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Effect of pH on survival, reproduction, egg viability and growth rate of five closely related rotifer species

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Abstract In the laboratory we examined the effect of pH (5–10 with one interval) on survival, reproduction, egg viability and growth rate (intrinsic growth rate—r_m and population growth rate—r) of five *Brachionus* rotifer species (*B. calyciflorus*, *B. quadridentatus*, *B. urceolaris*, *B. patulus* and *B. angularis*). The pH was shown to exert a major influence on egg viability and growth rate (r_m and r) for each species. The age-specific survivorship curves within a species were not significantly different at pH 6–10. The optimal pH for each species is near-neutral pH (pH 6–8), and the fecundity decreased as the pH deviated from these values. For each *Brachionus* species, there was no significant difference between age-specific fecundity curves at pH 7 and 8. At acid pH (pH 5 or 6) higher egg mortality was observed for each species. The r_m and population r of the five *Brachionus* species incubated at different pHs were significantly influenced by pH. The pH supporting the highest r_m or r was obtained at pH 6–8, but varied due to species. In this study *B. urceolaris* and *B. patulus* could tolerate a broad range of pH, while the populations of *B. calyciflorus*, *B. quadridentatus* and *B. angulari* declined at acid conditions.

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Introduction

Numerous studies have attempted to elucidate the responses of aquatic animals to different pH. Among these, results of field experiments and laboratory bioassays verified the lethal or sublethal effects of pH values of above 9 or below 6 on zooplankton species (O'Brien and deNoyelles 1972; Potts and Fryer 1979; Alibone and Fair 1981; Mitchell and Joubert 1986; Mitchell 1992; Vijverberg et al. 1996; Wang et al. 1997; Locke and Sprules 2000). In natural water bodies, due to the photosynthetic activity by algae and the respiration of aquatic animals, the pH usually fluctuates between 6 and 9. It is only under certain circumstances, such as biogeochemical activities of bacteria in acid mine drainage, poor acid neutralizing capacity in bogs and acid rain or well photosynthetic ability by specific algae species at high pH in eutrophic ponds, that the pH of these water bodies is more acid or more alkaline than usual levels (O'Brien and deNoyelles 1972; Wetzel 2001; Sigee 2005).

Compared to lethal effects of extreme pH, sublethal effects of pH on zooplankton species are more common. Sublethal influences of hydrogen or hydroxyl ion have been noted as impairing survival, growth, reproduction and feeding of zooplankton species (reviewed in Locke 1991; Mitchell 1992; Vijverberg et al. 1996). Considering the differential responses of zooplankton species to pH, the sublethal effects of pH indirectly alter the species interactions (e.g., competition, predator-prey) (Hessen et al. 1995; Fischer and Frost 1997; Locke and Sprules 2000), and result in changes of distribution and abundance of populations and species, which ultimately influence the community structure (Kiesecker 1996).

Rotifers are an important part of zooplankton communities. Many species in this phylum can tolerate a broad range of pH values with their peak occurrence ranging from pH 4.5 to 8.5 (Bērziņš and Pejler 1987). Interspecific differences in pH tolerance can be expected to alter biotic interactions among different rotifer species, shifting the competitive ability between species and regulating predation pressure (Mitchell and Joubert 1986; Frost et al. 1998). In response to long-term pH perturbations, rotifer communities exhibit changes and differences in species composition, distribution and abundance (Frost et al. 1998). Moreover, in closely related rotifer species, extensive niche overlap that results in strongest interspecific competition may occur (Schoener 1983). Apart from biotic interactions, abiotic factors such as pH can also determine the competitive outcome among different species (Hessen et al. 1995; Pehek 1995).

To assess how rotifer communities alter in response to changing pH conditions and how the pH modifies the competitive outcome among closely related species, it is necessary to quantify the direct effect of pH on life history characteristics and population growth rate of each species. In the present work, we examined the effects of moderate pH (pH 5–10) on survival, reproduction, egg viability and population growth rate of five common *Brachionus* rotifer species viz. *B. calyciflorus* Pallas, *B. quadridentatus* Hermann, *B. urceolaris* Müller, *B. patulus* Müller and *B. angularis* Gosse.

Materials and methods

Collection and origin of rotifers

We obtained rotifer clones of five *Brachionus* species from resting eggs in dried sediment collected from an artificial freshwater pond (ca. 70 m^2) in Beijing, China (39°57′ N; 116°21′ E). An amount of sediment (ca. 0.5 kg) was placed in a beaker and mixed with about 500 ml inorganic medium (pH $\approx$ 7.3) (see Gilbert 1963) containing green algae *Chlorella pyrenoidosa* that was cultured in SE medium (FACHB-Collection 2005). Every day all the water in the beaker was checked under a dissecting microscope and then returned to the beaker. *B. calyciflorus*, *B. quadridentatus*, *B. urceolaris*, *B. patulus* and *B. angularis* hatched out simultaneously (within 3–5 days) from the flooded sediment.

One newly hatched individual of each *Brachionus* species was isolated and allowed to reproduce parthenogenetically to obtain a culture of genetically identical individuals. The rotifers were cultured successively in the inorganic medium, and food alga *C. pyrenoidosa* was added to the culture medium at a density of 4×10^6 cells ml^{-1}. The culture medium was renewed every 2 days. Before use in the treatments all the *Brachionus* rotifer clones were cultured in the laboratory for at least a month and were in exponential growth phase. All rotifer and algal cultures, experimental incubations and hatching of resting eggs in dried sediment were kept at 20 ± 1.0°C in a 14:10 (L:D) photoperiod (illuminance $\approx$ 50 μEin m^{-2} s^{-1}) in a diurnal growth chamber.

The average body sizes of these five *Brachionus* species [body length (l) and width (w) in µm, mean ± standard deviation, n = 100] of *B. calyciflorus*, *B. quadridentatus*, *B. urceolaris*, *B. patulus* and *B. angularis* were: 196 ± 12 (l), 156 ± 8 (w); 188 ± 7 (l), 189 ± 9 (w); 183 ± 13 (l), 153 ± 16 (w); 145 ± 8 (l), 152 ± 7 (w) and 130 ± 7 (l), 115 ± 7 (w), respectively.

Variation of pH within 24 h

To asses the magnitude of possible pH variation within the interval the medium was renewed, and we monitored pH over a period of 24 h. We placed a 100-ml beaker, containing 80 ml culture medium (with no rotifer and alga), with required pH (pH 5–10 with one interval) in the diurnal growth chamber. All pH series consisted of three replicates. The pH of the culture medium, measured with pH meter (DELTA-320) at 20°C, was adjusted by adding NaOH (0.1 mol l^{-1}) and HCl (0.1 mol l^{-1}) into the medium following the method described in Mitchell (1992). Every 4 h, the pH of the medium was recorded. Fluctuations of pH within 24 h were relatively small in the pH range 5–8, but much larger for pH 9 and pH 10 (Fig. 1). Hence, we probably overestimated the value of pH 9 and 10 in our experiment.

Life table studies

To test the effect of pH (pH 5–10 with one interval) on the life table demography of the five *Brachionus* species, we designed experiments as follows. Prior to the treatments, a number of egg-bearing amictic females of each *Brachionus* species was isolated and incubated at a density of 5 ind. ml^{-1} in the culture medium with required pH (5, 6, 7, 8, 9 and 10) and food concentration (*C. pyrenoidosa* at 4×10^6 cells ml^{-1}). After being acclimated to the required pH for 24 h, 36 newly hatched rotifers of each *Brachionus* species (old <8 h) were randomly caught and separately piped into culture plates, containing 0.2 ml fresh culture medium with appropriate pH-algal food combinations for treatment incubation. The experiment design consisted of a total 30 (= 6 pHs × 5 species) culture plates.

To minimize the pH fluctuations in the rotifer culture medium and the adverse influence to individuals by algal culture medium, *C. pyrenoidosa*, in the exponential growth phase, were separated from the growth medium by centrifuging for 10 min at 3,000 × rpm, counted, and suspended in the rotifer culture medium with required concentration. Concentrated algae solutions were stored in the dark at 4°C, and used within 10 days of harvest.

Everyday, surviving females with attached eggs were transferred to fresh medium with appropriate pH-algal food combinations, and the number of eggs and neonates was recorded and used to calculate the life history parameters described below. Furthermore, egg mortality of each individual was also noted. The experiment was terminated when all individuals died.

The intrinsic growth rate (r_m) was calculated following the formulae described in Krebs (1994): $\sum e^{-rx} l_x m_x = 1$, where x is the age interval in days, l_x is the proportion of organisms surviving at the start of the age interval x and m_x is the number of offspring produced per day per female aged x. The mean and variation of r_m were based on 500 Jackknife samples of individual survivorship and fecundity schedules (Meyer et al. 1986). Since the egg viability of freshwater organism is greatly affected by pH (see Vijverberg et al. 1996), we computed the r_m', assuming all eggs are viable and will result in living neonates, with the method described above. During the experiments all individuals of *B. angularis* died without producing offspring in the first few days at pH 5. Thus, these data were removed from the results.

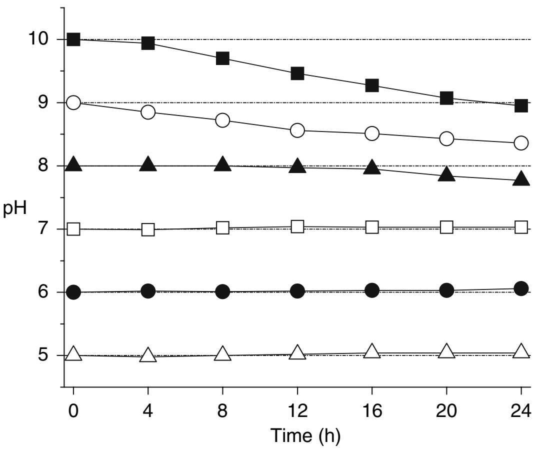


Fig. 1 The change of pH in culture medium within 24 h. Shown are mean ± standard error values based on three replicate recordings. Error bars that are not apparent are too small to be shown

Population growth studies

To establish effects of pH (pH 5–10 with one interval) on the population growth rate (r) of five *Brachionus* species, we placed five neonates (old <8 h) of each *Brachionus* species in culture plates containing 5-ml culture medium with required pHs (5, 6, 7, 8, 9 and 10) and food concentration (*C. pyrenoidosa* at 4×10^6 cells ml^{-1}). Every day all the living individuals in the container were transferred to fresh medium with appropriate pH-algal food combinations. After 5 days, the experiments were terminated and the total number of rotifers in the container was counted. Other procedures in acclimation and treatment incubations were the same as in the life table studies. All the experimental treatments consisted of four replicates. The experiment design consisted of a total 120 (= 6 pHs × 5 species × 4 replicates) culture plates.

We obtained population growth rate (r) with the equation: $r = (\ln N_t - \ln N_0)/t$, where N_0 and N_t are the initial and final population densities and t is the incubation time in days. During the experiments all individuals of *B. angularis* and *B. calyciflorus* died without producing offspring at pH 5. Therefore, we removed these data from the results.

Data analysis

We used non-parametric Mann-Whitney *U*-tests to compare pairwise the effect of pH on fecundity and age-specific survivorship. The effect of pH on egg mortality of each species was tested with the chi-square test. Differences in intrinsic growth rate (r_m) and population growth rate (r) were analyzed with factorial ANOVA for pH effects. The differences between r_m (actual intrinsic population growth rate) and r_m' (intrinsic population growth rate assuming all eggs are viable) were tested with the chi-square test. All statistical analyses were carried out using the statistical package SPSS version 12.0.

Results

For each *Brachionus* species, pairwise comparisons showed that the age-specific survivorship curves were

Table 1 Results of Mann–Whitney *U*–tests performed for age-specific survivorship curves under different pH

Species		pH 10	pH 9	pH 8	pH 7	PH 6
B. calyciflorus	pH 5	–0.609 ns	–1.250 ns	–1.107 ns	–1.546 ns	–1.052 ns
	pH 6	–0.408 ns	–0.176 ns	–0.176 ns	–0.412 ns	
	pH 7	–1.077 ns	–0.263 ns	–0.176 ns		
	pH 8	–0.638 ns	–0.058 ns			
	pH 9	–0.899 ns				
B. quadridentatus	pH 5	–2.475*	–1.921 ns	–2.723**	–2.509*	–2.395*
	pH 6	–0.057 ns	–0.586 ns	–0.586 ns	–0.227 ns	
	pH 7	–0.341 ns	–0.835 ns	–0.208 ns		
	pH 8	–0.454 ns	–1.173 ns			
	pH 9	–0.738 ns				
B. urceolaris	pH 5	–0.254 ns	–0.023 ns	–1.014 ns	–1.152 ns	–0.691 ns
	pH 6	–0.208 ns	–0.648 ns	–0.508 ns	–0.485 ns	
	pH 7	–0.716 ns	–1.041 ns	–0.046 ns		
	pH 8	–0.601 ns	–1.087 ns			
	pH 9	–0.440 ns				
B. patulus	pH 5	–0.709 ns	–0.281 ns	–0.250 ns	–1.789 ns	–0.904 ns
	pH 6	–0.101 ns	–0.507 ns	–0.499 ns	–0.993 ns	
	pH 7	–0.939 ns	–1.424 ns	–1.408 ns		
	pH 8	–0.367 ns	–0.062 ns			
	pH 9	–0.429 ns				
B. angularis	pH 5	–3.076**	–3.326**	–1.642 ns	–2.673**	–2.442*
	pH 6	–0.376 ns	–0.835 ns	–0.705 ns	–0.147 ns	
	pH 7	–0.167 ns	–0.688 ns	–0.913 ns		
	pH 8	–1.056 ns	–1.535 ns			
	pH 9	–0.542 ns				

Shown are the values of Z

ns, non-significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

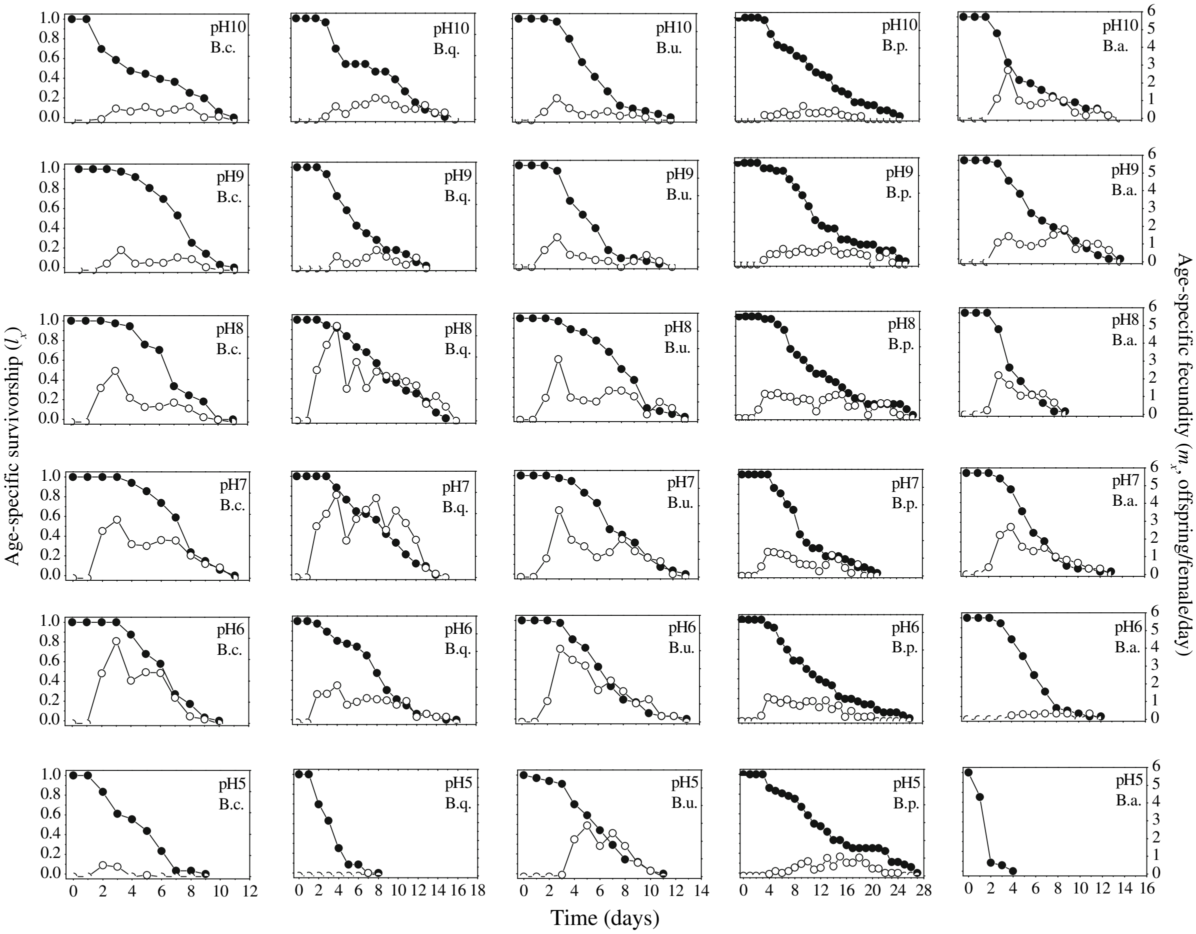


Fig. 2 Age–specific survivorship (filled circle) and age–specific fecundity (open circle) curves of five *Brachionus* species at each pH treatment. B.c.—*B. calyciflorus*, B.q.—*B. quadridentatus*, B.u.—*B. urceolaris*, B.p.—*B. patulus*, B.a.—*B. angularis*

not significantly different at pH 6–10 (Table 1, Fig. 2). The survivorship curves showed heavy mortalities at pH 5 in *B. quadridentatus* and *B. angularis*, but not in *B. calyciflorus*, *B. urceolaris* and *B. patulus* (Table 1, Fig. 2).

Higher fecundity was obtained at pH 6–8 in *B. calyciflorus*, *B. quadridentatus*, *B. urceolaris*, *B. patulus* and at pH 7–10 in *B. angularis* (Fig. 2). At low pH (5), *B. urceolaris* had higher fecundity than the other *Brachionus* species, and at high pH (10), much higher fecundity was observed in *B. angularis*. For each *Brachionus* species, there was no significant difference between age-specific fecundity curves at pH 7 and 8 (Table 2, Fig. 2). The fecundity curves of *B. calyciflorus* and *B. quadridentatus* showed great variation between low pH (5) and circum-neutral pH (6–9); however, these were not the cases in *B. urceolaris* and *B. patulus* (Table 2).

The difference of egg mortality was not obvious at pH 6–10 in *B. calyciflorus* ($\chi^2_{B.c.} = 6.636$, df = 4, $P = 0.156$, Fig. 3), *B. urceolaris* ($\chi^2_{B.u.} = 5.707$, df = 4, $P = 0.222$) and *B. patulus* ($\chi^2_{B.p.} = 4.50$, df = 4, $P = 0.343$); however, when pH decreased to 5, a marked increment in egg mortality was observed in these three *Brachionus* species ($\chi^2_{B.c.} = 146.83$, $\chi^2_{B.u.} = 120.67$, $\chi^2_{B.p.} = 58.57$, df = 5, $P < 0.001$). For *B. angularis* and *B. quadridentatus*, egg mortality increased significantly as pH decreased from neutral or alkaline pH (7–10) to acid pH (5 and 6) ($\chi^2_{B.a.} = 345.67$, $\chi^2_{B.q.} = 260.67$, df = 5, $P < 0.001$).

The intrinsic growth rate (r_m) and population growth rate (r) of five *Brachionus* species were

Table 2 Results of Mann–Whitney *U*–tests performed for age-specific fecundity curves under different pH

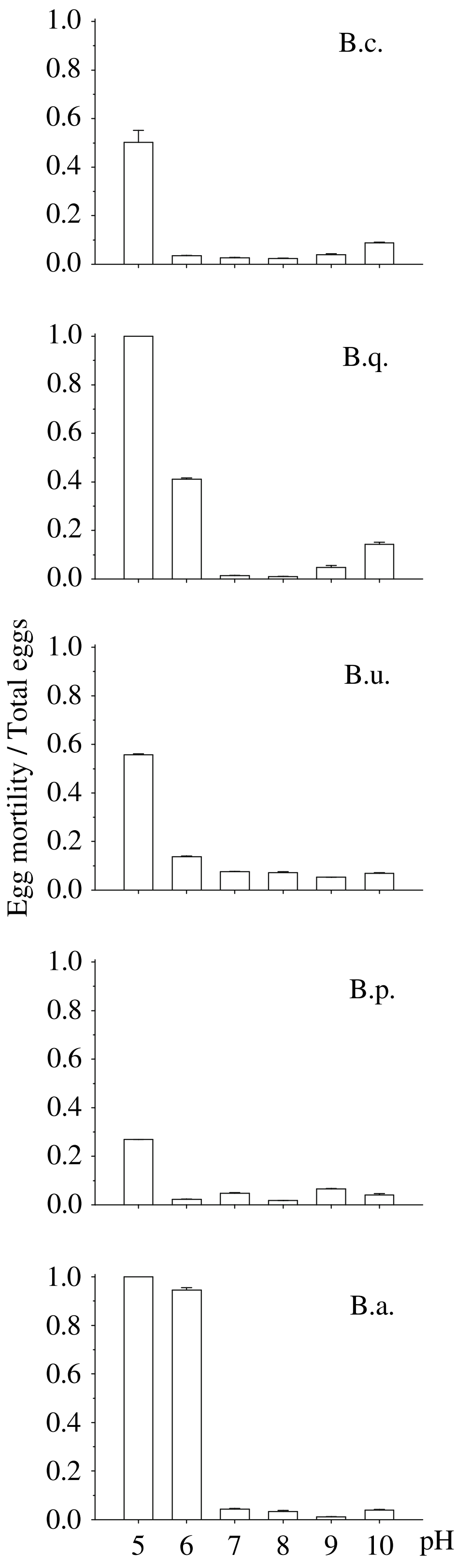
Species		pH 10	pH 9	pH 8	pH 7	PH 6
B. calyciflorus	pH 5	–1.914 ns	–1.827 ns	–2.654**	–2.807**	–2.391*
	pH 6	–1.082 ns	–1.001 ns	–0.351 ns	–0.001 ns	
	pH 7	–1.717 ns	–1.580 ns	–0.669 ns		
	pH 8	–1.339 ns	–0.995 ns			
	pH 9	–1.025 ns				
B. quadridentatus	pH 5	–4.083***	–2.839**	–4.329***	–4.000***	–4.293***
	pH 6	–1.436 ns	–2.576*	–1.123 ns	–1.211 ns	
	pH 7	–1.942 ns	–2.695**	–0.086 ns		
	pH 8	–2.474*	–3.171**			
	pH 9	–1.815 ns				
B. urceolaris	pH 5	–0.332 ns	–0.379 ns	–1.145 ns	–1.308 ns	–1.262 ns
	pH 6	–1.511 ns	–1.536 ns	–0.162 ns	–0.023 ns	
	pH 7	–1.976*	–1.860 ns	–0.069 ns		
	pH 8	–1.720 ns	–1.650 ns			
	pH 9	–0.071 ns				
B. patulus	pH 5	–1.940 ns	–0.727 ns	–1.699 ns	–0.640 ns	–0.711 ns
	pH 6	–1.861 ns	–0.157 ns	–1.031 ns	–0.729 ns	
	pH 7	–0.717 ns	–0.799 ns	–1.855 ns		
	pH 8	–3.012**	–1.230 ns			
	pH 9	–2.072*				
B. angularis	pH 5					
	pH 6	–2.344*	–2.772**	–0.832 ns	–2.130*	
	pH 7	–0.134 ns	–0.267 ns	–1.260 ns		
	pH 8	–1.083 ns	–1.444 ns			
	pH 9	–0.762 ns				

Shown are the values of Z

ns, non-significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

greatly influenced by pH (two-way ANOVA, $F_{rm} = 277.01$, $F_r = 487.23$, df = 5, $P < 0.001$, Figs. 4 and 5). The pH supporting the highest r_m or r was obtained at pH 6–8, but varied in values due to species (Fig. 4). *B. calyciflorus* and *B. urceolaris* had the highest r_m and r at pH 6, while *B. quadridentatus*, *B. patulus* and *B. angularis* attained the highest r_m or r at neutral pH (7 or 8). At neutral pH (7 and 8) *B. quadridentatus* had higher r_m and r than other species, while *B. urceolaris* at more acid and alkaline pH (5 and 10) attained higher r_m and r than other species (Figs. 4 and 5).

The difference between r_m and r_m' was not marked at pH 6–10 in *B. calyciflorus* ($\chi^2 = 0.193$, df = 4, $P = 0.996$), *B. quadridentatus* ($\chi^2 = 3.674$, df = 4, $P = 0.452$), *B. urceolaris* ($\chi^2 = 0.743$, df = 4, $P = 0.946$) and at pH 7–10 in *B. angularis* ($\chi^2 = 0.057$, df = 3, $P = 0.996$). However, this difference was obvious when we compared the r_m and r_m' at all pH levels (pH 5–10 in *B. calyciflorus*, *B. quadridentatus*, *B. urceolaris* and pH 6–10 in *B. angularis*) ($\chi^2_{B.c.} = 48.62$, $\chi^2_{B.q.} = 51.422$, $\chi^2_{B.u.} = 17.23$, df = 5, $P < 0.01$; $\chi^2_{B.a.} = 70.63$, df = 4, $P < 0.001$). These data showed that the difference of r_m and r_m' at low pH (5 in *B. calyciflorus*, *B. quadridentatus*, *B. urceolaris* and pH 6 in *B. angularis*) was significant in *B. calyciflorus*, *B. quadridentatus*, *B. urceolaris* and *B. angularis*. For *B. patulus*, no pronounced difference between r_m and r_m' was detected at experimental pH treatments ($\chi^2_{B.p.} = 1.043$, df = 5, $P = 0.959$).



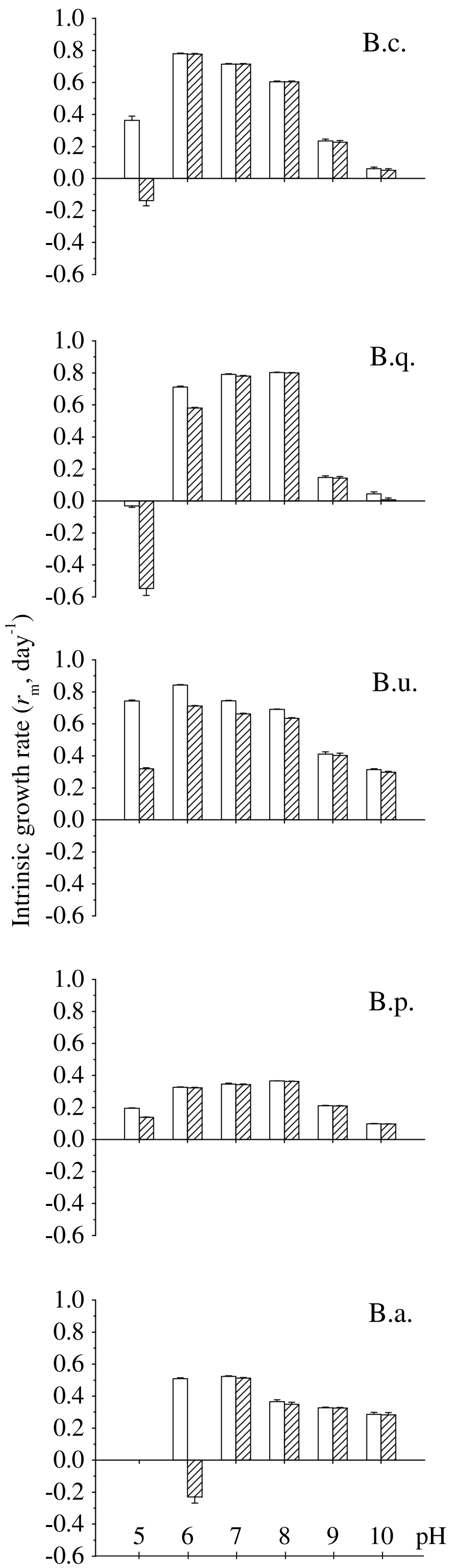
◀ **Fig. 3** Data on egg mortality divided by total eggs (open bar) of five *Brachionus* species at each pH treatment. Shown are mean ± standard error values based on 36 individuals. Error bars that are not apparent are too small to be shown. See the caption in Fig. 2 for the meaning of abbreviations

Discussion

The distribution and abundance of rotifers are confined by pH (see Wallace and Snell 2001). For the genus *Brachionus*, *B. angularis*, *B. calyciflorus* and *B. quadridentatus* are believed to be common alkaline species (see Sládeček 1983; Bērziņš and Pejler 1987), while *B. patulus* and *B. urceolaris* have been found in more acidic waters (Myers 1937; Parsons 1968; Horvath and Hummon 1980; McConathy and Stahl 1982; Bērziņš and Pejler 1987). Our results are consistent with these field investigations that *B. patulus* and *B. urceolaris* can tolerate more acid pH (5) than *B. angularis*, *B. calyciflorus* and *B. quadridentatus* (Figs. 2, 4, and 5).

The responses to pH (especially low pH) of rotifers seem to be consistent at a community level (Frost et al. 1998). Considering the differential responses of various taxa to pH, rotifer communities may vary due to the conditions of water bodies. The genus *Brachionus* is known for its tolerance to high pH (Ahlstrom 1940; Sládeček 1983; Mitchell and Joubert 1986); therefore, they dominate the rotifer community in eutrophic waters (see Sládeček 1983). However, in oligo-trophic or acid-stress waters, the dominant taxa will be those that can survive and reproduce at low pH conditions such as *Cephalodella*, *Keratella* and *Trichocerca* (Sládeček 1983; Brett 1989; Gonzalez and Frost 1994; Frost et al. 1998; Deneke 2000).

The distribution of the genus *Brachionus* is confined to waters with pH ≥ 6.6 (Ahlstrom 1940), although some species in this genus (e.g., *B. urceolaris*) can tolerate more acid conditions (Deneke 2000). At low pH conditions (pH < 6), feeding, respiration, and sodium balance of *Brachionus* may be impaired greatly (Kring and O'Brien 1976; Potts and Fryer 1979; Alibone and Fair 1981), which resulted in high egg mortality, low individual survival and negative population growth rate in some species of *Brachionus* (present work, Figs. 2–5). Although *B. patulus* and *B. urceolaris* had positive population growth rate (r_m or r) at pH 5 (Figs. 4 and 5), their survival and reproduction decreased greatly at pH



◀ **Fig. 4** Data (mean ± standard error) on intrinsic growth rate (r_m) of five *Brachionus* species at each pH treatment. Striped bar—r_m based on life table data; Open bar—assuming all eggs are viable and result in living neonates (r'_m). Error bars that are not apparent are too small to be shown. See the caption in Fig. 2 for the meaning of abbreviations

below 5 (no individual can survive to 12 h at pH 4, personal observations). These may be the main reasons to impede the distribution and abundance of this taxon in acidic waters.

The response of *B. calyciflorus* to pH received extensive studies (Mitchell and Joubert 1986; Mitchell 1992; Wang et al. 1997; Xi and Huang 1999). At moderate pH (5–10), although a typical bell-shaped curve was often observed in the response of *B. calyciflorus* to pH, optimum pH supporting the maximum population growth rate varied among these studies, ranging from 7.5 to 9.5 (Mitchell 1992; Wang et al. 1997; Xi and Huang 1999). Furthermore, in the present study *B. calyciflorus* attained the highest growth rate at a lower pH (6) (Figs. 4 and 5). The biotic and abiotic factors of the habitats where these *B. calyciflorus* clones were initially isolated may vary greatly. The different responses to pH of these clones are likely due to the intra-specific differences among zoogeographical populations, as some data revealed that the responses of ecotypes to pH would match their habitats of origin (Price and Swift 1985; Gonzalez and Frost 1994).

Within a particular community the interactions among different competitors or between predator and prey will be altered when species differ in their response to changing abiotic conditions (Chesson 1986). Many studies have been focused on the pH-mediated biotic interactions in aquatic ecosystems (Susan et al. 1993; Hessen et al. 1995; Pehek 1995; Kiesecker 1996; Locke and Sprules 2000). On one hand, due to anthropogenic factors (e.g., eutrophication or acid rain), the pH will be more acid or alkaline than usual levels (pH < 6 or > 9) in natural waters. The extreme increase or decrease of pH will decrease the abundance of those species that are more sensitive in both survival and reproduction to the change of pH, for example, *B. angularis*, *B. calyciflorus* and *B. quadridentatus* (present work), which will increase the relative competitive ability of less sensitive species (e.g., *B. patulus* or *B. urceolaris* in the present work). On the other hand, in our study the differentiation of *Brachionus* species in response to

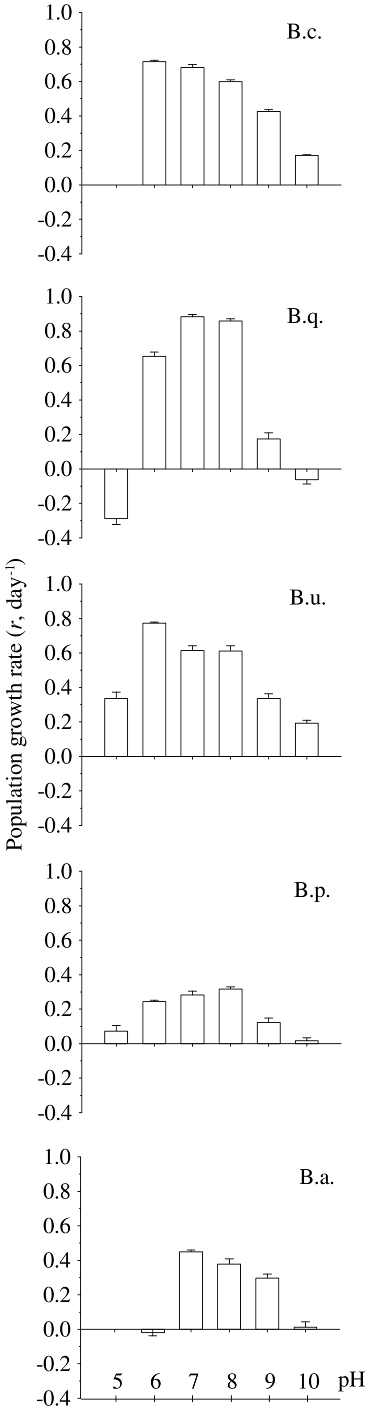


Fig. 5 Data on population growth rate (r) of five *Brachionus* species at each pH treatment. Shown are mean ± standard error values based on four replicate recordings. Error bars that are not apparent are too small to be shown. See the caption in Fig. 2 for the meaning of abbreviations

pH indicates that the pH may be an important abiotic factor in regulating the species composition of rotifers in a community, since some studies have revealed that when competing species differ in the sensitivity to pH, the compensatory dynamics (substitution among species) will occur between or among these species in relation to pH fluctuations (Klug et al. 2000).

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