiny ones as *Keratella*. In contrast, the large species, *Mesocyclops pehpeiensis*, has a strong impact on rotifers, but this impact is less selective (Chang & Hanazato, 2005; Nagata & Hanazato, 2006). Thus,

the lack of predation of cyclopoid copepods on the rotifer species in our study is because of the small size of *A. royi* and because *B. rotundiformis* is a loricate rotifer. The coexistence of *B. rotundiformis* and the harpacticoid copepod *Tigriopus japonicus* without any significant effect has been reported earlier (Hagiwara et al., 1995).

Susceptibility of rotifers to interference by larger copepods *P. annandalei*: selective predation and/or adaptive response

We observed (our unpublished data) that *A. royi* could capture *B. rotundiformis*, and *P. annandalei* could efficiently ingest *B. rotundiformis* at 1.8 ± 0.2 ind. h^{-1} copepod $^{-1}$. This explains the significantly negative effect of *P. annandalei* on the *B. rotundiformis* population. Some workers have shown calanoid copepods to be efficient predators on rotifers (Williamson, 1987; Lapesa et al., 2004; Feike & Heerkloss, 2009) and their eggs (Lapesa et al., 2004; Ramos-Rodriguez & Conde-Porcuna, 2004). Calanoids ingest rotifers to enhance both their survival and their reproduction at low planktonic food densities (Williamson & Butler, 1986; Stoecker & Egloff, 1987). Further, we substantiate that predators have a more pronounced impact at lower food concentrations: *B. rotundiformis* with *P. annandalei* exhibited lower population growth at low food levels. Therefore, rotifer predation by calanoid copepods depends on food level in addition to rotifer type, size, and morphology (Williamson, 1987; Lapesa et al., 2004). This finding is supported by the observations of

Pagano et al. (1999) who have reported that *Apocyclops panamensis* increases its predation on rotifers in the absence of seston food. Smaller, soft-bodied iloricat rotifers are more vulnerable to copepod predation than the larger and loricate ones, even though Hagiwara et al. (1995) found that the co-existence of the harpacticoid copepod *Tigriopus japonicus* did not affect the population growth of *B. rotundiformis*.

The increase in rotifer body size has been attributed to the nutritional state and developmental phase (Sarma & Rao, 1987; Yúfera & Pascual, 1989) and to the predation impact by copepods (Baião et al., 1999). Increased food concentration is known to increase rotifer body size (Sarma & Rao, 1987; Galindo et al., 1993) and vice versa (Galindo et al., 1993). However, increased body size with increased food level occurs only until an optimal food concentration is reached (Galindo et al., 1993). In this last study, *B. rotundiformis* were larger during the log-phase than during the K-phase as for the congeneric rotifer *B. patulus* (Sarma & Rao, 1987). Increased prey size decreases vulnerability to invertebrate predators (Gliwicz & Pijanowska, 1989). *P. annandalei* is primarily considered to be herbivorous (Chen et al., 2006), but it has also the ability to utilize ciliates and smaller rotifers, even in the presence of algae (S.H. Cheng's personal observation). In this study, the increased lorica volume of the rotifer in the presence of *P. annandalei* (its potential predator) reflects either adaptive response of rotifer for avoiding predation or a selection of smaller sized rotifers by the copepod.

Conclusion

In summary, the population peaks and growth rate of *B. rotundiformis* are adversely affected by increasing salinity level, decreasing food level, and the presence of crustacean zooplankters. *B. rotundiformis* realized its maximum growth rate at high food level and at salinity levels of 10 and 20, which are in the range of optimal salinity for this species (Hagiwara et al., 1995; Cheng et al., 2004). The presence of *A. royi* and *D. aspinosum* do not negatively affect the development of *B. rotundiformis*, but *P. annandalei* does. Thus, mixed cultures of both *D. aspinosum* and *A. royi* do not show any adverse effects on the rotifer

species in the culture. Therefore, in live feed aquaculture, the culture of *B. rotundiformis* together with *D. aspinosum* and *A. royi* is possible.

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