CrossMark

ROTIFERA XIV

Life table demography of *Asplanchna brightwellii* Gosse, 1850 fed with five different prey items

Gustavo Emilio Santos-Medrano · Daniel Robles-Vargas · Saraí Hernández-Flores · Roberto Rico-Martínez

Abstract We conducted life table experiments on the freshwater rotifer *Asplanchna brightwellii* to analyze its demography when fed with prey items from several taxonomic groups (cladocerans, protozoans, and rotifers) and under two different temperature regimes (20 and 25°C); the aim of the study was to determine the preferred prey for *A. brightwellii* in terms of fitness (evaluated as reproductive success) among five cladoceran, protozoan, and rotifer preys, and to test which temperature (20 or 25°C) is better for life table parameters of *Asplanchna*. Our analysis identified *Brachionus calyciflorus* as the preferred prey for *A. brightwellii* based on life table statistics, ingestion rate and electivity indices. The greatest values for net reproductive rate and intrinsic growth rate were achieved when *A. brightwellii* was fed *B. calyciflorus*. Greater reproductive values (R_o and r) were found at 25°C than at 20°C for *A. brightwellii* across the five prey species. We found significant differences in the ingestion rate and electivity index among zooplanktonic and benthic preys. The influence of temperature, the cost of predation, and how prey selection by *A. brightwellii* is influenced by: biomass, size, and swimming speed; they are discussed hoping to gain a better understanding of trophic transfers in zooplankton communities.

Keywords Predation costs · Aquatic ecology · Zooplankton ecology · Rotifer ecology · Invertebrate predation

G. E. Santos-Medrano · D. Robles-Vargas ·
S. Hernández-Flores · R. Rico-Martínez (✉)
Departamento de Química, Centro de Ciencias Básicas,
Universidad Autónoma de Aguascalientes, Avenida
Universidad 940, C.P. 20100 Aguascalientes, AGS,
Mexico
e-mail: rrico@correo.uaa.mx

Introduction

The Phylum Rotifera contains about 2,150 species (Dahms et al., 2011). This makes them one of the main zooplantonic components of freshwater ecosystems (Ramírez-Pérez et al., 2004). The rotifer *Asplanchna brightwellii* Gosse 1850, which belongs to the family Asplanchnidae (José de Paggi, 2002; Walsh et al., 2005), plays an important role in the nutrient dynamics of food webs through its predatory activity on protists (e.g., *Paramecium* and *Euglena*), rotifers (e.g., *Anuraeopsis*, *Brachionus*, *Keratella*), cladocerans, and ciliates (Sarma et al., 1998; Chang et al., 2010).

Asplanchna brightwellii reproduces mainly via parthenogenesis and is a viviparous and planktonic

species with worldwide distribution in eutrophic reservoirs (Gilbert, 1967; Walz, 1995; Walsh et al., 2005; Sarma et al., 2007; Guo et al., 2010). On occasion, this species reproduces sexually producing mictic eggs (or cysts) (José de Paggi, 2002). The sexuality and sexual reproduction of *A. brightwellii* is related to the concentration of α-tocopherol in the environment; this may act as predictor of favorable conditions for sexual reproduction such as high densities and adequate nutrition (Gilbert, 1980). The abundance of rotifers in natural waters is influenced by biotic and abiotic factors such as predation and temperature (Garza-Mouriño et al., 2005; Enríquez-García et al., 2009). Different strategies have been reported for avoiding predation from *Asplanchna*. These include rapid jumping movements, epizoic habits, and small size (Sarma & Nandini, 2007).

Dumont & Sarma (1995) analyzed the demography of *Asplanchna girodi* de Guerne, 1888 using *Anuraeopsis fissa* Gosse, 1851 as a prey species and concluded that survivorship parameters (e.g., mean lifespan and mean survivorship) were related to prey density. They also found that net reproductive rate and generation time, although not rate of population increase, were affected by prey abundance. Jiménez-Contreras et al. (2014) studied the demographic responses of *Asplanchna silvestrii* Daday, 1902 when cultured under five different light conditions using one prey species and two different prey densities; they found that regardless of prey density, the survivorship of *A. silvestrii* was affected mainly by photoperiod with the longest generation time being recorded when *A. silvestrii* was fed with a high prey density and kept in total darkness.

Prey ingestion in *A. brightwellii* has been studied from several perspectives. For example, Sarma (1993) offered *A. brightwellii* 16 different rotifer prey species from the genera *Anuraeopsis*, *Brachionus*, *Epiphanes*, *Filinia*, *Hexarthra*, *Lecane*, *Lepadella*, *Pompholyx*, *Proalides,* and *Trichocerca* and recorded their feeding responses (prey encounter, escape, capture, rejection, and ingestion). Later, Sarma et al. (2007) assessed the growth of *A. brightwellii* when fed with five different species of the genus *Brachionus*, mainly focusing on the relationship between spines on prey and consumption by the predator. Sarma & Nandini (2007) analyzed life table demography of *A. brightwellii* to test an ecological hypothesis of coexistence of small prey with large predators; for these studies, they used a

second predator species, *Asplanchna sieboldii* Leydig, 1854, and three prey species from the Family Brachionidae.

Temperature is an important factor whose importance is increasing due to concerns about global warming; climate change may have unexpected consequences because different species show unique responses to changes in environmental temperatures. An example is that increasingly warmer springs since 1962 have disrupted the trophic linkages between phytoplankton and zooplankton in Lake Washington (WA, USA) because of differing sensitivity to vernal warming (Winder & Schindler, 2004). Regarding studies in *Asplanchna*, photoperiod and temperature are important factors influencing prey consumption by *A. brightwellii* whose optimal temperature for prey consumption is 23°C (Guo et al., 2010). Pan et al. (2014) found that temperature affected significantly all the life table demographic parameters of *A. brightwellii* at four temperatures (16, 20, 24, and 28°C), but they only used one prey species; they found that depending on the life story parameter investigated, the best temperature would be 16, 20, or 24°C.

To date, there has been no work on rotifer predators where the emphasis of the life table experiments has been to find the best prey item in terms of influencing the life table variables of the predator. The intrinsic rate of increase, *r,* is the most widely used fitness measure in life history studies (Kozlowski, 1992). Green & Lan (1974) found *Brachionus calyciflorus* Pallas, 1766 to be the most eaten prey in an analysis of stomach content of 400 *A. brightwellii* specimens from a Javanese sewage pond. Sarma et al. (2003) stated that *B. calyciflorus* is the most common prey in many freshwater reservoirs. *A. sieboldii* has been shown to prefer *B. calyciflorus* and *Brachionus patulus* Pallas, 1766 as prey items over *Brachionus havanaensis* Rousselet 1911, and *Brachionus rubens* Ehrenberg 1838 (Nandini et al., 2003). A search of the mainstream scientific literature suggested that *B. calyciflorus* could be the preferred prey item for *A. brightwellii* because it is a planktonic species (and therefore, easy to capture and handle), and has been widely mentioned as a common prey of *A. brightwellii*. Therefore, the aim of this study was to explore the influence of two temperatures and five prey items of different species [one cladoceran, two rotifers, and two protozoans of different sizes and belonging to different communities (benthic and planktonic)], on

the life table demography of *A. brightwellii* to answer the question of what is the preferred prey item in terms of fitness for *A. brightwellii*. Our hypotheses were: (a) that *B. calyciflorus* would be the preferred prey item for *A. brightwellii* in terms of reproductive success (i.e., that the highest R_o and r values would be reached by *A. brightwellii* when fed with *B. calyciflorus*), (b) at 25°C most of the reproductive parameters of *A. brightwellii* would be higher than at 20°C.

Materials and methods

Life table experiments

The predatory rotifer *A. brightwellii* was collected at La Mezquitera, Aguascalientes (N 21.54545, W 102.19155). The species was grown in the laboratory for at least six months prior to experiments being undertaken. They were cultured in EPA medium (U.S.EPA, 1985) and fed five different prey items: (a) the benthic cladoceran *Alona guttata*, Sars 1862 (b) the planktonic protozoa *Paramecium bursaria* Ehrenberg 1836 and *Paramecium caudatum* Ehrenberg 1833, and (c) the rotifers *B. calyciflorus* (planktonic) and *Lecane papuana* Murray 1913 (benthic). We also studied the effect of two different temperatures (20 and 25°C) on ingestion at a prey density of 5 prey ml^{-1}.

Prey items were added daily to maintain the original prey density throughout the experiment. The life table started with the collection of asexual females of *A. brightwellii*. We observed the mothers every 2 h and assigned a mean value of 1 h to every individual born within each 2-h period until we collected 16 individuals. All mothers were acclimated to the relevant experimental temperature for at least 48 h before each experiment. All neonates came from different mothers, and were transferred to individual wells of a 24-well polystyrene plate (Corning®); these were incubated at the appropriate temperature in the dark. The total volume in each well was 2 ml. Sixteen individuals were studied at 25 or 20°C. Individuals were observed every 24 h and their neonates were counted and removed from the well. Instead of changing the original individuals to new wells with fresh food (a procedure that damages this species), half of the medium was replaced by fresh medium every 24 h.

The following parameters were analyzed: the number of 24-h intervals (x; days), mean duration of lifespan (D; h), mean generation time (G; h), net reproductive rate (R_o), and life expectancy (e_x; h). All these parameters were determined according to Krebs (1985). Reproductive value (V_x), mean generation time (G), net reproductive rate (R_o), and intrinsic growth rate (r) were calculated according to Krebs (1985) and Begon et al. (1996), using the following formulae:

$$\text{Survivorship}(l_x) = n_x/16$$
$$\times \, (\text{number of individuals per day})$$

$$\text{Mean fecundity}(m_x) = l_x/n_x$$
$$\times \, (\text{number of neonate rotifers produced per day})$$

$$\text{Reproductive value}(V_x) = l_x m_x$$

$$\text{Net reproductive rate}(R_o) = \sum (l_x m_x)$$

$$\text{Mean generation time}\,(G) = \sum \frac{(x l_x m_x)}{R_o}$$

$$\text{Intrinsic growth rate}\,(r) = \ln \frac{[n_{t_2} - n_{t_1}]}{(t_2 - t_1)},$$

where ln is the natural logarithm, n_x is number of individuals at time x, t_1 is time 1 in days, t_2 is the time 2 in days.

Ingestion rate

The test began by separating *A. brightwellii* into individual wells and starving them for 8 h at 25°C. Then, each *A. brightwellii* was placed in a well with the respective prey species at a concentration of 5 prey ml^{-1}, or 2.5 prey ml^{-1} in the case of *A. guttata*, in a total volume of 2 ml of EPA medium. After 30 min, all *A. brightwellii* individuals were removed and the number of live prey remaining in each well was counted. Experiments were repeated with each of the five prey species.

The ingestion rate (*IR*) (number of prey ingested in 30 min) of *A. brightwellii* was calculated as follows:

$$\text{IR} = \frac{P_i - P_f}{t}, \quad (\text{Castilho-Noll and Arcifa, 2007})$$

where t is the time (30 min), P_i is average number of prey at the beginning of the experiment, P_f is the average number of prey at the end of the experiment.

Electivity index

For prey dietary preferences, we used two different prey densities: (a) low density (15 prey ml^{-1}), distributed as follows: 10 individuals of each prey species except *A. guttata* (only 5 individuals per 3 ml), (b) high density (30 prey ml^{-1}) with the double that number of each prey species in 3 ml. The experiment consisted of 12 petri dishes: two prey densities, and six replicates for each prey item and density. In each petri dish, we placed one *A. brightwellii* pre-starved for 8 h. The petri dishes were placed in a bioclimatic chamber at 25°C and allowed to feed for 30 min. At the end of this period, *Asplanchna* was removed and the number of live prey remaining was recorded. Prey selectivity (*E*) was calculated using Ivlev's electivity index (Ivlev, 1961) as follows:

$$E = \frac{r - p}{r + p},$$

where *r* is the number of prey ingested by the predator, *p* is proportion of the food item remaining at the end of the experiment.

For *E*, values between −1 and 0 indicate negative selectivity and values between 0 and 1 indicate that the item had been selected.

Biomass determination

The dry weight of the six species of organisms was measured according to the protocol of Widbon (1984). Briefly, this method consisted of weighing 300 adult females of *A. brightwellii* (*n* = 2), 100 non-ovigerous adult females of *A. guttata*, 400 non-ovigerous adult females of *B. calyciflorus*, 350 non-ovigerous adult females of *L. papuana*, 8,000 individuals of *P. bursaria*, and 10,000 individuals of *P. caudatum* for each replicate (*n* = 5, except for *A. brightwellii*). The animals were weighed in small aluminum foil bowls of about 400 mg. Before weighing, each sample was rinsed carefully in double-distilled water and placed in the aluminum bowl using a pipette, together with a few drops of deionized water. The samples were dried at 60°C for about 12 h in a Fisher Scientific, Isotemp® 500 Series oven, cooled at room temperature (22°C) in a desiccator and weighed on two analytical balances (Chyo JK-200 and ADA 120/L) to determine the dry weight. Each sample was weighed twice and the average weight was noted. On each occasion, six to eight samples were processed simultaneously together with three control bowls, to which only the same amount of deionized water had been added. The dry weight thus obtained was divided by the number of organisms in the sample to calculate the average individual dry weight.

Speed measurements

To assess the speed of the organisms, we used the method proposed by Santos-Medrano et al. (2001) with slight modifications. We recorded movement of 10 different females with a Moticam 2300 camera attached to a microscope at ×50 magnification for several minutes in a 100 µl chamber. Then, the video was replayed with a clear acetate sheet taped to the monitor and the swimming path of a rotifer was traced for 10 s. A software INFINITY ANALYZE v 4.6 software was used to measure the length of the path traveled.

Morphometric measurements

For the size determinations, 10 images of each organism were captured with a Moticam 2300 camera attached to a microscope (Olympus) at ×20 magnification. Measurements were performed with Motic software Image Plus 2.0.

Statistical analysis

All of the statistical analyses were undertaken using the Statistica 7.0 (Statsoft Inc., 2004). To estimate the variability of life table statistics, 10,000 repetitions with bootstrap technique (XLSTAT 5.03 software) were used. These repetitions represent a good measure of the variability found in the actual replicates (*N* = 16). Levene's test for homogeneity of variance was significant, so we used non-parametric tests (Mann–Whitney *U* tests) to compare treatments. The data recorded in this study were examined using normalized principal component analysis (PCA). A simple $\log(x + 1)$ transformation was applied to stabilize the variance (Frontier, 1973). Pearson's Correlation Analysis was performed to select those variables with relevant levels of statistical significance (>0.75) in comparison to R_o. The Pearson's correlation matrix of all variables obtained in this work is included in Supplementary Table 1.

Results

Results from the life table demographic analysis of *A. brightwellii* fed with five different prey items are shown in Table 1. The greatest lifespan value (D) was obtained at 25°C when *A. brightwellii* was fed *B. calyciflorus*. However, the second to fourth greatest values for *D* were found at 20°C. The lowest *D* value was at 25°C when *Asplanchna* was fed *L. papuana*. The shortest mean generation time (*G*) corresponds to *Asplanchna* being fed with *Alona guttata* at 25°C, while the longest *G* was obtained when *A. brightwellii* was fed with *B. calyciflorus* at 25°C. The greatest values for net reproductive index (R_o) and intrinsic growth rate (*r*) were for *A. brightwellii* fed with *B. calyciflorus* at 25 and 20°C (Table 1). These initial results show that *B. calyciflorus* consumption resulted in the best reproductive performance of *A. brightwellii*. *P. bursaria* came as a distant second place in terms of best reproductive performance for *A. brightwellii* eating this species as prey for *A. brightwellii*, followed for *P. caudatum*, *L. papuana*, and then *A. guttata* (which produced negative *r* values in *A. brightwellii*). In general, slightly higher reproductive performance results were obtained at 25°C than at 20°C for *A. brightwellii* across the five different prey species.

A principal component analysis (PCA) was performed to analyze the hidden components among the data, and because a homoscedasticity test was negative. We started the analysis by comparing two variables, i.e., lifespan (*D*) and R_o (the average number of neonates for an individual in its life cycle). We found that R_o was the best parameter for evaluating the reproductive success of *A. brightwellii* when fed different prey species. The PCA is presented in Fig. 1a for 20°C and Fig. 1b for 25°C. Figure 1a clearly shows that *P. bursaria* is a good food for *A. brightwellii* at 20°C and influences several performance parameters of its predator, such as IR (best result), *G* (second best), *r* low (second best), and R_o (second best). Also in Fig. 1a, *B. calyciflorus* as prey influenced all variables selected for the analysis, but mainly *E* high, *r* high, V_x, *E* low, *D*, and e_x where the results of these parameters for *A. brightwellii* at 20°C are the highest. The same variables also influence *P. caudatum*. For two species, *A. guttata*, and *L. papuana*, there is little correlation with the parameters included in Fig. 1a. Figure 1b clearly shows that *B. calyciflorus* as prey influences several variables such as V_x, R_o, *E* low, *D*, and e_x, where the results of these parameters for *A. brightwellii* at 25°C are the ones that give the highest reproductive values; it also influences other variables with less significance like: *E* high, *r* high, *G*, and *r* low, where the results of these parameters for *B. calyciflorus* offered as prey to *A. brightwellii* at 25°C are also the ones that gives the

Table 1 Life table parameters for the rotifer *A. brightwellii*

Prey species	*D* (h)	*G* (h)	R_o	*r* low (d)	*r* high (d)
20°C					
A. guttata	88.50 ± 8.95	45.08 ± 3.43	0.42 ± 0.02	−0.21	−0.21
B. calyciflorus	136.50 ± 15.67	103.89 ± 3.42	4.75 ± 0.19	1.96 ± 0.12	2.95 ± 0.12
P. bursaria	100.50 ± 5.46	100.16 ± 6.09	1.72 ± 0.13	1.41 ± 0.07	0.81 ± 0.27
P. caudatum	117 ± 11.77	66.14 ± 2.54	1.18 ± 0.04	1.21 ± 0.15	1.85 ± 0.12
L. papuana	109.50 ± 6.56	70.82 ± 4.44	1.11 ± 0.07	0.69 ± 0.13	−0.21
25°C					
A. guttata	70.50 ± 6.25	31.56 ± 2.59	0.29 ± 0.03	−0.21	−0.21
B. calyciflorus	213 ± 13.30	116.84 ± 2.18	7.13 ± 0.14	1.98 ± 0.08	2.68 ± 0.01
P. bursaria	97.33 ± 6.57	74.40 ± 4.24	0.56 ± 0.03	0.91 ± 0.08	1.09 ± 0.09
P. caudatum	81 ± 4.83	41.18 ± 4.02	1.33 ± 0.12	0.12 ± 0.01	0.71 ± 0.09
L. papuana	67.50 ± 5.46	32.35 ± 3.00	0.27 ± 0.03	0.14 ± 0.28	−0.21

Values are the mean ± standard error $N = 16$. Bootstrap was performed and set at 10,000 re-samples. The bootstrap values are not shown but are very similar to actual values. *h* hour, *d* day

Abbreviations correspond to: mean lifespan (*D*), mean generation time (*G*), intrinsic growth rate (*r*), and net reproductive index (R_o)
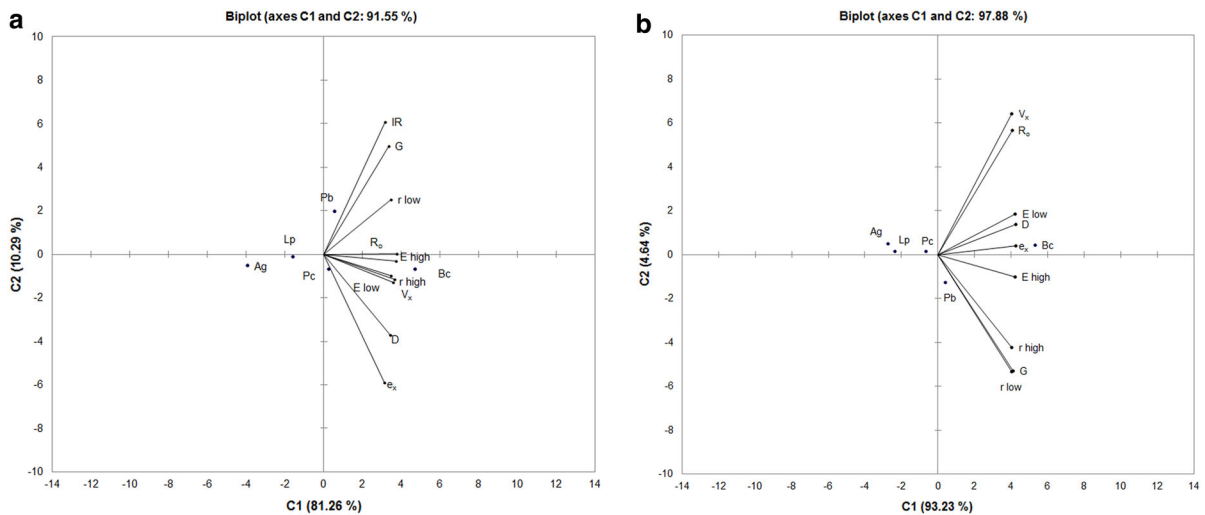
Fig. 1 Principal Component Analysis of variables best correlated with R_o ($P \geq 0.75$). *1a* is the analysis at 20°C and *1b* corresponds to 25°C. Abbreviations are: *G* mean generation time (h); R_o net growth rate; e_x life expectancy; *D* mean lifespan (h); V_x reproductive value; *E low* electivity index at low prey density; *E high* electivity index at high prey density; *r low*

intrinsic growth rate at low prey density (individuals days^{-1}); *r high* intrinsic growth rate at high prey density (individuals days^{-1}); *IR* ingestion rate (prey eaten min^{-1}). *Ag*, *Alona guttata*; *Bc*, *Brachionus calyciflorus*; *Lp*, *Lecane papuana*; *Pb*, *Paramecium bursaria*; *Pc*, *Paramecium caudatum*

highest reproductive values. For three species: *A. guttata*, *L. papuana*, and *P. caudatum,* there is very little correlation with the parameters included in Fig. 1b.

A more detailed analysis of the main *A. brightwellii* demographic parameters in relation to daily changes is shown in Fig. 2. The highest reproductive values (V_x) correspond to *A. brightwellii* fed with *B. calyciflorus* after 72 h, irrespective of temperature, while the lowest V_x values are those of *A. guttata*, in agreement with the values found in Table 1. Life expectancy (e_x) values are greatest when *A. brightwellii* is fed on *B. calyciflorus* at 25 and 20°C, respectively, followed by *A. brightwellii* fed on *P. bursaria* at 25°C. Perhaps the most relevant difference for the predator regarding the influence of temperature, and prey item is observed in the survivorship curve at 25°C (Fig. 2). When *A. brightwellii* is fed *B. calyciflorus* at 25°C, survivorship increases substantially in comparison with all other treatments. In fact, after 144 h, all *A. brightwellii* fed with other prey items are dead, *A. brightwellii* fed with *B. calyciflorus* continues to survive up to 288 h (Fig. 2). During the life table analysis, we recorded the presence of *A. brightwellii* males in a few treatments: (a) when fed *B. calyciflorus* at 20°C (6.57%) and 25°C (5.98%), (b) when fed *P. bursaria* at 25°C (25%).

We obtained the size, dry weight, and swimming speed of *A. brightwellii* and the five prey species to determine if they have an influence on prey choice and demography of *A. brightwellii* (Table 2). Two replicates were obtained for *A. brightwellii* dry weight, and the values were found to be similar to that obtained by Dumont et al. (1975). Dry weight was important to design the experiments and compare *A. brightwellii* consumption among the prey items. As expected, the *A. brightwellii* with a maximum length of 563 μm is the largest species followed by the cladoceran *A. guttata* with a maximum length of over 376 μm. The two protozoans and rotifer species were all less than 200 μm in length (Table 2). Regarding dry weight, *A. guttata* is heavier than *A. brightwellii*, which is slightly heavier than *B. calyciflorus*. The presence of a thick shell in *A. guttata* probably explains its higher weight compared to *A. brightwellii*, even though *A. brightwellii* was the longest animal used in this work. An analysis of swimming speed shows that *P. bursaria* is the fastest swimmer in terms of both absolute speed (mm s^{-1}) and relative speed (body lengths s^{-1}) (Table 2).

The results of the ingestion rate experiment (Fig. 3) show that *A. brightwellii* fed with *P. bursaria* had a
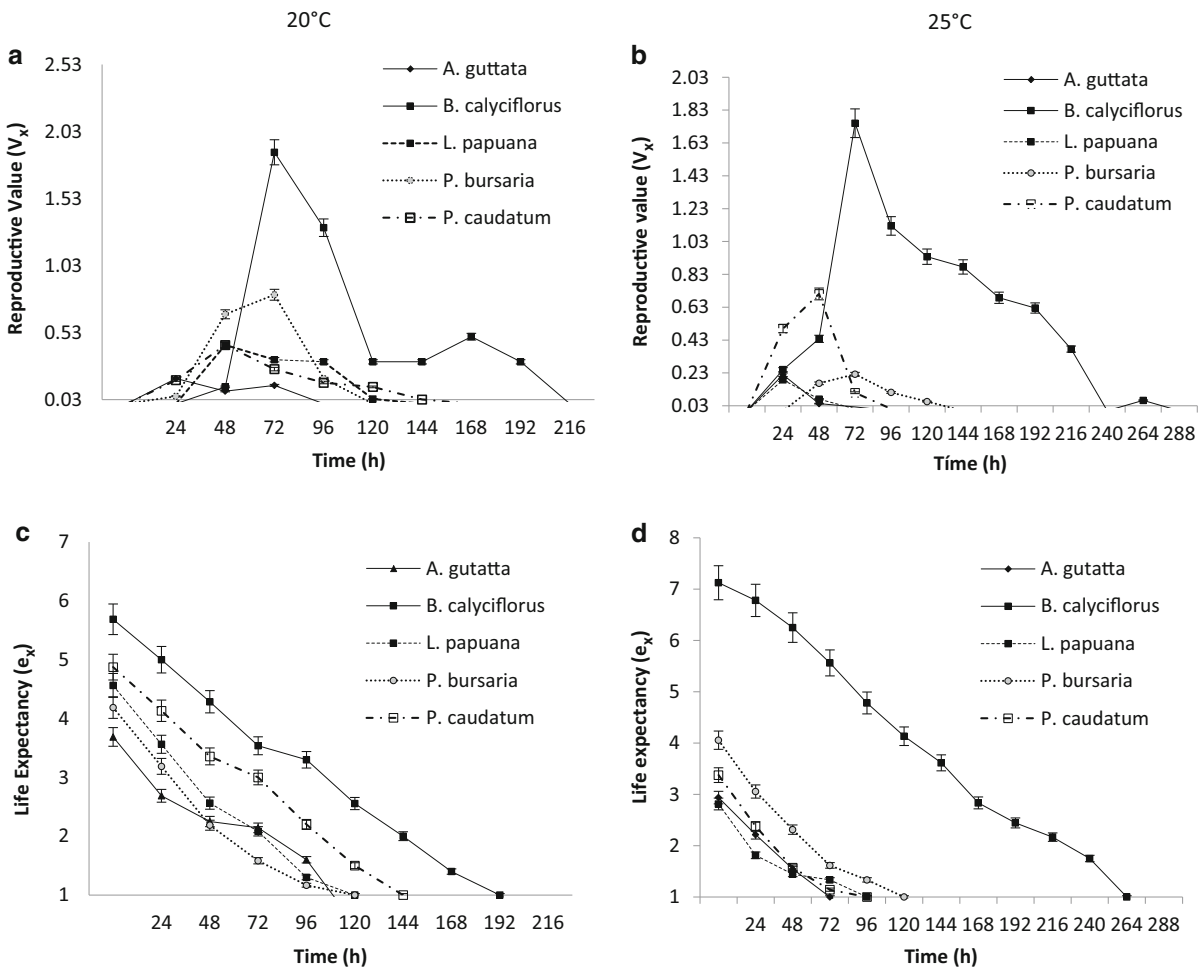
Fig. 2 Reproductive value (V_x) and life expectancy (e_x) of *A. brightwellii* fed with five different prey items. Mean and one standard error are shown ($N = 16$)

Table 2 Morphometric characteristics and swimming speed of the different organisms used in this work

Parameters	A. brightwellii	A. guttata	B. calyciflorus	L. papuana	P. bursaria	P. caudatum
ML (μm)	563.62 ± 65.85	376.01 ± 42.13	181.13 ± 25.82	113.13 ± 4.92	127.32 ± 7.68	171.50 ± 14.89
MW (μm)	273.61 ± 37.10	229.26 ± 29.39	131.34 ± 14.45	94.34 ± 3.05	56.43 ± 7.95	48.40 ± 5.53
DW (μg ind^{-1})	1.75 ± 0.35	4.2 ± 0.83	1.37 ± 0.44	0.68 ± 0.17	0.16 ± 0.02	0.18 ± 0.01
SS (mm s^{-1})	0.99 ± 0.27	1.61 ± 0.36	0.77 ± 0.21	0.63 ± 0.07	1.78 ± 0.23	1.03 ± 0.27
SSBL (s^{-1})	1.76 ± 0.51	4.28 ± 1.19	4.25 ± 1.42	5.57 ± 0.67	14.01 ± 1.76	5.9 ± 1.97

Abbreviations are: Maximum Length (ML), $N = 20$; maximum width (MW), $N = 20$; dry weight (DW), $N = 5$ except for *A. brightwellii* where $N = 2$; swimming speed (SS) as mm s^{-1} and swimming speed in terms of body length s^{-1} (SSBL), $N = 10$; Values are mean ± one SD

higher ingestion rate (IR) than those fed with *B. calyciflorus* in terms of individuals ingested per 24 h period (Fig. 3a). However, in terms of dry weight, *A. brightwellii* fed with *B. calyciflorus* had a higher IR

value than those fed with any other prey species (Fig. 3b). This result is consistent with the better performance in demographic terms of *A. brightwellii* fed with *B. calyciflorus* and *A. guttata* (Table 1). This
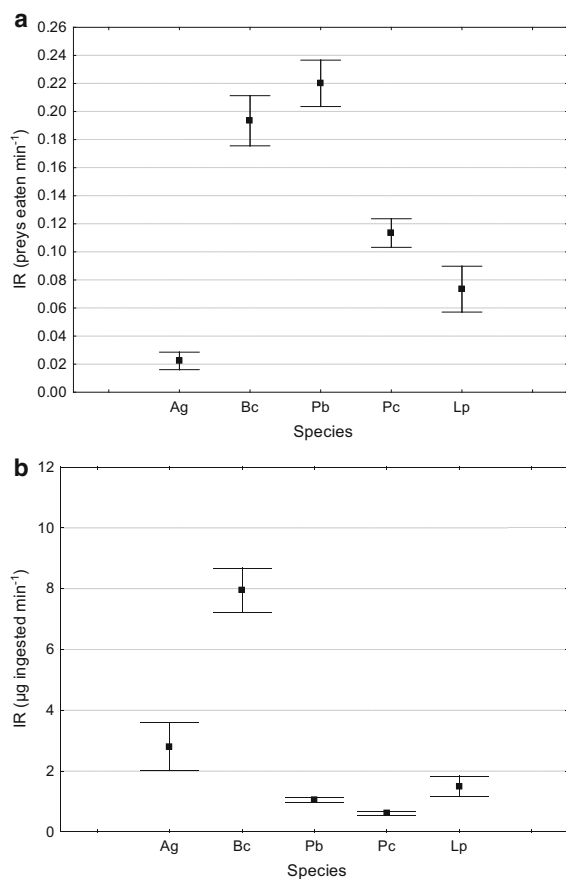
Fig. 3 Ingestion rate (IR) of *A. brightwellii* feed separately with five different prey items. Mean ± standard error; *N* = 15. **a** Results in terms of individuals ingested (preys eaten min^{-1}), **b** Results in terms of dry weight ingested (μg ingested min^{-1}). Species names are abbreviated as follows: *Ag*, *Alona guttata*; *Bc*, *Brachionus calyciflorus*; *Pb*, *Paramecium bursaria*; *Pc*, *Paramecium caudadum*; *Lp*, *Lecane papuana*

suggests that dry weight (hence biomass) is one of the driving forces influencing prey choice of *A. brightwellii*.

The results of the Electivity Index (*E*) experiment are shown in Fig. 4. There was almost no significant difference between low- and high-density experiments (ANOVA, *P* < 0.05). When a mixed group of prey was offered to *A. brightwellii*, there was a clear preference for *B. calyciflorus* at both low and high densities over all other species (Fig. 4). There was no significant difference between *B. calyciflorus* at low and high densities for this experiment. The second preference was for both of the *Paramecium* species at the lower density and for *P. bursaria* at the higher density. *A. guttata* and *L. papuana* were least preferred at both prey densities (Fig. 4).
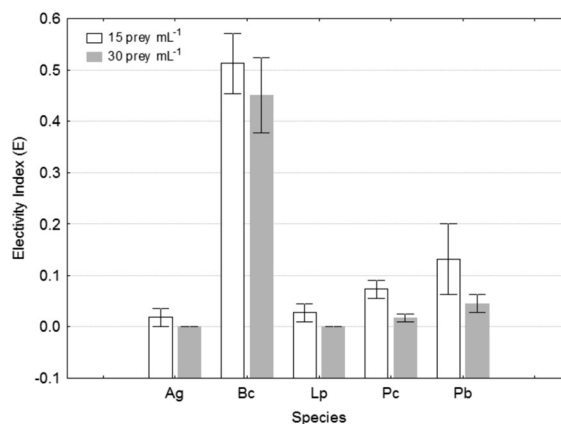

Fig. 4 Electivity Index (*E*) of *A. brightwellii* on five prey items at two food densities. *Bar* corresponds to mean values. *Vertical lines on bars* indicate one standard error *N* = 6. Species are abbreviated as follows: *Ag*, *Alona guttata*; *Bc*, *Brachionus calyciflorus*; *Pb*, *Paramecium bursaria*; *Pc*, *Paramecium caudadum*; *Lp*, *Lecane papuana*

Discussion

The demographic analysis (highlighted by the PCA results), the ingestion rate (when based on dry weight), and the Electivity Indices suggest that *B. calyciflorus* is the preferred prey for *A. brightwellii*. The results of the ingestion rate experiment based on dry weight suggest that this may be because *B. calyciflorus* is a good quality food for *A. brightwellii*. The results of the Electivity Index experiments suggest that *B. calyciflorus* being the slowest prey might also make it easier to catch. Results of the Electivity Index (*E*) showed that the two species with the lowest *E* values were *A. guttata* and *L. papuana*, the only benthic prey species. These results suggest that planktonic prey species are selected over benthic ones.

When we explored whether 25°C was a better temperature than 20°C for *B. calyciflorus*, we found significant differences for *D*, but not for R_o, V_x, and e_x (Table 3). When we explored whether *B. calyciflorus* at 20 or 25°C was the best prey item for *A. brightwellii*, the answer was inconclusive. At 20°C there are almost no significant differences among parameters and species (Table 3). However, at 25°C, we found significant differences from *A. guttata* and *L. papuana* in all four parameters (*D*, R_o, V_x, and e_x) (Table 3). In the case of *P. bursaria*, there were significant differences in *D* and V_x and nearly significant for R_o and e_x (*P* = 0.06 and *P* = 0.07, respectively) (Table 3).

Table 3 Comparisons of *Brachionus calyciflorus* (Bc) as a prey for *Asplanchna brightwellii* compared to (*cf.*) other prey species offered using the Mann–Whitney *U* non-parametric test

Prey species	Temperature (°C)	D	R_o	e_x	V_x
Mann–Whitney *U* non-parametric test					
Ag *cf.* Bc	20	**0.015**	**0.06**	0.31	**0.028**
Pb *cf.* Bc	20	0.56	0.48	0.25	0.19
Pc *cf.* Bc	20	0.25	0.32	0.68	0.16
Lp *cf.* Bc	20	0.14	0.43	0.52	0.16
Ag *cf.* Bc	25–20	**0.001**	**0.05**	**0.05**	**0.01**
Pb *cf.* Bc	25–20	**0.03**	**0.10**	0.25	**0.02**
Pc *cf.* Bc	25–20	**0.004**	0.57	0.17	0.06
Lp *cf.* Bc	25–20	**0.006**	**0.08**	**0.10**	**0.01**
Ag *cf.* Bc	25	**0.001**	**0.01**	**0.01**	**0.001**
Pb *cf.* Bc	25	**0.0001**	0.06	0.07	**0.003**
Pc *cf.* Bc	25	**0.0001**	0.27	**0.04**	**0.01**
Lp *cf.* Bc	25	**0.0001**	**0.03**	**0.02**	**0.001**
Ag *cf.* Bc	20–25	**0.0001**	**0.02**	0.06	**0.006**
Pb *cf.* Bc	20–25	**0.0001**	0.18	0.09	**0.04**
Pc *cf.* Bc	20–25	**0.0001**	0.10	0.28	**0.04**
Lp *cf.* Bc	20–25	**0.0001**	0.08	0.12	**0.02**
Bc *cf.* Bc	20–25	**0.002**	0.57	0.40	0.56

Probability values are reported for each comparison. Abbreviations are: *Alona gutatta* (Ag); *Lecane papuana* (Lp); *Paramecium bursaria* (Pb); *Paramecium caudatum* (Pc). Values in bold correspond to significant differences ($P < 0.05$)

Finally, for *P. caudatum,* there were significant differences on D, e_x, and V_x (Table 3). Therefore, these tests at least partially support our hypothesis that *B. calyciflorus* was the preferred prey item for *A. brightwellii* in terms of reproductive performance at 25°C from our analysis of life table experiments and that perhaps the lack of homogeneous variance in the data did not allow to find significant differences regarding R_o (in two cases), the variable most closely related to reproductive success from our point of view. Pan et al. (2014) also found heterogeneity in their results about correlations between temperature in the range of 16–28°C and reproductive parameters: lifespan, life expectancy, and mean generation time were higher at 16°C, whereas R_o and *r* were higher at 20°C. High positive correlations were found between ingestion rate (IR) and the demographic parameters of the life table experiment (D, G, R_o, and *r*) at both 20 and 25°C (Fig. 1a, b). Correlations were slightly higher at 25°C than at 20°C. Sarma (1993) also found *A. brightwellii* ingestion time was positively correlated with prey length. However, we found significant negative correlations between Electivity Index (*E*) (at low and high densities, respectively) and maximum length ($P < 0.001$). It seems likely that the longer animals are more difficult for *A. brightwellii* to handle, which increases energetic predation costs. Prey size

has been shown to explain patterns of predation in zooplanktonic communities (Brooks & Dodson, 1965). Predator success is highly correlated ($r^2 = 0.81$) with prey size when the copepod *Diaptomus pallidus* was offered seven rotifer preys (Williamson, 1987). Our results seem to agree with the results of both Brooks & Dodson (1965) and Williamson (1987).

Low encounter rates were suggested as the most likely explanation for *Asplanchna girodi* being unable to survive at 100 ind. ml^{-1} of the rotifer prey *Anuraeopsis fissa* (Dumont & Sarma, 1995). In our work, we too found significant differences between Electivity Index estimates at low and high densities ($P = 0.04$). However, our experiments lasted only 30 min, whereas Dumont & Sarma (1995) made observations every 12 h. Therefore, our results partially agree with those of Dumont & Sarma (1995) reflecting a better performance of the predator in presence of higher prey density. However, the difference in the experiment protocols means that we are unable to establish a density prey threshold to compare with the results of these authors. Jíménez-Contreras et al. (2014) found that high prey density was a significant factor increasing *r* in *Asplanchna silvestrii*; this agrees with the results of our work.

We found negative correlations between *A. brightwellii* IR and the swimming speed (both in

mm s^{-1} and body lengths s^{-1}) at low and high densities ($P < 0.05$). This is probably related to the escape response of the prey, with *B. calciflorus* being the slowest prey and probably the easiest to catch by *A. brightwellii*. Unfortunately, we did not analyze escape response or the different stages of prey capture and consumption as other authors have done in the past (Williamson, 1987). Therefore, this assumption cannot be proven.

Negative correlations were also found between IR, *E*, and dry weight (Table 3). These correlations might be explained, in part, by the presence of a hard shell in *A. guttata* (the heaviest prey). However, *L. papuana* (with a relatively hard lorica) was the lightest of all prey and yet had the second lowest *E*. Therefore, other factors besides lorica hardness and dry weight explain the *E* results.

In our experiments with starved *A. brightwellii*, IR ranged from 0 to 10 prey hour^{-1} for the five prey species; these data are in good agreement with those of Sanders & Wickham (1993) who recorded an IR for *A. brightwellii* of 1–5 prey hour^{-1}.

Dry weight calculations are important because they help determine metabolic and physiologic processes (Dumont et al., 1975). Our results (which include dry weight determinations) allow a better understanding of trophic transfers in zooplankton communities, since dry weight is considered in calculations of the ingestion rate and is of particular importance in terms of aquatic toxicology since lead can be biomagnified in food webs whose top predators are invertebrates like *Asplanchna* (Rubio-Franchini et al., 2008; Rubio-Franchini & Rico-Martínez, 2011). Predator–prey dynamics are related to biomass changes (Persson et al., 2001) and to food requirements and population growth rate (Stemberger & Gilbert, 1984); in both cases, dry weight determination can be important to obtain better models for relating body size and energetics to predation (Chi & Forrest, 2015).

In conclusion, *A. brightwellii* is a predatory species that feeds selectively when offered five different prey types belonging to three different taxa (cladocerans, protozoans, and rotifers) at the same time. The demographic parameters measured (ingestion rate and Electivity Index) suggest that *A. brightwellii* prefers *B. calciflorus* as its prey. There is also a preference for zooplankton over benthic prey species. Few differences were observed when demographic experiments were conducted at 20 or 25°C. The results

of our analysis of ingestion rate in relation to dry weight suggest that dry weight of prey should be included in future discussions of ingestion rate and life table parameters.

References

Begon, M., J. L. Harper & C. P. Townsend, 1996. Ecology: Individuals, Populations, and Communities, 3rd ed. Blackwell Scientific, Oxford.

Brooks, J. L. & S. I. Dodson, 1965. Predation, body size, and composition of plankton. Science 150: 28–35.

Castilho-Noll, M. S. M. & M. S. Arcifa, 2007. *Chaoborus* diet in a tropical lake and predation of microcrustaceans in laboratory experiments. Acta Limnologica Brasiliensia 19: 163–174.

Chang, K. H., H. Doi, Y. Nishibe & S. Nakano, 2010. Feeding habits of omnivorous *Asplanchna*: comparison of diet composition among *Asplanchna herricki*, *A. priodonta* and *A. girodi* in pond ecosystems. Journal of Limnology 69: 209–216.

Chi, S. & S. B. Forrest, 2015. Linking body size and energetics with predation strategies: a game theoretic modeling framework. Ecological Modeling 316: 81–86.

Dahms, H. U., A. Hagiwara & J. S. Lee, 2011. Ecotoxicology, ecophysiology, and mechanistic studies with rotifers. Aquatic Toxicology 101: 1–12.

Dumont, H. J. & S. S. S. Sarma, 1995. Demography and population growth of *Asplanchna girodi* (Rotifera) as a function of prey (*Anuraeopsis fissa*) density. Hydrobiologia 306: 97–107.

Dumont, H. J., I. Van de Velde & S. Dumont, 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. Oecologia 19: 75–97.

Enríquez-García, C., S. Nandini & S. S. S. Sarma, 2009. Seasonal dynamics of zooplankton in Lake Huetzalin, Xochimilco (Mexico City, Mexico). Limnologica 39: 283–291.

Frontier, S., 1973. Etude statistique de la dispersion du zooplancton. Journal of Experimental Marine Biology and Ecology 12: 229–262.

Garza-Muriño, G., M. Silva-Briano, S. Nandini, S. S. S. Sarma & M. E. Castellanos-Páez, 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 516: 169–179.

Gilbert, J. J., 1967. Control of sexuality in the rotifer *Asplanchna brightwellii* by dietary lipids of plant origin. Proceedings of the Natural Academy of Sciences of the United States of America 57: 1218–1225.

Gilbert, J. J., 1980. Female polymorphism and sexual reproduction in the rotifer *Asplanchna*: evolution of their relationship and control by dietary alpha-tocopherol. American Naturalist 116: 409–431.

Green, J. & O. B. Lan, 1974. *Asplanchna* and the spines of *Brachionus calciflorus* in two Javanese sewage ponds. Freshwater Biology 4: 223–226.

Guo, R., T. W. Snell & J. Yang, 2010. Studies of the effect of environmental factors on the rotifer predator-prey system in freshwater. Hydrobiologia 655: 49–60.

Ivlev, V. S., 1961. Experimental Ecology of the Feeding of Fishes. Yale University Press, New Haven, CT.

de Paggi, J., 2002. Guides to the identification of the Microinvertebrates of the Continental Waters of the World. Rotifera. Volumen 6: Asplanchnidae, Gastropodidae, Lindiidae, Microcodidae, Synchaetidae, Trochosphaeridae and Filinia. Backhuys Publishers, Leiden.

Jíménez-Contreras, J., S. S. S. Sarma, S. Nandini & A. Urquieta-Ordoñez, 2014. Effect of circadian cycle and prey density on the demography of the predator *Asplanchna silvestrii* (Rotifera). International Review of Hydrobiology 99: 133–140.

Krebs, C. J., 1985. Ecología: Estudio de la distribución y la abundancia, 2ª. Edición. Ed. Harla. México D.F., México

Kozlowski, J., 1992. Optimal allocation of resources to growth and reproduction: implication for age and size at maturity. Trends in Ecology and Evolution 7: 15–19.

Nandini, S., R. Pérez-Chávez & S. S. S. Sarma, 2003. The effect of prey morphology on the feeding behavior and population growth of the predatory rotifer *Asplanchna sieboldii*: a case study using five species of *Brachionus* (Rotifera). Freshwater Biology 48: 2131–2140.

Pan, L., X. Yi-Long, C. Hong-Yuan, B. Peng & W. Jin-Xia, 2014. Combined effects of temperature and prey (*Brachionus angularis*) density on life table demography and population growth of *Asplanchna brightwelli* (Rotifera). Annales de Limnologie – International Journal of Limnology 50: 261–268.

Persson, A., H. Lars-Anders, C. Brönmark, P. Lundberg, L. B. Pettersson, L. Greenberg, P. A. Nilsson, P. Nyström, P. Romare & L. Tranvik, 2001. Effects of enrichment on simple aquatic food webs. The American Naturalist 157: 654–669.

Ramírez-Pérez, T., S. S. S. Sarma & S. Nandini, 2004. Effects of mercury on the life table demography of the Rotifer *Brachionus calyciflorus* Pallas (Rotifera). Ecotoxicology 13: 535–544.

Rubio-Franchini, I., J. S. Mejía & R. Rico-Martínez, 2008. Determination of lead in samples of zooplankton, water, and sediments in a Mexican reservoir: evidence for lead biomagnification? Environmental Toxicology 23: 459–465.

Rubio-Franchini, I. & R. Rico-Martínez, 2011. Evidence of lead biomagnification in invertebrate predators from laboratory and field experiments. Environmental Pollution 159: 1831–1835.

Sanders, R. W. & S. A. Wickham, 1993. Plantonic protozoa and metazoa: predation, food quality and population control. Marine Microbial Food Webs 7: 197–223.

Santos-Medrano, G. E., R. Rico-Martínez & C. A. Velázquez-Rojas, 2001. Swimming speed and Reynolds numbers of eleven freshwater rotifer species. Hydrobiologia 446(447): 35–38.

Sarma, S. S. S., 1993. Feeding responses of *Asplanchna brightwellii* (rotifera): laboratory and field studies. Hydrobiologia 255(256): 275–282.

Sarma, S. S. S., S. Nandini & H. J. Dumont, 1998. Feeding preference and population growth of *Asplanchna brightwelli* (Rotifera) offered two non-evasive prey rotifers. Hydrobiologia 361: 77–87.

Sarma, S. S. S., E. L. Pavón-Meza & S. Nandini, 2003. Comparative population growth and life table demography of the rotifer *Asplanchna girodi* at different prey (*Brachionus calyciflorus* and *Brachionus havanaensis*) (Rotifera) densities. Hydrobiologia 491: 309–320.

Sarma, S. S. S. & S. Nandini, 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.

Sarma, S. S. S., G. García-Martínez & S. Nandini, 2007. Population growth of *Asplanchna brightwellii* (Rotifera) fed prey species having different morphological defenses. Journal of Freshwater Ecology 22: 667–676.

Stemberger, R. S. & J. J. Gilbert, 1984. Body size, ration level, and population growth in *Asplanchna*. Oecologia 64: 355–359.

Walsh, E. J., R. L. Wallace & R. J. Shiel, 2005. Toward a better understanding of the phylogeny of the Asplanchnidae (Rotifera). Hydrobiologia 546: 71–80.

Walz, N., 1995. Rotifer populations in plankton communities: energetics and life history strategies. Experientia 51: 437–453.

Widbon, B., 1984. Determination of average individual dry weights and ash-free dry weights in different sieve fractions of marine meiofauna. Marine Biology 84(101): 108.

Williamson, C. E., 1987. Predator-prey interactions between omnivorous diaptomid copepods and rotifers: the role of prey morphology and behavior. Limnology and Oceanography 32: 167–177.

Winder, M. & D. E. Schindler, 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. Ecology 85: 2100–2106.