0971-4693/94 US $ 5.00
Allelopathy Journal 21 (1): 95-106 (2008)
Table: 1, Figs : 4

Combined effects of temperature, food availability and predator's (A*splanchna girodi*) allelochemicals on the demography and population growth of *Brachionus havanaensis* (Rotifera)

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(Received in revised form: November 26, 2007)

ABSTRACT

We studied the influence of asplanchnin (a non-toxic kairomone from the predator *Asplanchna girodi*) on the selected populations of prey *Brachionus havanaensis* cultured at two algal densities ($0.5x10^6$ cells mL^{-1} and $2x10^6$ cells mL^{-1} of *Chlorella vulgaris*) and at two temperatures (15° and 25°C). At 15°C, the allelochemicals decreased the survival and offspring production of *B. havanaensis* at same food levels. Both gross and net reproductive rates were about 50% lower at 15°C than at 25°C. In the absence of asplanchnin, the rate of population increase (*r*) was highest (0.52 per day) at 25°C under 2 x 10^6 cells mL^{-1} of *Chlorella.* While in the presence of asplanchnin, the *r* was negative (-0.09 per day) at 15°C, at 0.5 x 10^6 cells mL^{-1}. At higher temperature and higher food density, life history variables of *B. havanaensis* did not show adverse impact of asplanchnin. At 15°C under two food levels, *B. havanaensis* populations decreased in the presence of asplanchnin. However, at 25°C, *B. havanaensis* grown at low food level showed similar population densities (ca. 100 ind. mL^{-1}) regardless of the presence of asplanchnin. At 25°C and high food level, *B. havanaensis* had very low densities in the presence of *Asplanchna* than in controls. Thus, we showed the importance of food density and temperature as variables to evaluate the impact of predators' allelochemicals on the prey demographic characteristics.

Key words: Algae, allelochemical, asplanchnin, demography, population growth, predator-prey interaction, rotifer, temperature, zooplankton.

INTRODUCTION

Studies of allelopathic interactions in predator-prey systems in freshwater ecosystems are largely confined to vertebrates (such as fish) and crustaceans (such as cladocerans) (19,40). However, in freshwater ecosystems, rotifers are generally more abundant than crustaceans and are less susceptible to fish predation, except during the larval stages (2-3 weeks) (38). Intra-zooplankton predation studies have shown the importance of direct prey consumption by predators on the plankton structure in freshwater bodies (4). There are about 2000 rotifer species known worldwide, of these only few

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genera (families Notommatidae, Asplanchnidae and Atrochidae) are predatory and feed on other rotifer species (15,36).

Asplanchna and *Asplanchnopus* often capture larger cladocerans and smaller rotifers (20,21). The prey rotifers subjected to *Asplanchna* predation, show changes in their morphology and behaviour (11). While vertebrates (essentially fish) may result in smaller body sizes of their brachionid prey and invertebrates (carnivorous zooplankton and insect larvae) lead to large-bodied individuals (5). Thus, *Brachionus* is vulnerable to depredation, hence, it has developed diverse adaptive characteristics, to minimize predation-related mortality (31).

Asplanchna changes the morphology of its prey rotifers by releasing the allelochemical asplanchnin, which is a low molecular weight heat-labile protein (11). This allelochemical induces spine elongation and increasing the body size (length and width) of its brachionid prey by acting on the parthenogenetic eggs (which are still in the embryonic stage in the germarium) (9). The adaptive significance of phenotypes with spines induced by predators' allelochemicals is clear; it reduces the probability of mortality due to predation (25). Nevertheless, the reason for the predominance of phenotypes with spines and smaller-bodied individuals in absence of the invertebrate predators is not clear (33,35). The induced defences have a cost for the prey, which can be avoided in absence of predator (19). On the other hand, if phenotypic changes have high costs, then they may become counterproductive for the survival of a population, especially under unfavourable food and temperature levels and therefore such costs, if any, should be minimum and hence difficult to measure, especially at individual level (37).

Population level studies on rotifers (such as changes in densities or demographic parameters using life tables) provide greater flexibility and sensitivity to quantify trade offs between reproduction and somatic growth under changing environmental conditions including the presence of allelochemicals from predators such as *Asplanchna* (23,38). *Brachionus calyciflorus* undergoes morphological changes in relation to asplanchnin, without a reproductive cost (35), while another rotifer *Keratella testudo* experiences a reproductive cost for allelochemicals (34).

Brachionus havanaensis is most common brachionid rotifers in Mexico and in nature shows considerable variations in the body length and spine length in the presence of its predator *Asplanchna* (8). Laboratory experiments have also confirmed spine induction in *B. havanaensis* by *Asplachna girodi* (24). However, it is not known if these changes are associated with some reproductive costs (i.e., reduced population growth rates or egg output). Therefore, we aimed to quantify the changes in population densities and life history parameters (mean lifespan, gross and net reproductive rates, generation time and the rate of population increase) of *B. havanaensis* in the presence of its predator *A. girodi.* Since both temperature and algal food level also influence the population dynamics of *B. havanaensis*, we evaluated the combined effects of these factors and the allelochemicals obtained from *A. girodi*. Further, if the morphological changes of the prey induced by *A. girodi* do not represent a reproductive cost, then the variations in the population variables of *B. havanaensis* would be similar, when grown alone or in the presence of predator's allelochemicals.

MATERIALS AND METHODS

Biological material

The prey (*Brachionus havanaensis*) and the predator (*Asplanchna girodi*) were isolated from the lake Xochimilco (Mexico City) and separately cultured using moderately hardwater (EPA medium). The EPA medium was prepared by dissolving 96 mg $NaHCO_3$, 60 mg $CaSO_4$, 60 mg $MgSO_4$ and 4 mg KCL in 1 litre of distilled water (39). The single celled green alga *Chlorella vulgaris* was used as food (offered daily at $1X10^6$ cells mL^{-1}) for *B. havanaensis*. *C. vulgaris* was batch-cultured in 2 L transparent bottles using defined nutrient medium (Bold's basal medium) (1). Log phase algae were harvested, centrifuged at 3000 rpm for 5 min, rinsed and resuspended in distilled water. The stock algal density was estimated using haemocytometer. For *A. girodi*, we daily offered the prey brachionids (a mixture of *Brachionus patulus* and *B. havanaensis* at a density of 5-10 ind. mL^{-1}). We simultaneously conducted both life table demography and population growth experiments using two algal concentrations ($0.5X10^6$ and $2X10^6$ cells mL^{-1}) under two temperature regimes (15° and 25°C) and in the presence and absence of asplanchnin.

Life table demography experiments

The experiments were conducted in 100 mL capacity glass jars, each with 50 mL medium containing one of the two chosen algal concentrations and set at 15° or 25°C. Life table experiments were conducted using neonate *B. havanaensis* (2 ± 1 h following hatching) and 6 replicates (cohorts) for each treatment. Each cohort contained 20 neonates in 20 mL medium individually introduced into the test jars using a finely drawn Pasteur pipette under a stereomicroscope (SMZ 645 Nikon, Japan) at a magnification of 20X. In treatments with allelochemical, we inserted a small mesh cage (pore size 50 μm) containing two juvenile individuals of *A. girodi* so that only the asplanchnin but not the predators could freely pass into the medium. Thus, predators were in continuous but indirect contact with their prey throughout the experimental period. The predators in the cages were fed using a few individuals of *Brachionus patulus*, a prey species different from that used in the experiments. The density of *B. patulus* used in the cages was not energetically sufficient for the predator to reproduce but to keep it active in the test jars (26). In treatments without allelochemicals we also kept the mesh in a similar way but without *Asplanchna*. In all treatments, we used 48 test jars (2 temperatures X 2 algal food levels X 2 allelochemical levels (presence and absence) X 6 replicates). Following initiation of the experiment, at every 12 h intervals, we collected data on the number of individuals of the original cohort alive and the number of offspring produced, if any. The dead individuals and the offspring produced were removed from the test jars. The medium was 100% replaced with appropriate algal density after every 24 h. In treatments containing allelochemicals, the predators were also replaced by fresh batch of immature *A. girodi* individuals. The experiments were discontinued after every individual of the original cohort had died.

The data obtained for 12 h were pooled for 24 h and standard life history variables were derived (average lifespan, life expectancy at birth, gross reproductive rate, net reproductive rate, generation time and the rate of population increase). Age-specific

survivorship and fecundity curves were plotted. The following formulae were used for deriving the life history variables (16):

l_x = Proportion of survivorship per day
m_x = Proportion of offspring produced per female per day

$$\text{Life expectancy: } e_x = \frac{T_x}{n_x}$$

Where, T_x = number of individuals per day
n_x = number of living individuals at the initiation and the age x (days)

$$\text{Gross reproductive rate } = \sum_0^\infty m_x$$

$$\text{Net reproductive rate } R_o = \sum_0^\infty l_x \cdot m_x$$

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

Rate of population increase, Euler-Lotka equation (solved iteratively)

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

where r = rate of population increase per day, w = age at maturity (days)

Differences in the life history variables of *B. havanaensis* under different treatments were evaluated statistically using three-way analysis of variance ANOVA and *post hoc* (Tukey) tests (Statistica Ver. 7, USA).

Population growth experiments

For population growth experiments, we used the same temperature-food density-asplanchnin combinations as used for life table experiments. However, here for each treatment, we used 4 replicates. Thus for population growth experiment, we used a total of 32 test jars [2 food levels X 2 temperatures X 2 allelochemical levels (presence and absence) X 4 replicates]. Into each of the test jar, we introduced *B. havanaensis* at an initial density of 1 ind. mL^{-1}.

Following initiation of the growth experiment, we daily counted the number of *B. havanaensis* individuals (either total count or two aliquots of 0.2 to 1 mL, depending on the prey density) and medium was 100% replaced by fresh medium containing appropriate algal food as described for life table experiments. In treatments containing allelochemicals,

the predators were also replaced by fresh batch of individuals. The experiments were discontinued after 25 days, by that time populations of *B. havanaensis* in most replicates began to decline. Based on the data collected, we obtained peak population density and the rate of population increase (*r*) for each replicate separately. The following formula (32) was used to derive population growth rates: $r = (lnN_t - lnN_o)/t$, where: r = rate of population growth, N_o = initial population density; N_t = final population density, t = time in days. ANOVA and multiple comparison tests, as mentioned above were used to evaluate the differences in the peak population densities and population growth rates of *B. havanaensis* grown under different treatments.

RESULTS AND DISCUSSION

The age specific survivorship curves indicated that the survival of *B. havanaensis* diminished remarkably at 25°C than at 15°C, regardless of presence or absence of predator's allelochemical. Increase in temperature had also shortened the duration of life of *B. havanaensis.* In addition, at 15°C and under both the tested food levels the survival of *B. havanaensis* was shorter due to the predator's kairomone (Figure 1). The age-specific fecundity curves showed (Figure 2) that at 15°C the offspring production was low (1 and 2 eggs per female per day), but almost constant and for a longer duration (2 to 3 weeks) during the female lifespan at both low and high algal food levels. At 25 °C, this tendency changed towards a higher fecundity (2 and 3 offspring per female per day for shorter duration (<10 days). The influence of predator's infochemicals on the fecundity was not clear at 25°C, while at 15°C and at low algal food density, the offspring production was lower than in treatments containing no allelochemicals from the predator.

Data on the selected life history variables of *B. havanaensis* grown with and without asplanchnin are presented in Table 1. The average lifespan and life expectancy were longer at 15°C than at 25°C regardless of the predator's allelochemical in the medium and at the two algal food densities. However, both these variables were higher at 2 x 10^6 cells mL^{-1} than at 0.5 x 10^6 cells mL^{-1}. Gross and net reproductive rates varied from 2-12 and 1-5 offspring per female per day, respectively. Generally, both gross and net reproductive rates were about 50% lower at 15°C than at 25°C under comparable food levels. Generation time varied from 3 to 8 days depending on the treatment; at lower temperature, it was longer. The rate of population increase was highest (0.52 per day) at 25°C under 2 x 10^6 cells mL^{-1} algal density and in the absence of predator's allelochemicals in the medium. On the other hand, the *r* was negative (-0.09 per day) at 15°C, at 0.5 x 10^6 cells mL^{-1} and in the presence of asplanchnin.

The results of 3-way ANOVA showed significant effect ($p<0.05$) of temperature and food availability on the survival-related (average lifespan and life expectancy at birth) and reproduction-related variables (gross and net reproductive rates, generation time and rate of population increase) of *B. havanaensis*. Asplanchnin had a significant effect only on reproductive variables. Except for gross reproductive rate, the interaction of food x temperature was significant for the rest of the life history variables. The interaction of asplanchnin x food level or temperature was not significant (except generation time and the rate of population increase). The interaction of temperature x food concentration x

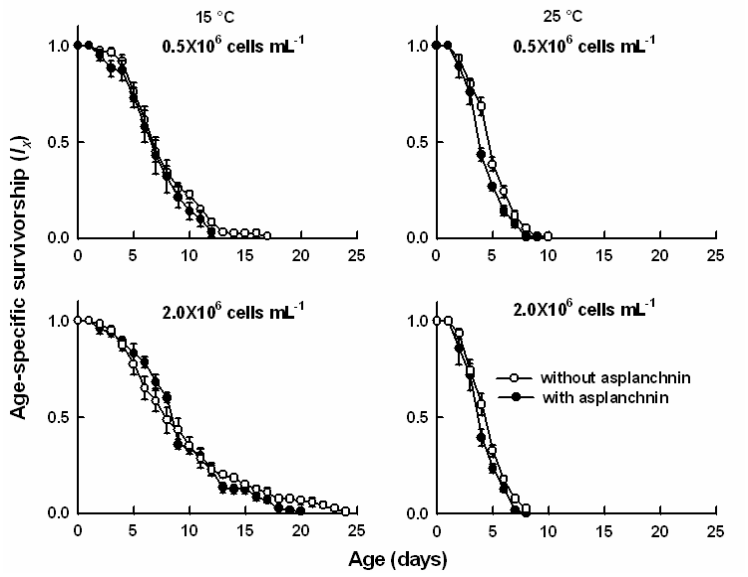

Figure 1. Age-specific survivorship (l_x) curves of *Brachionus havanaensis* grown at two algal densities, under two temperature regimes, and in the absence ( ) or presence ( ) of asplanchnin in the medium. Shown are the mean±standard errors based on six replicates (cohorts).

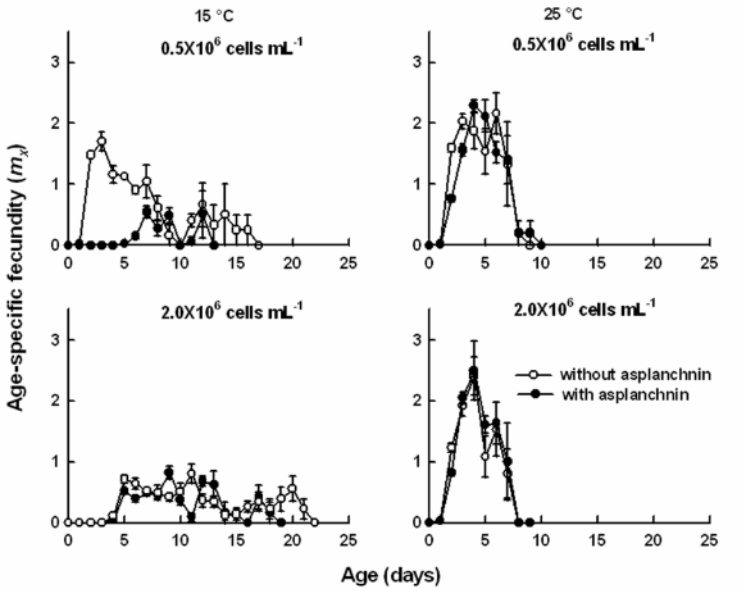

Figure 2. Age-specific fecundity (m_x) curves of *B. havanaensis* grown at two algal densities, under two temperature regimes, and in the absence ( ) or presence ( ) of asplanchnin in the medium. Shown are the mean±standard errors based on six replicates (cohorts).

allelochemical was significant only for gross reproductive rate and the *r*. The results of multiple correlations showed all the tested variables were significantly affected by the temperature, food level or the presence of asplanchnin ($p<0.05$, Table 1, Tukey test).

Table 1. Selected life history variables of *B. havanaensis* cultured in the absence or presence of asplanchnin from the predator *A. girodi* at two temperatures and under two food densities (FD x 10^6 cells mL^{-1} of *C. vulgaris*). Data with the same letters are not significantly different ($p>0.05$, Tukey test).

Treatment	FD	Life history variables					
		ALS days	LEB days	GRR	NRR	GT days	*r*/day
				15° C			
No asplanchnin	0.5	7.8±0.2[a]	7.4±0.2[a]	4.2±0.3[a]	1.4±0.1[a]	7.4±0.2[a]	0.04±0.01[a]
With asplanchnin	0.5	7.2±0.5[a]	6.7±0.5[a]	2.1±0.5[b]	0.6±0.1[b]	7.5±0.3[a,b]	-0.09±0.04[b]
No asplanchnin	2.0	9.7±0.5[b]	9.2±0.5[b]	7.2±0.3[c]	2.6±0.27[c]	8.3±0.2[b]	0.12±0.02[a]
With asplanchnin	2.0	9.5±0.3[b]	9.0±0.3[b]	5.4±0.4[a]	2.1±0.15[a,c]	7.9±0.1[b]	0.10±0.01[a]
				25° C			
No asplanchnin	0.5	5.2±0.2[c]	4.7±0.2[c]	8.3±0.6[c]	4.4±0.29[d]	3.4±0.1[c]	0.49±0.02[c]
With asplanchnin	0.5	4.8±0.1[c]	4.3±0.1[c]	10.1±0.3[d]	4.0±0.18[e]	3.7±0.1[c,d]	0.41±0.01[d]
No asplanchnin	2.0	4.8±0.1[c]	4.3±0.1[c]	11.8±1.7[d]	5.0±0.21[f]	3.4±0.1[c]	0.52±0.01[c]
With asplanchnin	2.0	4.6±0.1[c]	4.1±0.1[c]	9.6±0.4[d]	4.0±0.1[e]	3.4±0.1[c]	0.44±0.01[d]

ALS = average lifespan; LEB = life expectancy at birth; GRR = gross reproductive rate, offspring per female per lifespan; NRR = survival weighted offspring per female per lifespan; GT = generation time; and r: rate of population increase per day

Population growth curves *of B. havanaensis* grown under different food levels, temperature and in the presence of asplanchnin are presented in Figure 3. The temperature had far more greater effect than food level on the population growth of *B. havanaensis*. At 15°C under both the algal food levels, *B. havanaensis* populations crashed, while under similar conditions and in the absence of asplanchnin, the rotifers showed some growth, although much lower compared to that at higher temperature. At 25°C, rotifers grown at low food level showed similar population densities regardless of the presence of asplanchnin in the medium. At higher food level and at this temperature, rotifers grown in the presence of allelochemical from the predator had much lower densities. The *r* derived from population growth data varied from -0.47 to +0.54 per day depending on the treatment. Results of multiple comparisons showed that the *r* was significantly affected by temperature, food level or the presence of asplanchnin ($p<0.05$, Tukey test, Figure 4).

During the last two decades, the study of aquatic systems has acquired a new dimension with the discovery of infochemicals that can be detected by the aquatic organisms. Among these infochemicals, kairomones and other allelochemicals are emitted by both herbivorous and predatory zooplankton (14,19). The potential prey zooplankton species has the ability to detect these substances and to change its morphological and life history strategies so as to maximize its fitness (12,33). It is known that *B. havanaensis*, like other species of *Brachionus* such as *B. calyciflorus*, *B. bidentatus*, and *B. patulus* increases its body size and spine lengths in the presence of *Asplanchna* (13,24). Nevertheless, costs associated with such changes in the morphology remained unknown.

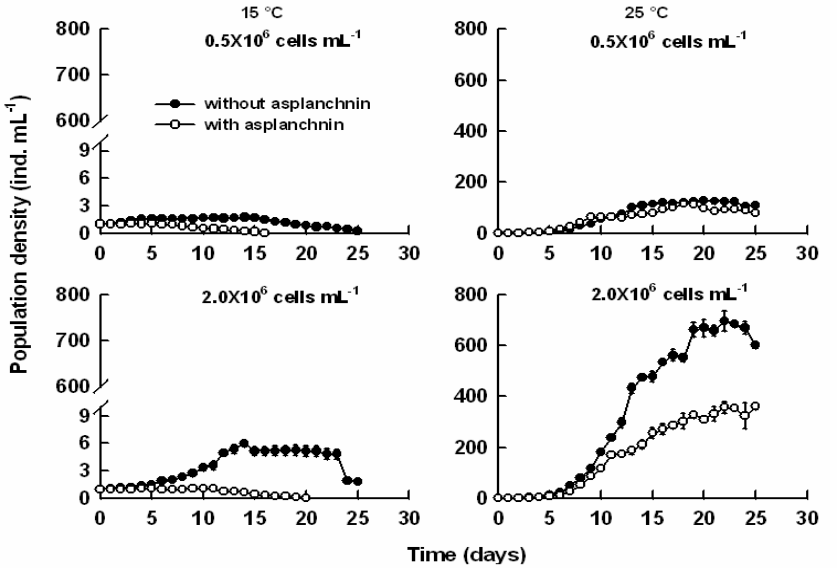

Figure 3. Population growth curves of *B. havanaensis* cultured at two algal densities, under two temperature regimes, and in the absence ( ) or presence ( ) of asplanchnin in the medium. Shown are the mean±standard errors based on six replicates.

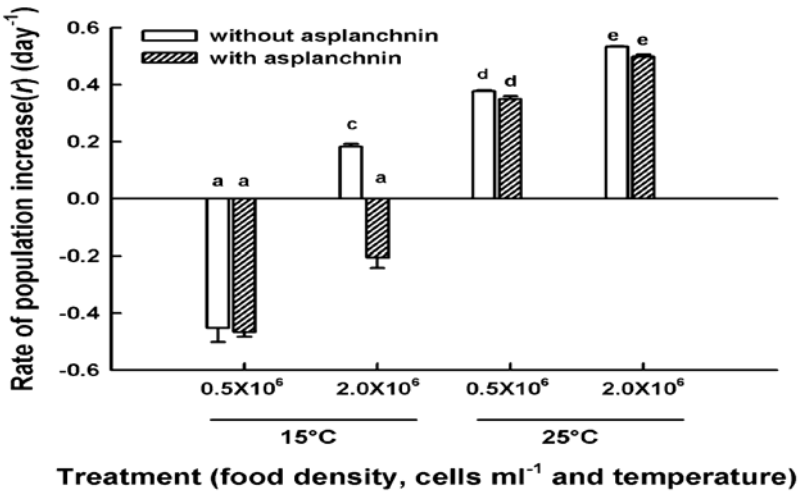

Figure 4. Rate of population increase (*r* per day, derived from growth curves) of *B. havanaensis* cultured at two algal densities, under two temperature regimes, and in absence ( ) or presence ( ) of asplanchnin in the medium. Shown are the mean±standard errors based on six replicates. Bars with the same letter are not significantly different ($p>0.05$, Tukey test).

Based on life table experiments, Gilbert (10) did not observe significant changes in the survival or reproduction of long-spined *B. calyciflorus* when compared to short-spine morphs. On the other hand, Conde-Porcuna and Declerk (2) have found that the induction of spine lengths in *Keratella quadrata* is negatively related with its fecundity, suggesting that some reproductive costs are associated with spine production.

We did not quantify the concentration of asplanchnin in the medium. However, the predator density used in cages was sufficient to induce spine production in *Brachionus* and within range of temperature chosen here, asplanchnin production appears to be similar (19,24). There is also sufficient evidence to show that the asplanchnin is continuously produced by *Asplanchna* (13). Since in the test jars, *A. girodi* was continuously in contact with *B. havanaensis*, it is possible that a constant level of asplanchnin was present in the test jars. Pavón-Meza et al. (24) have cultured *B. havanaensis* in the presence of *A. girodi* (indirect contact) at 3 temperature levels (15, 20 and 25°C) and under 3 algal food concentrations (0.5×10^6, 1.0×10^6 and 2.0×10^6 cells mL^{-1}). They observed that the posterior spine length of *B. havanaensis* has increased significantly by about 58% due to allelochemicals from *Asplanchna*, which was similar at the three temperatures. In addition, the interactions of food x temperature, or predator´s presence x temperature have remained non-significant for the body size or spine length of *B. havanaensis*. This suggests that the production and/or permanence of asplanchnin in the culture jars are essentially similar in all treatments containing the predators. It is therefore possible here too that temperature could have little effect on the asplanchnin levels in our jars. In this study, the presence of allelochemicals had no significant effect on the average lifespan or the age at first reproduction of *B. havanaensis* grown under a given food level- temperature combination. However, reproductive variables (gross and net reproductive rates, and the rate of population increase) were adversely affected by the asplanchnin especially at low food level and low temperature. Since in the nature, food quantity, temperature vary considerably through seasons (17), the predator's allelochemicals on brachionid rotifers could also vary, possibly from no effect to strong adverse impact. Therefore, our results suggest the inclusion of food concentration and temperature as important variables while evaluating the impact of predator's allelochemicals on the demographic characteristics of prey species.

The reduction in the reproductive parameters of *B. havanaensis* as a result of allelochemicals from *Asplanchna* appears to be a general tendency with the infochemicals from other predators too. For example, Enríquez-García et al. (6) have reported significant reduction in the gross and net reproductive rates as well as the rate of population increase of *B. havanaensis* when exposed to infochemicals obtained from vertebrate (salamander axolotl, *Ambystoma mexicanum*) or invertebrate (copepod *Acanthocyclops robustus*) predator-conditioned-medium. In treatments containing no allelochemicals, the range of life demographic variables obtained here or the patterns of survivorship and fecundity agree with the data available for *B. havanaensis* in literature (22). In addition, as compared to 25°C, *B. havanaensis* had longer lifespan and lower reproductive output at 15°C. Reduction in reproductive rates and enhanced duration of survival at lower temperatures as a common feature for the pantropical genera of rotifers including *Brachionus* (28,38), which was also observed in our study.

Unlike the fixed zooplankton samples, rotifers in test jars need to be quantified as rapidly as possible to minimize effects due to counting stress. While whole count is ideal,

it is often not practical, especially with the smaller rotifers such as *Anuraeopsis* and *Brachionus* which reach high densities and hence aliquot samples are recommended (38). Since the population in the test jars often increase, varying quantities of aliquots have been chosen depending on the density (13). There is often a close relation between the density estimated from aliquots and that based on whole sample count and the differences in these estimations generally appear statistically non-significant (38). We therefore used two aliquots of 0.2 to 1 mL in order to quantify changes in the population densities of *B. havanaensis*. Population growth curves obtained here for *B. havanaensis* are typical for most brachionids. For example, when *B. patulus* was grown under 4 x 10^6 cells mL^{-1} at 15°C, the rotifer populations crashed from an initial density of about 50 ind. mL^{-1} to <1 ind. mL^{-1} and the growth rates became negative, while the same species at 25°C increased to a peak density of about 600 ind. mL^{-1} (27). In the present work, *B. havanaensis* also showed reduced population densities and even negative growth rates at 15°C. This suggests that just like *B. patulus*, *B. havanaensis* is adapted to temperatures higher than 15°C in nature. The growth rates of *Brachionus* may vary from 0.1 to 2.0 depending on the species and culture conditions (30). Negative growth rates indicate the adverse environmental conditions or stress (7). Considering that 15°C is unfavourable for *B. havanaensis* (23), the presence of asplanchnin could be an additional stress on the population growth rates.

The reduced population growth rates (due to decreased gross and net reproductive rates, as evident from the life table demography described earlier) of *B. havanaensis* in the presence of allelochemicals from *Asplanchna* may be related to the changes in the energy allocation for somatic growth vs. reproduction. Thus, since *B. havanaensis* shows increased body size and spine lengths (8,22) with increasing availability of food from the medium, a higher portion of the assimilated energy could be expected for somatic growth causing decreased egg output. When the available energy was much limited at 15°C and under low algal food level, the growth rates of *B. havanaensis* became negative, which indicates a stressful condition (7).

CONCLUSIONS

Our results showed that asplanchnin had a significant effect on the reproduction but not on survival-related variables of *B. havanaensis*, when cultured at low temperature and low algal food density. The rate of population increase derived from demography and population growth data showed also adverse impact of asplanchnin, especially at low temperature and low algal density. At higher temperature and higher food density, asplanchnin did not adversely effect both survivorship and reproduction-related variables of *B. havanaensis*. We showed the importance of considering food density and temperature as variables for evaluating the impact of predators' allelochemicals on the prey demographic characteristics.

ACKNOWLEDGEMENTS

We thank Dr. Ana Luisa Anaya for inviting us to contribute to this special issue. We are grateful to an anonymous reviewer for the constructive criticism on our manuscript and Dr. Francisco J. Espinosa-García for editorial corrections. E. Lucía Pavón-Meza thanks the Mexican National Council for Science and Technology (CONACyT- 128436) for a doctoral scholarship.

REFERENCES

1. Borowitzka, M. A. and Borowitzka, L. J. (1988). *Micro-algal Biotechnology*. Cambridge University Press, London. 477 pp.
2. Conde-Porcuna, J.M. and Declerck, S. (1998). Regulation of rotifer species by invertebrate predators in a hypertrophic lake: selective predation on egg-bearing females and induction of morphological defences. *Journal of Plankton Research* **20**: 605-618.
3. Dumont, H.J. and Sarma, S.S.S. (1995). Demography and population growth of *Asplanchna girodi* (Rotifera) as a function of prey (*Anuraeopsis fissa*) density. *Hydrobiologia* **306**: 97-107.
4. Dumont, H.J., Tundisi, J.G. and Roche, K. (Eds) (1990). *Intrazooplankton Predation*. Developments in Hydrobiology No. 60. Kluwer Academic Publishers, Dordrecht, The Netherlands. 256 pp.
5. Duncan, N. (1989). Food limitation and body size in the life cycle of planktonic rotifers and cladocerans. *Hydrobiologia* **186/187**: 11-28.
6. Enríquez-García, C., Chaparro-Herrera, D.J., Nandini, S. and Sarma, S.S.S. (2007) Life history strategies of *Brachionus havanaensis* subject to kairomones of vertebrate and invertebrate predators. *Chemistry and Ecology* **23**: 303-313.
7. Forbes, V.E. and Calow, P. (1999). Is the per capita rate of increase a good measure of population-level effects in ecotoxicology? *Environmental Toxicolology and Chemistry* **18**: 1544-1556.
8. Garza-Mouriño, G., Silva-Briano, M., Nandini, S., Sarma, S.S.S. and Castellanos-Páez, M.E. (2005) Morphological and morphometrical variations of selected rotifer species in response to predation: a seasonal study of selected brachionid species from Lake Xochimilco (Mexico). *Hydrobiologia* **546**: 169-179.
9. Gilbert, J.J. (1966). Rotifer ecology and embryological induction. *Science* **151**: 1234-1237.
10. Gilbert, J. J. (1980). Further observations on developmental polymorphism and its evolution in the rotifer *Brachionus calyciflorus*. *Freshwater Biology* **10**: 281-294.
11. Gilbert, J. J. (1998). Kairomone-induced morphological defenses in rotifers. In :*The Ecology and Evolution of Inducible Defences* (Eds., R. Tollrian and C. D. Harvell), pp. 127–141. Princeton University Press, Princeton, USA.
12. Glazier, D.S. and Calow, P. (1992). Energy allocation rules in *Daphnia magna*: Clonal and age differences in the effects of food limitation. *Oecologia* **90**: 540-549.
13. Halbach, U. and Halbach-Keup, G. (1974). Quantitative beziehungen zwischen phytoplankton und der populationsdynamik des rotators *Brachionus calyciflorus* Pallas. Befunde aus laboratoriumsexperimenten und freilanduntersuchungen. *Archiv für Hydrobiologie* **73**: 273-309.
14. Havel, J. E. (1987). Predator-induced defenses: a review. In: *Predation: Direct and Indirect Impacts on Aquatic Communities* (Eds., W.C. Kerfoot, and A. Sih,). pp. 263-272. Princeton University Press. Princeton, USA.
15. Koste, W. (1978). *Rotatoria. Die Rädertiere Mitteleuropas. Ein Bestimmungswerk begründet von Max Voigt.*, Bornträger, Stuttgart, Germany. Vol. 1. 673 pp., Vol. 2. 234 pp.
16. Krebs, C.J. (1985). *Ecology; The Experimental Analysis of Distribution and Abundance*. 3rd Ed. Harper & Row, New York. 592 pp.
17. Lampert, W. and Sommer, U. (1997) *Limnoecology*: *The Ecology of Lakes and Streams*. Oxford University Press, New York, 382 pp.
18. Lara-Resendiz, R.A. (2004). Efecto indirecto del depredador *Asplanchna brightwelli* (Gosse) sobre el crecimiento poblacional, tabla de vida y morfometría de *Brachionus calyciflorus* Pallas y *Brachionus macracanthus* (Daday) (Rotifera: Brachionidae). B.Sc. Thesis, National Autonomous University of Mexico, Mexico City, Mexico. 48 pp.
19. Lass, S. and Spaak, P. (2003). Chemically induced anti-predator defences in plankton: a review. *Hydrobiologia* **491**: 221-239.
20. Nandini, S., Pérez-Chávez, R. and Sarma, S.S.S. (2003). The effect of prey morphology on the feeding behaviour and population growth of the predatory rotifer *Asplanchna sieboldi*: A case study using five species *of Brachionus* (Rotifera). *Freshwater Biology* **48**: 2131-2140.
21. Nandini, S. and Sarma, S.S.S. (2005) Life history characteristics of *Asplanchnopus multiceps* (Rotifera) fed rotifer and cladoceran prey. *Hydrobiologia* **546**: 491-501.
22. Pavón-Meza, E.L., Sarma, S.S.S. and Nandini, S. (2005). Combined effects of algal (*Chlorella vulgaris*) food level and temperature on the demography of *Brachionus havanaensis* (Rotifera): A life table study. *Hydrobiologia* **546**: 353-360.

23. Pavón-Meza, E.L. (2007). *Estrategias de la Historia de Vida del Rotífero Brachionus havanaensis Rousselet con Relación a Temperatura, Concentración de Alimento Y Depredación.* Doctoral Thesis, National Autonomous University of Mexico, Mexico City, Mexico. 115 pp.
24. Pavón-Meza, E.L., Sarma, S.S.S. and Nandini, S. (2007). Combined effects of temperature, food (*Chlorella vulgaris*) concentration and predation (*Asplanchna girodi*) on the morphology of *Brachionus havanaensis* (Rotifera*). Hydrobiologia* **593**: 95-101.
25. Pourriot, R. (1974). Predator-prey relationships in rotifers: Effect of the predator (*Asplanchna brightwelli*) on the morphology of the prey (*Brachionus bidentata*). *Annales D Hydrobiologie* **5**: 43-55.
26. Sagrario, M.H. (2003). *Efecto de la Densidad de la Presa Brachionus calyciflorus* Pallas *sobre el Crecimiento Poblacional del Depredador Asplanchna brightwelli* (Gosse). B.Sc. Thesis, National Autonomous University of Mexico, Mexico City, Mexico. 60 pp.
27. Sarma, S.S.S. and Rao, T.R. (1990). Population dynamics of *Brachionus patulus* Müller (Rotifera) in relation to food and temperature. *Proceedings of the Indian Academy of Sciences (Animal Sciences)* **99**: 335-343.
28. Sarma, S.S.S. and Rao, T.R. (1991) The combined effects of food and temperature on the life history parameters of *Brachionus patulus* Muller (Rotifera). *Internationale Revue gesamten Hydrobiologie* **76**: 225-239.
29. Sarma, S.S.S. (1993). Feeding responses of *Asplanchna brightwelli* (Rotifera): laboratory and field studies. *Hydrobiologia* **255/256**: 275-282.
30. Sarma, S.S.S., Larios-Jurado, P.S. and Nandini, S. (2001). Effect of three food types on the population growth of *Brachionus calyciflorus* and *Brachionus patulus* (Rotifera: Brachionidae). *Revista de Biología Tropical* **49**: 75-82.
31. Sarma, S.S.S. and Nandini, S. (2007). Small prey size offers immunity to predation: a case study on two species of *Asplanchna* and three brachionid prey (Rotifera). *Hydrobiologia* **593**: 67-76.
32. Sibly, R.M. and Hone, J. (2002). Population growth rate and its determinants: An overview. *Philosophical Transactions of the Royal Society, London* **B357**: 1153-1170.
33. Stemberger, R. S. and Gilbert, J.J. (1987). Defenses of planktonic rotifers against predators. In: *Predation: Direct and Indirect Impacts on Aquatic Communities* (Eds., W.C. Kerfoot, and A. Sih,). pp. 227-239. Princeton University Press. Princeton, USA.
34. Stemberger, R. S. (1988). Reproductive costs and hydrodynamic benefits of chemically induced defenses in *Keratella testudo*. *Limnology and Oceanography* **33**: 593-606.
35. Stemberger, R. S. (1990). Food limitation, spination and reproduction in *Brachionus calyciflorus*. *Limnology and Oceanography* **85**: 33-44.
36. Thorp, J.H. and Covich, A.P. (Eds) (2001). *Ecology and Classification of North American Freshwater Invertebrates*. 2nd Ed., Academic Press, San Diego. 1038 pp.
37. Tollrian, R. (1995). Predator-induced morphological defenses: costs, life history shifts, and maternal effects in *Daphnia pulex*. *Ecology* **76**: 1691-1705.
38. Wallace, R.L., Snell, T.W., Ricci, C. and Nogrady, T. (2006). *Rotifera Part 1: Biology, Ecology and Systematics. Guides to the Identification of the Microinvertebrates of the Continental Waters of World*. Kenobi Productions Gent, Belgium / Backhuys, The Netherlands. 299 pp.
39. Weber, C. I. (1993). *Methods to Measure the Acute Toxicity of Effluents and Receiving Waters to Freshwater and Marine Organisms*. 4th ed. United States Environmental Protection Agency, Cincinnati, Ohio, EPA/600/4-90/027F, xv + 293 pp.
40. Zaret, T. (1980). *Predation and Freshwater Communities*. Yale University Press, London. 187 pp.