Combined effects of algal (*Chlorella vulgaris*) food level and temperature on the demography of *Brachionus havanaensis* (Rotifera): a life table study

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Abstract

We evaluated the combined effects of food (0.5×10^6, 1.0×10^6 and 2.0×10^6 cells ml^{-1} of *Chlorella vulgaris*) and temperature (15, 20 and 25 °C) on life history variables of *B. havanaensis*. Regardless of *Chlorella* density there was a steep fall in the survivorship of *B. havanaensis* at 25 °C. Both food level and temperature affected the fecundity of *B. havanaensis*. At any given food level, rotifers cultured at 15 °C showed extended but low offspring production. At 25 °C, offspring production was elevated, the duration of egg laying reduced and the fecundity was higher during the latter part of the reproductive period. The effect of food level was generally additive, at any given temperature, and higher densities of *Chlorella* resulted in higher offspring production. Average lifespan, life expectancy at birth and generation time were 2–3 times longer at 15 °C than at 25 °C. At 20 °C, these remained at intermediate levels. The shortest generation time (about 4 days) was observed at 25 °C. Gross and net reproductive rates and the rate of population increase (r) increased with increasing temperature and generally, at any given temperature, higher algal food levels contributed to higher values in these variables. The r varied from 0.11 to 0.66. The survival patterns and lower rates of reproduction at 15 °C suggest that the winter temperatures (10–15 °C) prevailing in many waterbodies in Mexico City allow this species to sustain throughout the year under natural conditions.

Introduction

Brachionus havanaensis Rousselet is a widely distributed freshwater rotifer in the American continent including Mexico (Ahlstrom, 1940; De Ridder, 1981). Its ability to tolerate a wide range of temperature and food concentrations and its role as an important prey item for certain invertebrate predators, such as *Asplanchna*, make this rotifer an important zooplankton species in both tropical and high altitude freshwater water bodies of Mexico (Torres-Orozco & Zanatta, 1998).

Information pertaining to the ecology of this species is mostly based on field collections. However, a few laboratory studies have focused on its role as prey for *Asplanchna* (Nandini et al., 2003; Sarma et al., 2003a). Like some other spined species of *Brachionus*, such as *B. calyciflorus* and *B. quadridentatus*, *B. havanaensis* too is capable of showing variation in posterior and anterior spine length in response to *Asplanchna* predation (Garza-Mouriño et al., 2005). However, survival of this species is related not only to its anti-predatory adaptations, but also to its high reproductive

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potential enabling it to compete with other members of Brachionidae (*Keratella cochlearis*, *K. tropica*, *B. budapestinensis* and *B. calyciflorus*) with which it often co-occurs.

Two important factors controlling life history traits of several rotifer genera including *Brachionus* are food and temperature (Edmondson, 1965). Food effects may be evaluated by considering nutritional quality or abundance (Enrique-García et al., 2003). Numerous studies on the effect of algal quality on herbivorous rotifers and other zooplankton species (Rothhaupt, 1990; Gulati & DeMott, 1999; DeMott et al., 2001; Ramos-Rodríguez & Conde-Porcuna, 2003) generally show that the algae grown in medium containing low amounts of certain elements (e.g. phosphorus), have low nutritional value for zooplankton. However, in many eutrophic tropical waterbodies it is doubtful if algae suffer from a lack of essential nutrients such as N, P and K (Ramírez-García et al., 2002). With regard to algal density, it is generally believed that an increase in the concentration of edible algal food enhances the offspring production. This is true for certain brachionid species, such as *B. calyciflorus* (Sarma et al., 1999). Sarma & Nandini (2001) have shown that increasing *Chlorella* density from 0.25×10^6 to 4.0×10^6 cells ml^{-1} caused decreased egg in the rotifer *B. variabilis*. Therefore, generalizations based on a few taxa may not be applicable to an entire family or even to a given genus. Thus, the evaluation of variable food levels for *B. havanaensis* is important to understand changes in life history parameters (such as lifespan, age-specific survivorship, fecundity and generation time).

For ectothermic organisms like rotifers, temperature affects metabolic processes (Halbach, 1973): higher temperature accelerates egg hatching, age at maturity and rate of egg production but shortens lifespan. Lower temperatures usually have the opposite effect on these variables (Sarma & Rao, 1991). In nature both food level and temperature act synergistically. While the relative allocation of energy intake to reproduction is a function of both the quantity of food available and food consumed, its magnitude varies in relation to temperature (Sarma & Rao, 1990).

The objective of the present study was to evaluate the combined effects of food level and temperature on survivorship and reproductive performance of *B. havanaensis*.

Materials and methods

A single parthenogenetic individual of *B. havanaensis* was isolated from the National Canal of Lake Xochimilco (Mexico City) and cultured on *Chlorella vulgaris* (Strain No. CL-V-3 Algal Department, CICESE, Ensenada, Baja California, Mexico) using moderately hardwater (EPA medium) prepared by dissolving 96 mg NaHCO$_3$, 60 mg CaSO$_4$, 60 mg MgSO$_4$ and 4 mg KCl in 1 l of distilled water (Anonymous, 1985). *Chlorella* was cultured in 2 l transparent bottles using Bold's basal medium (Borowitzka & Borowitzka, 1988). Log phase algae were harvested, concentrated by centrifugation at 3000 rpm and resuspended in distilled water. Algal density was measured using a haemocytometer. Rotifers were cultured in 20 l glass aquaria, fed every day using alga at a concentration of about 1×10^6 ml^{-1}. The medium in aquaria was changed every other day. Rotifer mass cultures were maintained at 22 ± 2 °C under continuous, diffused fluorescent illumination.

Prior to conducting experiments, small cultures (about 1 l) of *B. havanaensis* were maintained at least for a week at the three chosen temperatures (low, 15 °C; medium, 20 °C; and high, 25 °C). To obtain neonates of known age, we filtered rotifers during the exponential phase using 80 μm mesh and collected parthenogenetic eggs. Neonates and small individuals of *B. havanaensis*, if any, were removed immediately. Neonates hatching within 3 h following removal were used in the experiments. Standard cohort life table experiments were conducted at three temperatures and three *Chlorella* densities (low, 0.5×10^6; medium, 1.0×10^6; and high, 2.0×10^6 cells ml^{-1}). For each temperature and food level combination, we used six replicates. Thus, the experimental design consisted of 54 transparent jars of 50 ml capacity. We introduced 20 neonates into each jar for each temperature and *Chlorella* density combination. Following inoculation, we counted and removed neonates born during the successive observations at 12 h intervals. Simultaneously, dead adults were removed. The number of eggs carried by each female and loose eggs were also recorded. The surviving females were transferred every 24-h to fresh test jars containing *C. vulgaris* at the appropriate level and corresponding temperature. The experiments were discontinued when all *B. havanaensis*

had died. The number of eggs and neonates of each 24 h interval were pooled and considered as the daily offspring production for calculating life history variables. We used standard formulae (Krebs, 1985) to derive the selected life history variables (survivorship and fecundity curves, average lifespan and net reproductive rate, generation time and rate of population increase). The survivorship and reproductive variables were analyzed statistically using two-way analysis of variance (ANOVA) following Sokal & Rohlf (2000).

Results

The survivorship curves (l_x) and age-specific offspring production (fecundity, m_x) of *B. havanaensis* grown under different algal food densities and temperatures are shown in Fig. 1. Regardless of *Chlorella* density there was a steep decline in survivorship of *B. havanaensis* at 25 °C. At 15 and 20 °C, although the survival of the test individuals was longer, the curves showed a nearly constant mortality with age. The effect of food level was not apparent, although an increase in *Chlorella* density did increase the longevity of rotifers at 20 °C.

Both food level and temperature affected the fecundity of *B. havanaensis*. At all three food levels, the rotifers cultured at 15 °C showed extended but low offspring production. With a temperature increase to 20 °C, the fecundity increased during the early reproductive period. With a further increase in temperature to 25 °C, offspring production was elevated during the latter part of the reproductive period and the duration of egg laying was reduced. The effect of food level was generally additive, in that at any given temperature, higher densities of *Chlorella* increased offspring production. Females carrying three eggs were observed only at 20 °C.

The age-specific life expectancy curves generally showed increased mortality with increasing age of rotifers at 15 and 25 °C but at the intermediate temperature (20 °C) there was a slight increase in the life expectancy after 10 days. There was no apparent effect of food level (Fig. 2). The average lifespan, life expectancy at birth and the generation times were all 2–3 times longer at 15 °C than at 25 °C. At 20 °C, these remained at intermediate levels. The shortest generation time, about 4 days, was observed at 25 °C. Gross and net reproductive rates increased with increasing temperature and also higher algal food levels generally
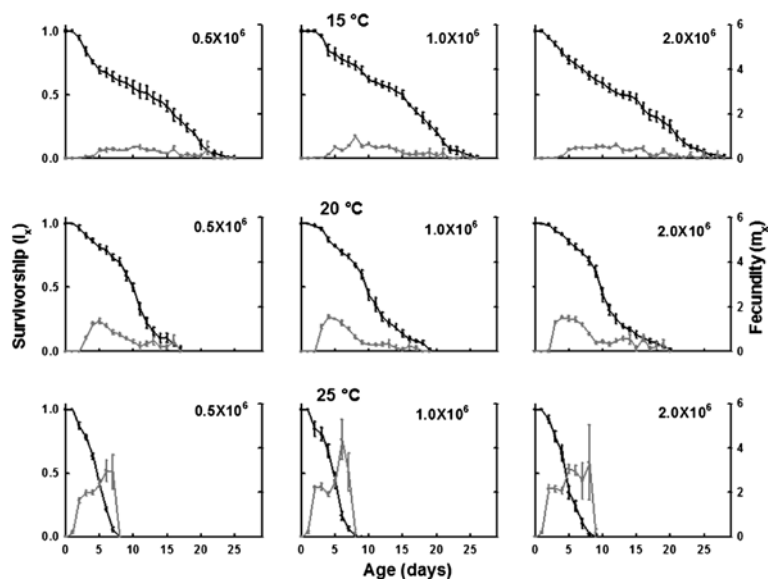

Figure 1. Age-specific survivorship (l_x) and fecundity (m_x) curves of *B. havanaensis* cultured using three different food densities (0.5×10^6, 1.0×10^6 and 2.0×10^6 cells ml^{-1} of *Chlorella*) and each of these at three temperatures (15, 20 and 25 °C). Shown are the mean ± SE of six replicates.
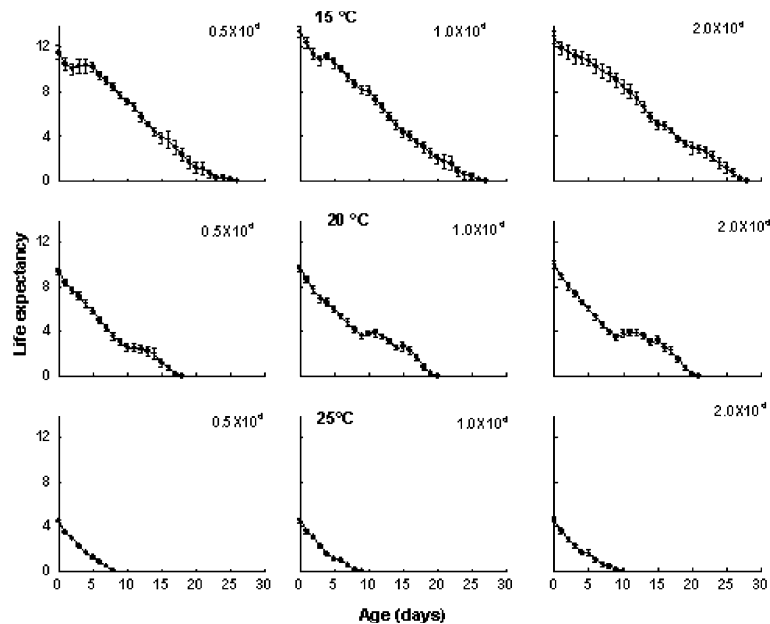
Figure 2. Age-specific life expectancy curves of *B. havanaensis* cultured using three different food densities (0.5×10^6, 1.0×10^6 and 2.0×10^6 cells ml^{-1} of *Chlorella*) and each of these at three temperatures (15, 20 and 25 °C). Shown are the mean ± SE of six replicates.

contributed to higher rates (Table 1). Regardless of food density and temperature, the rate of population increase (*r*) varied from 0.11 to 0.66. For all *Chlorella* densities, increase in temperature resulted in increased *r*. The effect of food level on *r* in general was that increased food level resulted in higher population growth rates (Fig. 3).

Both food density and temperature had statistically significant effect on average lifespan, gross and net reproductive rates, generation time and the rate of population increase ($p < 0.01$, Two way ANOVA, Table 2). However, the interaction between food level and temperature was not significant ($p > 0.05$) for the measured life history traits.

Discussion

Brachionus havanaensis has been recorded in high elevation ponds (2000 m above sea level) in and around Mexico City and in tropical regions in the southeastern states of Mexico (Torres-Orozco & Zanatta, 1998; Flores-Burgos et al., 2003). Temperature ranges from ~10 to 30 °C. Our study covers the wide temperature range as well as the

range of food concentrations that occurs in the waterbody from which this rotifer was originally collected. In addition, these food concentrations have been used for life history assessment in many brachionid rotifers (e.g., *B. calyciflorus*: Sarma et al., 1999, *B. macracanthus*: Sarma & Nandini, 2002, *B. rubens*: Sarma et al., 2003b) thus facilitating comparison within this genus.

Among survivorship variables, median lifespan (or $0.5l_x$) and average lifespan ($= \Sigma l_x$) have received considerable attention because of their role in the evolution of lifespan. These two measures are not identical but are closely related (Sarma & Rao, 1991). King (1982) has hypothesized that for iteroparous organisms, including rotifers, the median lifespan is twice the generation time, regardless of culture conditions. When this was applied to some other rotifer species (Sarma & Rao, 1991) and crustaceans (Anaya-Soto et al., 2003), a significant correlation was, indeed, observed although the slope deviated from 2, as also found in the present study (figure not presented). Increases in temperature have been shown to reduce the lifespan in many rotifer species (Halbach, 1973; Sarma & Rao, 1991), a trend also observed in the present study. When temperature was increased

Table 1. Selected life history traits of *B. havanaensis* in relation to different temperatures and algal food (*Chlorella*) concentrations

| Food density (×10⁶ cells ml⁻¹)	Average lifespan	Life expectancy at birth	Gross reproductive rate	Net reproductive rate	Generation time
15 °C					
0.5	12.03 ± 0.07	11.53 ± 0.61	5.61 ± 0.22	2.82 ± 4.38	9.71 ± 0.14
1.0	13.89 ± 0.47	13.39 ± 0.47	7.39 ± 0.49	4.38 ± 0.33	9.54 ± 0.20
2.0	13.89 ± 0.47	12.94 ± 0.55	7.07 ± 0.41	3.59 ± 0.19	10.26 ± 0.27
20 °C					
0.5	9.89 ± 0.24	9.39 ± 0.24	9.16 ± 0.67	5.83 ± 0.42	6.13 ± 0.21
1.0	10.16 ± 0.30	9.66 ± 0.30	9.54 ± 0.65	6.54 ± 0.37	5.67 ± 0.12
2.0	10.49 ± 0.30	9.99 ± 0.30	12.18 ± 0.66	7.68 ± 0.28	5.99 ± 0.08
25 °C					
0.5	4.98 ± 0.08	4.48 ± 0.08	14.11 ± 0.65	6.25 ± 0.19	3.65 ± 0.09
1.0	5.02 ± 0.25	4.52 ± 0.25	16.55 ± 1.10	7.21 ± 0.71	3.53 ± 0.11
2.0	5.11 ± 0.25	4.61 ± 0.25	18.64 ± 2.77	7.61 ± 0.65	3.71 ± 0.06

Mean ± SE of six replicates.
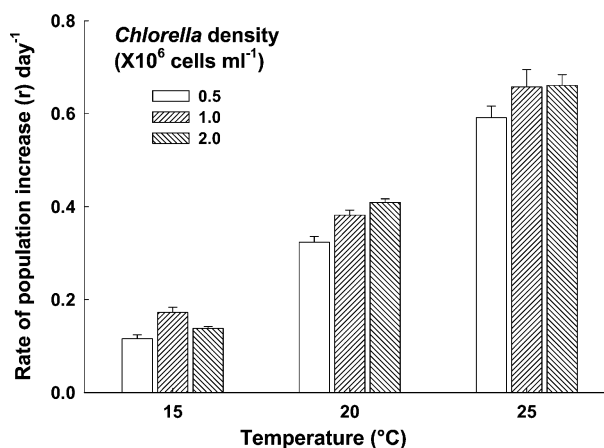
Figure 3. Rate of population increase (day⁻¹) of *B. havanaensis* cultured using three different food densities (0.5×10^6, 1.0×10^6 and 2.0×10^6 cells ml⁻¹ of *Chlorella*) and each of these at three temperatures (15, 20 and 25 °C). Shown are the mean ± SE of 6 replicates.

from 15 to 25 °C, the average lifespan decreased by 2/3. Our observation that an increase in temperature by about 10 °C reduced the rotifer lifespan considerably is similar to reports on other rotifer species (Sarma & Rao, 1991; Sanoamuang, 1993). Regardless of food concentration and temperature, the average lifespan of brachionid rotifers appears to vary from 10 to 25 days at temperatures of 20–25 °C (Nogrady et al., 1993); our study indicates that *B. havanaensis* also falls within this range. Age-specific life expectancy generally decreases with increasing age of the individuals in a cohort population; in certain cases,

however, elevated values at certain days during the lifespan have been documented (Sarma et al., 2003b). We also observed this for *B. havanaensis* at 20 °C, especially at higher food level.

Age-specific fecundity curves observed for *B. havanaensis* are similar to those for other brachionid rotifers, e.g. *B. calyciflorus* (Halbach, 1973) and *B. plicatilis* (King, 1982). The pattern of offspring production in rotifers appears to depend on the conditions in which they are reared (Nogrady et al., 1993). For example, at high temperatures, the duration of egg laying and the rate of egg production are rapid. On the other hand, at

Table 2. Statistical evaluation using two-way analysis of variance (ANOVA) on selected life history traits of *B. havanaensis* fed *Chlorella* at three densities under three temperatures (see Table 1)

Source	DF	SS	MS	F-ratio
Average lifespan				
Temperature (A)	2	601.148	300.57	383.67 ***
Food density (B)	2	5.749	2.87	3.67 **
Interaction of A × B	4	6.247	1.56	1.99 ns
Error	45	34.471	0.77	
Gross reproductive rate				
Temperature (A)	2	874.71	437.35	58.38 ***
Food density (B)	2	81.314	40.66	5.43 ***
Interaction of A × B	4	23.78	5.94	0.79 ns
Error	45	329.516	7.32	
Net reproductive rate				
Temperature (A)	2	128.304	64.15	63.4 ***
Food density (B)	2	17.991	9.00	8.89 ***
Interaction of A × B	4	5.729	1.43	1.42 ns
Error	45	44.52	0.99	
Generation time				
Temperature (A)	2	354.664	177.33	1135.73 ***
Food density (B)	2	1.387	0.69	4.44 **
Interaction of A × B	4	0.938	0.23	1.5 ns
Error	45	6.87	0.15	
Rate of population increase				
Temperature (A)	2	2.208	1.1	531.48 ***
Food density (B)	2	0.043	0.02	10.28 ***
Interaction of A × B	4	0.008	0.0	0.99 ns
Error	45	0.091	0.0	
Highest value of egg ratio (eggs/female)				
Temperature (A)	2	1.036	0.52	14.55 ***
Food density (B)	2	0.827	0.41	11.62 ***
Interaction of A × B	4	0.189	0.05	1.33 ns
Error	45	1.566	0.03	

DF = degrees of freedom, SS = sum of squares, MS = mean square, F = F-ratio..Levels of significance: ***$p < 0.001$; **$p < 0.01$; ns = non-significant ($p > 0.05$).

lower temperatures, both these are lower. This is evident in the fecundity of *B. havanaensis*, where egg production was observed for about 20 days at 15 °C and this was reduced to 15 and 10 days at 20 and 25 °C, respectively. The number of eggs daily produced by *Brachionus* varies from 2 to 6 eggs (Duncan, 1989). We observed about 1–5 eggs female^{-1} day^{-1}. Enhanced egg production with increasing food concentration, as observed in *B. havanaensis*, is similar to *B. calyciflorus* (Guisande & Mazuelos, 1991) but differs in *B. variabilis* where

an inverse relation has been reported (Sarma & Nandini, 2001). Gross and net reproductive rates of *B. havanaensis* were lower than those reported for *B. calyciflorus* but similar to those reported for *B. macracanthus* (Sarma & Nandini, 2002). A 15 °C food level did not enhance gross or net reproductive rates even though the food was not limiting, which suggests that temperature had an overriding influence on the offspring production.

The rate of population increase (*r*) is considered to be influenced by factors like food level, temper-

ature or toxicants (Forbes & Calow, 1999). While *Brachionus* has *r* values in the range of 0.1–2.0 day^{-1}, many species have $r < 0.5$ day^{-1} (Sarma et al., 2001). Our *r*-values varied by a factor of 6 (0.11–0.66 day^{-1}). Since both net reproductive rate and the *r* were positive, *B. havanaensis* appears to be capable of increasing its population density even at low temperature.

The lack of a significant influence of the interaction between food level and temperature on any of the tested life history traits of *B. havanaensis* is an interesting observation. In our life table study, neonates were continuously removed and hence the surviving adults did not experience resource limitations as observed in the case of population dynamics studies. Thus, even if both population growth and life table demography studies are conducted under similar conditions, some factors have a greater effect than the others e.g., rate of population increase, as documented for other brachionid rotifers (Sarma & Rao, 1990, 1991; Sarma et al., 2003b). The lack of a significant interaction of food level and temperature on the life history traits of *B. havanaensis* found by us may be attributed to this phenomenon. Lastly, the fact that *B. havanaensis* showed enhanced reproductive output at 20 and 25 °C but much lower output at 15 °C, suggests that this species is adapted to tropical conditions, though it is capable of maintaining itself at temperatures lower than 15 °C (Flores-Burgos et al., 2003).

The strain of *B. havanaensis* used in this study was apparently adapted to higher temperatures. The increase in temperature and the algal food level enhanced egg output which was eventually reflected in higher net reproductive and population growth rates. The survival patterns and lower rates of reproduction at 15 °C suggest that the winter temperatures (10–15 °C) prevailing in many waterbodies in Mexico City allow this species to flourish and maintain its population until spring and summer optima.

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