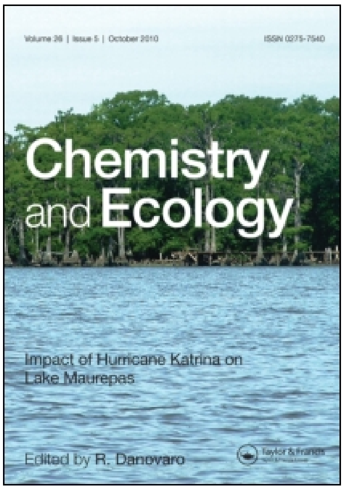

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Life-history strategies of *Brachionus havanaensis* subject to kairomones of vertebrate and invertebrate predators

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We evaluated the different life-history strategies of the rotifer *Brachionus havanaensis* in the presence of vertebrate (salamander axolotl, *Ambystoma mexicanum*) or invertebrate (copepod *Acanthocyclops robustus*) predator using population growth and life-table demography at two algal food levels (0.5×10^6 and 1.0×10^6 cells ml^{-1} of *Chlorella vulgaris*). Generally, increased food availability resulted in higher densities of *B. havanaensis*. At any algal food level, *B. havanaensis* grown in the presence of kairomones showed higher population abundances than controls. Within the kairomone treatments, rotifers grown using *A. mexicanum*-conditioned medium showed a higher population growth than those using *A. robustus* medium. The average lifespan of *B. havanaensis* varied from 6 to 13 d, depending on the presence or absence of kairomones and the algal food density, the shortest being in treatments containing kairomones from *Ambystoma*. Gross (19–22 offspring female^{-1}) and net reproductive rates (11 offspring female^{-1}) were significantly higher in the *Ambystoma*-conditioned medium than in the other treatments including controls (9–10 and 6–7 offspring female^{-1}, respectively). Generation time (4–6 d) was influenced by algal density as well as the presence of kairomones. *B. havanaensis* had the shortest generation time in *Ambystoma*-conditioned medium. The rate of population increase of *B. havanaensis* varied from 0.34 to 0.87 d^{-1}, with higher values in treatments containing *Ambystoma*-conditioned water. The total lorica length, anterior, and posterior spine lengths of *B. havanaensis* were significantly higher in the presence of kairomones from both vertebrate and invertebrate predators than in controls. In general, there was a greater lorica and spine length of *B. havanaensis* due to *Ambystoma* infochemicals than those from *Acanthocyclops*.

Keywords: Kairomone; Zooplankton; Demography; Predation

1. Introduction

Zooplankton communities are subject to intense predation stress. The direct influences are due to the physical interaction between two species, while the indirect impacts are generally

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via infochemicals [1]. Among freshwater zooplankton, rotifers are not only common but also at times numerically more abundant than other groups such as cladocerans and copepods. Rotifers are small metazoans, measuring 50–1500 μm, and covered by a cuticle made of sclero-proteins which in certain taxa is developed into lorica with or without anterior and posterior spines. They have a ciliated corona which helps in locomotion, and along with a modified pharynx (trophi) in feeding as well. The majority of rotifers are cyclical parthenogens [2]. Though there are about 120 genera of rotifers, most studies in relation to feeding ecology, behaviour, demography, ecotoxicology, and aquaculture have been conducted on *Brachionus*. This is because of the wide distribution of this genus, ease of culture and maintenance, and the availability of a large morphological, physiological, ecological, and genetic database. Under natural conditions, brachionids are subject to intense vertebrate (such as fish larvae) and invertebrate (such as *Asplanchna* and *Chaoborus*) predation pressure [3]. Globally, there are about 40 species of the genus *Brachionus*, of which 15 have been recorded from Mexico [4]. *Brachionus havanaensis* is a common rotifer in freshwater bodies in Mexico. This species is known to exhibit phenotypic plasticity in several traits when subject to different food levels, temperature ranges, and predation stress [5, 6].

Lake Xochimilco is a wetland with a complex system of canals and shallow lakes (maximum depth about 2 m) in Mexico City. The rotifer diversity is higher in comparison with cladocerans or copepods in this water body [7]. It is also inhabited by several species of fish and is home to the endemic salamander, *Ambystoma mexicanum*. Rotifers are thus subject to predation pressure from invertebrates (such as cyclopoid copepods) and vertebrates (such as larval fish and *Ambystoma*). Invertebrate predators generally have a stronger impact in structuring their prey community, since they show both numerical and functional responses within a short time [8]. Rotifers, common in Lake Xochimilco, form part of the diet of larval *A. mexicanum* and the adults of *Acanthocyclops robustus.* They show different morphological adaptations against predators. For example, enhanced body size and spine lengths under pressure from invertebrates helps minimize capture by predators [9]. These phenotypic responses imply shifts in life history strategies and changes in survivorship and reproduction patterns [10].

Infochemicals emerging from predators also influence life-history traits of zooplankton. A relatively large set of information is available on the demographic characters of *Daphnia* in relation to fish-conditioned medium [11]. Thus, when *Daphnia* spp. are subject to the presence of infochemicals released from fish, the cladocerans tend to produce large but few offspring, which ensures a higher probability of survival in nature [12]. For rotifer species, lower reproductive rates and a larger size at birth in the presence of invertebrate kairomones are known [13]. However, less information is available on the indirect impact of many invertebrate predators on rotifers including *Acanthocyclops robustus*, a common cyclopoid copepod in canals of Xochimilco. Although this copepod is known to feed on *Brachionus havanaensis*, the impact of its infochemicals on the life history variables for this rotifer is not known. In our field samples, we have also observed that *B. havanaensis* and the adult *A. robustus* have both a sympatric and synchronic distribution at different sites of Lake Xochimilco almost throughout the year.

In this study, we analysed the differences in the life history strategies of *B. havanaensis* subject to indirect predation stress via infochemicals from two coexisting predators *Ambystoma mexicanum* and *Acanthocyclops robustus*.

2. Materials and methods

The brachionid rotifer *Brachionus havanaensis* was originally isolated from Lake Xochimilco and maintained for more than 6 months prior to experimentation. The rotifers were fed green alga *Chlorella vulgaris*, which was batch-cultured in 2 l transparent bottles using Bold's medium [14]. For experiments we used two algal levels of 0.5×10^6 and 1.0×10^6 cells ml^{-1}, estimated using a haemocytometer. The carbon content of the food at these algal levels is similar to those found in the Mexican eutrophic waterbodies including Xochimilco lake [15]. For mass culture of rotifers and for experiments, we used reconstituted moderately hard-water (EPA medium), which was prepared by dissolving 0.9 g of $NaHCO_3$, 0.6 g of $CaSO_4$, 0.6 g of $MgSO_4$, and 0.04 g of KCl in 1 l of distilled water [16].

The predators, also obtained from the lake Xochimilco, were grown separately using EPA medium. For *A. robustus*, we offered a mixture of *Chlorella vulgaris* and the rotifer *Brachionus calyciflorus* as the diet. Juveniles of *A. mexicanum* were reared in the laboratory using mixed zooplankton species (cladocerans, *Moina macrocopa, Daphnia pulex* and *Ceriodaphnia dubia* and rotifers *B. havanaensis* and *B. calyciflorus*). In order to obtain the conditioned medium, we maintained each predator species in 2 l jars containing about 1.5 l of EPA medium without food for 12–24 h, depending on the predator type. The density of *A. robustus* was about 1000 ind. l^{-1}, while for *A. mexicanum* it was 10 ind. l^{-1}. Using a mesh of 20-μm pore size, we filtered the medium from the jars containing the predators, which was used in the experiments.

We conducted simultaneously population-growth and life-table demography experiments on *B. havanaensis*. The experimental design and test conditions were similar for both experiments: 50-ml transparent jars containing 20 ml of medium, two algal food densities (0.5×10^6 and 1.0×10^6 cells ml^{-1} of *Chlorella vulgaris*), three treatments (control, *A. robustus*-conditioned medium and *A. mexicanum*-conditioned medium), and four replicates for each treatment; pH: 7.0–7.5, temperature $23 \pm 1\,^{\circ}\text{C}$, continuous but diffused fluorescent illumination, and the medium and algal food in the test jars replaced 100% daily. The reason for daily 100% replacement of the medium was in order to prevent the accumulation of metabolites and to ensure a constant level of infochemicals and algal food density in the test jars.

For population-growth studies, we introduced a mixed age group of 20 individuals of *B. havanaensis* into each of the 24 test jars (three treatments × two food levels × four replicates) under a stereomicroscope at 20× using a finely drawn Pasteur pipette. Following initiation of growth experiments, we estimated daily the density of *B. havanaensis* from either the total count or two aliquots of 1–5 ml, depending on the density. After density estimation, the rotifers were transferred to fresh jars containing the appropriate test medium and the chosen algal density. Experiments continued for 3 weeks, by which time most rotifer populations in the test jars began to decline. Based on the data collected, we derived the rate of population increase (r) using the regression between log natural population density over time [17]. On the last day of the growth experiments, the rotifers from each test jar were fixed in 4% formalin. Using a calibrated ocular micrometer, we measured body length, width, anterior, and posterior spine lengths of about 20 egg-bearing individuals from each replicate under a compound microscope (Nikon Eclipse) at 400×.

For the life-table experiments, we introduced 20 neonates (<2 h after hatching from parthenogenetic eggs) into each of 24 test jars. Following initiation of the experiment, we counted and transferred surviving members of the original cohort every day to fresh jars containing the appropriate test medium. Neonates and dead adults, when present, were counted and discarded. Experiments continued until the last individual of each cohort died. From the survivorship and fecundity data, we calculated variables such as average lifespan (ALS), gross (GRR) and net reproductive rates (R_0), generation time (T), and the rate of population increase per day (r) using the following formulae [18]:

$$\text{Gross reproductive rate (GRR)} = \sum_{0}^{\infty} m_x \tag{1}$$

$$\text{Net reproductive rate } R_o = \sum_{0}^{\infty} l_x \cdot m_x \tag{2}$$

$$\text{Generation time: } T = \frac{\sum l_x \cdot m_x \cdot x}{R_o}. \tag{3}$$

Rate of population increase (r), Euler equation

$$\sum_{x=w}^{n} e^{-rx} \cdot l_x \cdot m_x = 1, \tag{4}$$

where l_x is the probability of an individual surviving to an age class, m_x is the age-specific fecundity, R_o is the average number of offspring per female, and r is the growth rate of the population.

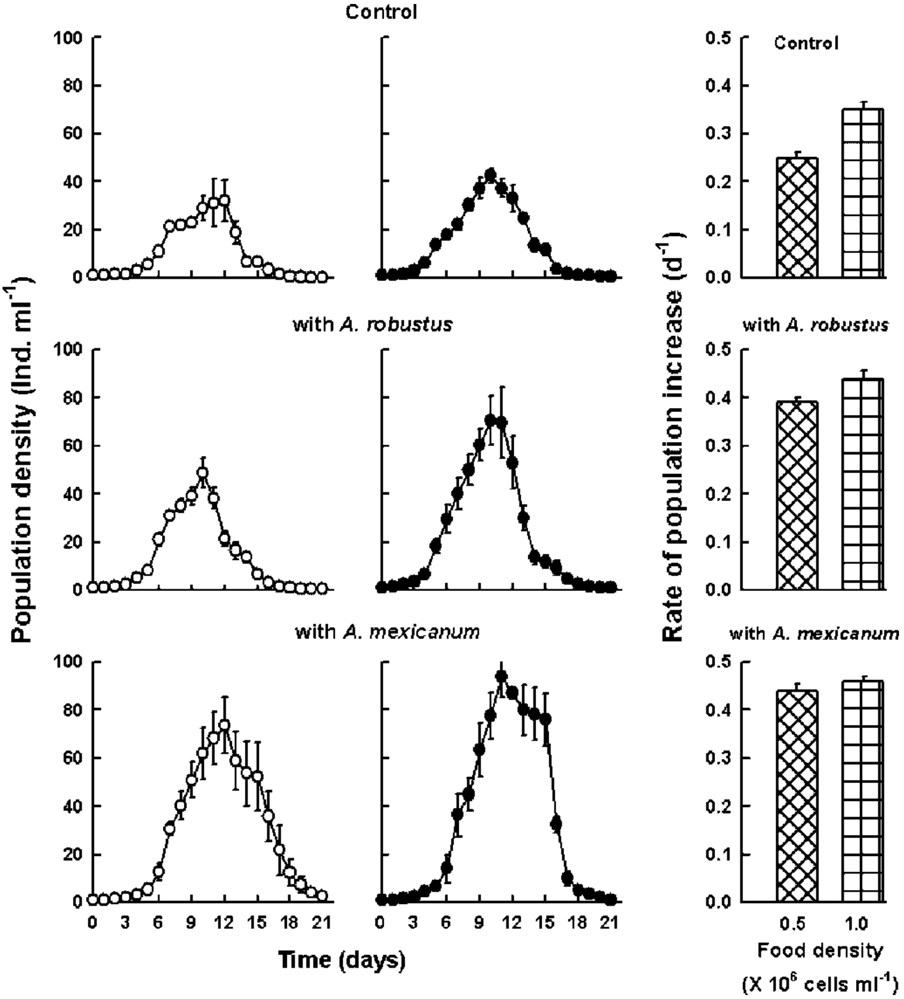

Figure 1. Population growth curves of *B. havanaensis* grown at two algal densities (open circles, 0.5×10^6 and closed circles 1.0×10^6 cells ml^{-1} of *Chlorella vulgaris*) and in the presence or absence of predator-conditioned medium. Shown are the mean ± standard errors based on four replicates. The rate of population increase derived from population growth is shown in bars.

An analysis of variance (ANOVA) was used to quantify the differences in the selected life-history variables and the morphometric data of *B. havanaensis* under different treatments. Post hoc (Tukey test) analysis was used for multiple comparisons utilizing the software Statistica ver. 5.

3. Results

The population growth curves and the rate of population increase (r) of *B. havanaensis* grown under different food densities and in the presence of kairomones from *A. robustus* and *A. mexicanum* are presented in figure 1. Regardless of the presence of kairomones, an increase in the availability of algal diet resulted in an increased abundance of *B. havanaensis*. Similarly, regardless of the density of algal food, *B. havanaensis* grown in the presence of kairomones showed higher population abundances than controls. Rotifers grown using *A. mexicanum*-conditioned medium showed a higher population growth than those using *A. robustus* medium. The trends in the population growth were largely reflected by the rate of population increase (r), which showed significantly higher values with increase in food level and in treatments containing kairomones from *Ambystoma* ($p < 0.05$, F test; table 1).

Data on the age-specific survivorship and fecundity curves of *B. havanaensis* grown under different algal food densities and in the presence of kairomones from the copepods and the salamanders are shown in figure 2. Regardless of *Chlorella* density, the survivorship of *B. havanaensis* was reduced in the presence of kairomones. There were no significant differences in survivorship patterns in relation to food level or the presence of kairomones. The

Table 1. Results of two-way analysis of variance (ANOVA) performed for the selected life-history variables of *Brachionus havanaensis* in relation to algal food level and the presence or absence of predators.

Variable rate of population increase	DF effect	MS effect	DF error	MS error	F ratio
Population growth					
Predator's presence (A)	2	6.37	18	1.67	3.80*
Food level (B)	1	72.25	18	1.67	43.12***
Interaction of $A \times B$	2	3.81	18	1.67	2.27 n.s.
Life-table study					
Average lifespan					
Predator's presence (A)	2	73.81	18	1.32	55.66***
Food level (B)	1	1.37	18	1.32	1.03 n.s.
Interaction of $A \times B$	2	3.41	18	1.32	2.57 n.s.
Gross reproductive rate					
Predator's presence (A)	2	319.97	18	3.69	86.70***
Food level (B)	1	1.65	18	3.69	0.44 n.s.
Interaction of $A \times B$	2	8.03	18	3.69	2.17 n.s.
Net reproductive rate					
Predator's presence (A)	2	40.79	18	2.41	16.92***
Food level (B)	1	7.76	18	2.41	3.22 n.s.
Interaction of $A \times B$	2	3.08	18	2.41	1.27 n.s.
Generation time					
Predator's presence (A)	2	7.51	18	0.34	21.70***
Food level (B)	1	9.56	18	0.34	27.61***
Interaction of $A \times B$	2	1.14	18	0.34	3.31 n.s.
Rate of population increase					
Predator's presence (A)	2	51.71	18	0.41	124.34***
Food level (B)	1	69.84	18	0.41	167.92***
Interaction of $A \times B$	2	48.37	18	0.41	116.30***

Note: $^{***}p < 0.001$; $^{*}p < 0.05$; n.s.: non-significant.

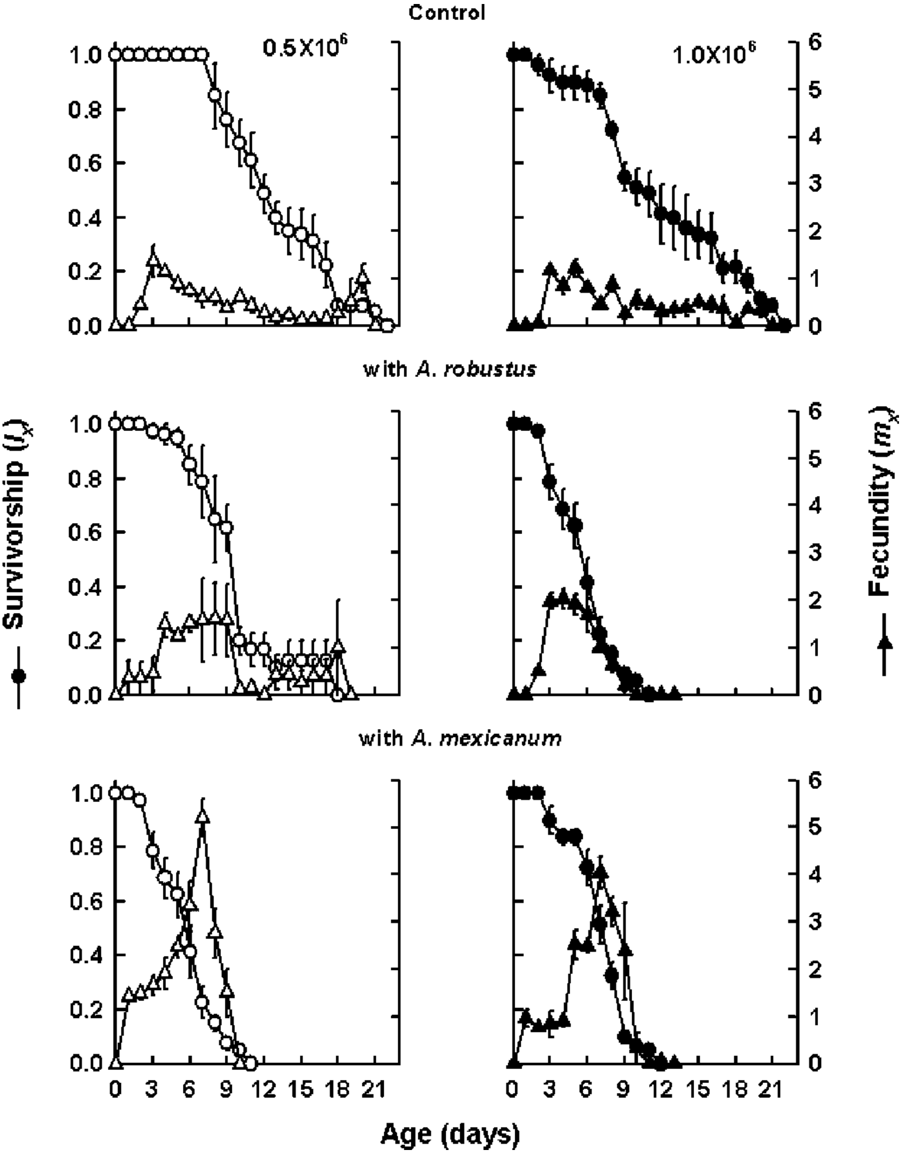

Figure 2. Age-specific survivorship and fecundity curves of *B. havanaensis* grown at two algal densities (open symbols, 0.5×10^6 and closed symbols 1.0×10^6 cells ml^{-1} of *Chlorella vulgaris*) and in the presence or absence of predator-conditioned medium. Shown are the mean ± standard errors based on four replicates (cohorts).

age-specific offspring production (m_x) in controls was low, but extended over the entire lifespan of *B. havanaensis*. On the other hand, in treatments containing kairomones, the fecundity was high, but for a shorter duration, and peaked around an age class of 6–9 d old.

Data on the selected life history variables are presented in table 2. The average lifespan varied from 6 to 13 d, depending on algal food density and presence or absence of kairomones. There was a significant impact of kairomones ($p < 0.001$) but not of food level ($p > 0.05$) on the average lifespan of *B. havanaensis* (two-way ANOVA, table 1). The average lifespan was shortest with treatments containing kairomones from *Ambystoma*. While there were no significant differences in the gross and net reproductive rates in relation to food level ($p > 0.05$), both

Table 2. Data on the selected life-history variables of *B. havananesis* grown at two algal food densities and with conditioned medium from *A. robustus* (*A.r.*) and *A. mexicanum* (*A.m.*).

	Life-history variable				
Treatment	ALS	GRR	R_o	T	r
Food level 0.5×10^6					
Without kairomone	$13.2 \pm 0.6^{\mathrm{a}}$	$9.2 \pm 1.0^{\mathrm{a}}$	$7.1 \pm 0.5^{\mathrm{a}}$	$6.0 \pm 0.3^{\mathrm{a,d}}$	$0.42 \pm 0.02^{\mathrm{a}}$
With *A.r.*	$9.1 \pm 0.3^{\mathrm{b,c}}$	$9.9 \pm 0.8^{\mathrm{b}}$	$9.2 \pm 0.8^{\mathrm{b}}$	$4.7 \pm 0.1^{\mathrm{a,e}}$	$0.54 \pm 0.02^{\mathrm{b}}$
With *A.m.*	$7.3 \pm 0.2^{\mathrm{b,e}}$	$19.0 \pm 1.2^{\mathrm{a}}$	$11.1 \pm 1.1^{\mathrm{a,b}}$	$4.8 \pm 0.1^{\mathrm{a,c}}$	0.70 ± 0.01^{c}
Food level 1.0×10^6					
Without kairomone	$12.2 \pm 1.1^{\mathrm{a,d}}$	$9.5 \pm 0.6^{\mathrm{a}}$	$6.3 \pm 0.6^{\mathrm{a}}$	$6.9 \pm 0.2^{d,f}$	$0.34 \pm 0.02^{\mathrm{a}}$
With *A.r.*	10.1 ± 0.4^{c}	$8.6 \pm 0.8^{\mathrm{b}}$	$6.7 \pm 0.5^{\mathrm{b}}$	$5.5 \pm 0.5^{\mathrm{b,c,e}}$	0.42 ± 0.02^{e}
With *A.m.*	$5.9 \pm 0.3^{d,e}$	$21.6 \pm 1.2^{\mathrm{a}}$	$11.0 \pm 0.9^{\mathrm{a}}$	$3.6 \pm 0.2^{\mathrm{a}}$	$0.87 \pm 0.02^{\mathrm{a}}$

Note: ALS: average lifespan (days); GRR: gross reproductive rate (offspring female^{-1} lifespan^{-1}); R_o: net reproductive rate (survival-weighted offspring female^{-1} lifespan^{-1}); T: generation time (days); r: rate of population increase (d^{-1}). Shown are mean ± standard error based on four replicates (cohorts). For a given variable, data containing similar alphabets are not significant ($p > 0.05$, Tukey test).

these variables were significantly higher in the *Ambystoma* conditioned medium than in the other treatments ($p < 0.001$). Generation time was influenced by algal density as well as the presence of kairomones, but their interaction was not significant ($p < 0.001$). The generation time of *B. havanaensis* was shortest at 1.0×10^6 cells ml^{-1} of *Chlorella* and in the presence of *Ambystoma*-conditioned medium. The rate of population increase from the demography experiments was higher at lower food levels except in the presence of *Ambystoma*-conditioned medium. There was a significant impact of the treatment, food level, and interaction of both on the rate of population increase of *B. havanaensis* ($p < 0.001$).

Data on lorica morphometry showed statistically significant differences ($p < 0.001$, one-way ANOVA) in the spine or total length of *B. havanaensis* in the presence of infochemicals as compared with controls (figure 3). The total body length and anterior and posterior spine

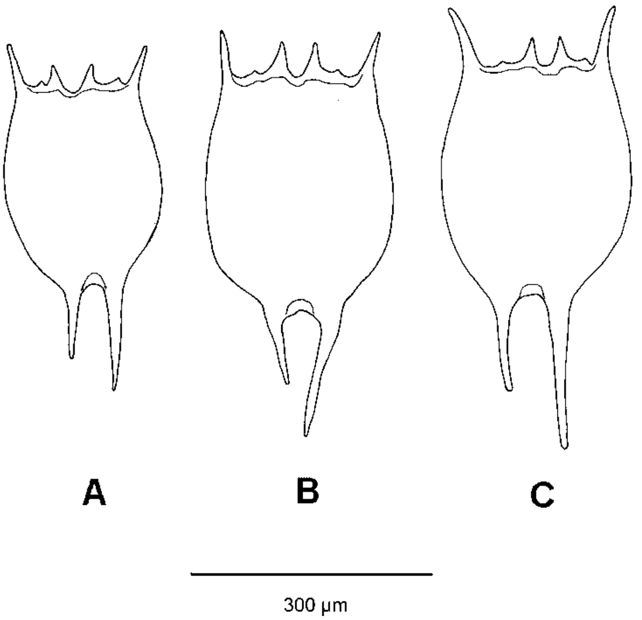

Figure 3. Lorica morphology of adult parthenogenetic female *B. havanaensis* cultured in controls (A) and in the presence of kairomones from *A. robustus* (B) or *A. mexicanum* (C). All figures were drawn on the same scale.

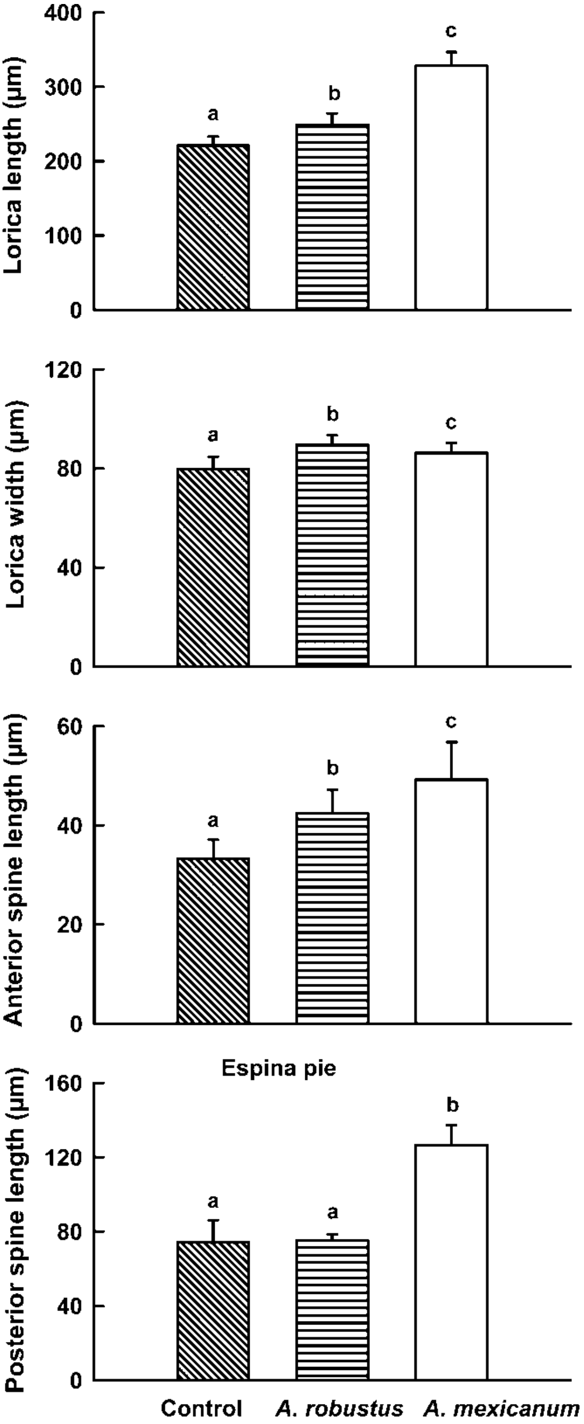

Figure 4. Morphometric data (lorica length, width, anterior spine length and posterior spine length, in µm) of adult parthenogenetic female *B. havanaensis* cultured in controls, and in the presence of kairomones from *A. robustus* or *A. mexicanum*. Shown are the mean ± standard errors based on 20 individuals of each treatment. For each variable, data carrying similar alphabets are not statistically significant ($p > 0.05$, Tukey test).

lengths were significantly higher in the presence of both vertebrate and invertebrate kairomones than in the controls. In general, there were greater body and spine lengths in the presence of *Ambystoma* infochemicals than those from *Acanthocyclops* (figure 4).

4. Discussion

Brachionus havanaensis showed a higher population abundance in the presence of kairomones from *A. mexicanum* than in controls or in copepod kairomone treatments. However, compared with controls, both predators caused an increased abundance of *B. havanaensis*, suggesting stimulation of rotifer population growth. Invertebrate kairomones are known to enhance offspring production in rotifers where a greater investment in reproduction as compared with controls is beneficial to offset loss from predation [19]. Normally, at higher population abundances, most rotifers produce males and resting eggs [2]. However, we did not observe the production of males or resting eggs, probably due to the fact that the peak population densities reached by *B. havanaensis* were below 100 ind. ml^{-1}. A previous study showed the production of males and resting eggs in *B. havanaensis* at densities above 200 ind. ml^{-1} [20]. Thus, the low peak densities of this species in this study are probably due to the fact that the rotifer populations had to invest more energy for spine elongation due to the presence of infochemicals.

It is well known that rotifer density increases with increasing algal food level, a fact also observed here. Many species of *Brachionus* such as *B. calyciflorus* [21], *B. patulus* [22], and *B. rubens* [23] generally show peak population abundances around 10–15 d when raised on alga levels of 0.5×10^6 to 1.5×10^6 cells ml^{-1} at 25 °C. In the present study, too, *B. havanaensis* reached peak abundances at about 10–12 d as was found in other studies [20]. The rate of population increase (r) (0.34–0.87 ind. d^{-1}) from the life-table study was generally higher than that obtained from the population growth experiment, which ranged from 0.25 to 0.45 ind. d^{-1}. The r derived from population growth studies is usually smaller than that derived from a demographic study, most likely due to the presence of intra-specific competition in the former and its absence in the latter [24]. Regardless of the study method used, r for most brachionid rotifers varies from 0.2 to 2.0 [25]. In this work, the r values obtained for *B. havanaensis* are thus within the range reported previously for *Brachionus* in general and *B. havanaensis* in particular [20].

Survivorship and offspring production are the two most important variables determining the fitness of a species [26]. Many herbivorous rotifers have an average lifespan of 10–25 d, and that recorded for *B. havanaensis* here agrees with previous reports [6]. A greater investment in reproductive output lowers the survivorship [27]. The life-history strategy adopted by a species also depends on the predation stress that it is subject to. *A. mexicanum* is known to feed maximally on *B. havanaensis* compared with other brachionids such as *B. calyciflorus, B. patulus*, and *B. rubens* [28]. We have also observed that *Acanthocyclops robustus* feeds on *B. havanaensis* but in lower numbers compared with *A. mexicanum*. This probably explains the different strategies (high reproduction and low survivorship vs. low reproduction and high survivorship) adopted by *B. havanaensis* in the presence of the vertebrate and invertebrate predator. It also explains the greater energy investment in size elongation in the presence of *Ambystoma* kairomones as compared with those from *Acanthocyclops*.

Changes in life-history variables of *Brachionus* in relation to kairomones from predators permit coexistence of prey with predators [3]. For example, elevated offspring in the presence of kairomones from vertebrate predators is expected to compensate for loss from predation [11]. On the other hand, reduced offspring production in the presence of invertebrate predation is possibly a shift in the energy allocation from reproduction to the development of anti-predator defences. In brachionid rotifers, the development of posterior spines and enhanced body size are directly related to the kairomones from the invertebrate predators including *Asplanchna* and cyclopoid copepods [3, 29]. However, previous studies indicate that species that already have large spines, such as *Brachionus macracanthus*, do not invest further in spine elongation as a defence against predation [30]. In our experiments we observed significantly longer spines of *B. havanaensis* subjected to predator's kairomones as compared with the controls. It therefore appears that *B. havanaensis* invests in a higher population growth as well as an increase in spine length, when subject to vertebrate or invertebrate predation stress. It remains to be seen whether similar life-history strategies are observed in other long-spined *Brachionus* species such as *B. diversicornis* or *B. falcatus*.

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