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Combined effects of temperature and prey (*Brachionus angularis*) density on life-table demography and population growth of *Asplanchna brightwelli* (Rotifera)

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Abstract – Predator–prey interactions play major and direct roles in the structuring of zooplankton communities. *Asplanchna* usually predates ciliates, rotifers, cladocerans and sometimes even copepods, its predation may drive not only the ecological, but also the evolutionary dynamics of prey populations. In the present study, the life-table demography and the population growth of *Asplanchna brightwelli* were investigated at four temperatures (16, 20, 24 and 28 °C) using *Brachionus angularis* as prey at four densities (10, 20, 30 and 40 ind.mL^{-1}). The results showed that temperature affected significantly all the life-table demographic parameters (age-specific survivorship and fecundity, average lifespan, life expectancy at hatching, generation time, net reproductive rate and intrinsic rate of population increase) and the population growth rate obtained from the population growth studies, prey density affected the generation time, the net reproductive rate, the intrinsic rate of population increase and the population growth rate, and the interaction between temperature and prey density affected the generation time and the population growth rate. Both the average lifespan and the life expectancy at hatching were the longest at 16 °C, the generation times were longer at lower temperatures (16 and 20 °C) and higher prey densities (30 and 40 ind.mL^{-1}), the net reproductive rates were higher at lower temperatures (16 and 20 °C) and 20–40 ind.mL^{-1} of *B. angularis*, and the population growth rates were higher at 20 °C under 20–40 ind.mL^{-1} of *B. angularis*.

Key words: *Asplanchna brightwelli* / life history / population growth / temperature / *Brachionus angularis* density

Introduction

Zooplankton in freshwater is mainly composed of protozoans, rotifers, cladocerans and copepods (Seoánes and Aguado, 1995), among which rotifers are noteworthy for their important role in the transfer of energy from primary producers to secondary and tertiary consumers in aquatic food webs. Most genera of rotifers are herbivorous, feeding on phytoplankton, whereas others are carnivorous feeding on ciliates, other rotifers and small crustaceans. Among all the carnivorous rotifers, most members of the rotifer genus *Asplanchna* Gosse are predatory, and their diet predominantly comprises a variety of prey species that include ciliates, rotifers, cladocerans and sometimes even copepods (Ejsmont-Karabin, 1974; Guiset, 1977; Williamson, 1983; Arndt, 1993). Although most crustacean zooplankton may escape predation by *Asplanchna* due to their large size, rotifers are more susceptible (Williamson, 1983). Therefore, *Asplanchna*-controlled changes in the abundance and diversity of herbivorous rotifers can be significant (Pourriot, 1977). As an important selective agent, predation by *Asplanchna* may drive not only the ecological but also the evolutionary dynamics of prey populations.

Asplanchna has been used as an important model organism for the laboratory study of predation feeding on a variety of prey (Williamson, 1983). Much literature is available on the food and feeding habits of *Asplanchna*, both from field and laboratory studies (reviewed in Dumont, 1977; Pourriot, 1977; Williamson, 1983; Arndt, 1993; Sarma, 1993; Conde-Porcuna and Sarma, 1995; Iyer and Rao, 1996; Nandini and Sarma, 1999; Nandini *et al.*, 2003; Sarma *et al.*, 2011). Although there are some data on the life-table demography and the population growth rate

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of *Asplanchna* as a function of prey levels (*e.g.*, Urabe, 1992; Dumont and Sarma, 1995; Conde- Porcuna and Declerck, 1998; Sarma *et al.*, 1998, 2002a, 2003; Nandini and Sarma, 1999, 2000; Nandini *et al.*, 2003), the combined effects of temperature and the prey level are inadequately studied (Verdone-Smith and Enesco, 1982).

Among the members of the genus *Asplanchna*, *A. brightwelli* Gosse is a cosmopolitan species, feeding on rotifer genera such as *Anuraeopsis* Lauterborn, *Brachionus* Pallas and *Keratella* Bory de St. Vincent (Urabe, 1992; Conde- Porcuna and Declerck, 1998; Sarma *et al.*, 1998). *B. angularis* Gosse is also a cosmopolitan species, and lacks morphological defences against *Asplanchna* predation. However, in subtropical shallow lakes, the population density of *B. angularis* is not controlled by *Asplanchna* (Wen *et al.*, 2011a, 2011b). Therefore, investigating the combined effects of temperature and prey (*B. angularis*) density on life-table demography and population growth of *A. brightwelli* could be helpful for the interpretation of seasonal changes of these zooplankton species under field conditions.

The developmental rate of poikilothermic animals increases with increasing temperature, and it is enhanced at suitable food levels. In the present study, the combined effects of four levels of temperature and prey level on the life-table demographic parameters and the population growth rate of *A. brightwelli* were investigated not only to find out the optimal condition for population growth, but also to test the hypothesis that at all the tested prey levels, both the survival and the generation time of *A. brightwelli* decrease with increasing temperature.

As usual, an organism utilizes its intake energy for survival, growth and reproduction. The relative allocation of intake energy to reproduction is obviously a function of the quantity of food available and consumed, and related with temperature because of its influence on the energetic costs of metabolism. Therefore, the present study will test another hypothesis that whether a prey level is suitable for the reproduction of *A. brightwelli* depends on the temperature and the negative effect of the unsuitable food level becomes greater with increasing temperature.

Material and methods

The predatory rotifer *A. brightwelli* (body length: 900 ± 50 μm) was isolated from Lake Fengming (Wuhu City, Anhui Province, China) in October, 2013. Four clonal populations were established with parthenogetic females individually, and were respectively maintained in 500 mL beakers with *B. angularis* (body length: 150 ± 25 μm) being exclusive food (at a density of 30 ind.mL^{-1}). *B. angularis* itself was mass cultured from a single clone using alga *Scenedesmus obliquus* (Turp.) Kütz at 1.0×10^6 cells.mL^{-1} as food. The alga was grown in semi-continuous culture using HB-4 medium that contained 200 mg $(NH_4)_2SO_4$, 15 mg K_2HPO_4, 15 mg $CaCl_2$, 80 mg $MgSO_4 \cdot 7H_2O$, 100 mg $NaHCO_3$, 25 mg KCl and 22.5 mg $FeCl_3 \cdot 6H_2O$ per 1000 mL of double-distilled water (Li *et al.*, 1959). Algal cells were harvested in the exponential phase of growth, centrifuged at 3000 rpm for 5 min, resuspended in distilled water and stored at 4 °C in a refrigerator for maintenance of rotifer cultures and experiments. Algal cell concentration was measured with a haemocytometer.

For routine maintenance of zooplankton cultures at 25 ± 1 °C as well as for conducting experiments we used moderate hard water which contained 100 mg KNO_3, 40 mg K_2HPO_4, 62 mg $MgSO_4 \cdot 7H_2O$ and 144 mg $Ca(NO_3)_2 \cdot 4H_2O$ in 1000 mL of 0.002 M NaH_2PO_4–Na_2HPO_4 buffer (pH 7.3) prepared in distilled water (Gilbert, 1963). Mass cultures of both *A. brightwelli* and *B. angularis* were changed with fresh moderate hard water every alternate day. In the cultures we usually obtained *A. brightwelli* at a density of 1 ind.mL^{-1} and *B. angularis* at 50 ind.mL^{-1}. Prior to starting the experiments, about 1 L of *A. brightwelli* and 2 L of *B. angularis* from cultures were separately maintained for about 2 weeks at four chosen temperatures (16, 20, 24 and 28 °C). Between 14 and 30 °C, *A. brightwelli* occurred in subtropical shallow lakes such as Lake Fengming (Xie., 2014).

For life-table experiments, we used four replicate (four clones) beakers with 15 mL medium of 25 mL capacity. Four (10, 20, 30 and 40. ind.mL^{-1}) densities of *B. angularis* were offered on the basis of preliminary experiments. Prey density was estimated on aliquot samples from mass cultures. Thus for life-table demography of *A. brightwelli* on *B. angularis*, we used 64 test beakers (four prey densities × four temperatures × four replicates). Into each test beaker we introduced ten neonates (< 4 h old) of *A. brightwelli* and desired density of prey. The experiments were conducted at four temperatures with continuous but diffused illumination. Observation was made at 12-h intervals, although food was added at every 24-h period. We counted and discarded the number of neonates born and dead adults. The surviving adults were transferred to fresh beakers containing appropriate prey density at corresponding temperature. The experiments were terminated when the last individual of each cohort died. Standard life tables were constructed following Poole (1974). The variables analyzed included age-specific survivorship and fecundity, average lifespan (LS), life expectancy at hatching (e_0), generation time (T), net reproductive rate (R_0) and intrinsic rate of population increase (r_m), using standard formulae according to Krebs (1985) and Pianka (1988):

$$\text{Net reproductive rate}\,(R_0) = \sum_0^\infty l_x m_x$$

$$\text{Generation time}\,(T) = \sum l_x m_x x / R_0$$

Intrinsic rate of population increase (r), first an approximation using:

$$r = \ln R_0 / T$$

For final calculation, we solved the equation:

$$\sum_{X=0}^{\infty} e^{-rx} l_x m_x = 1$$

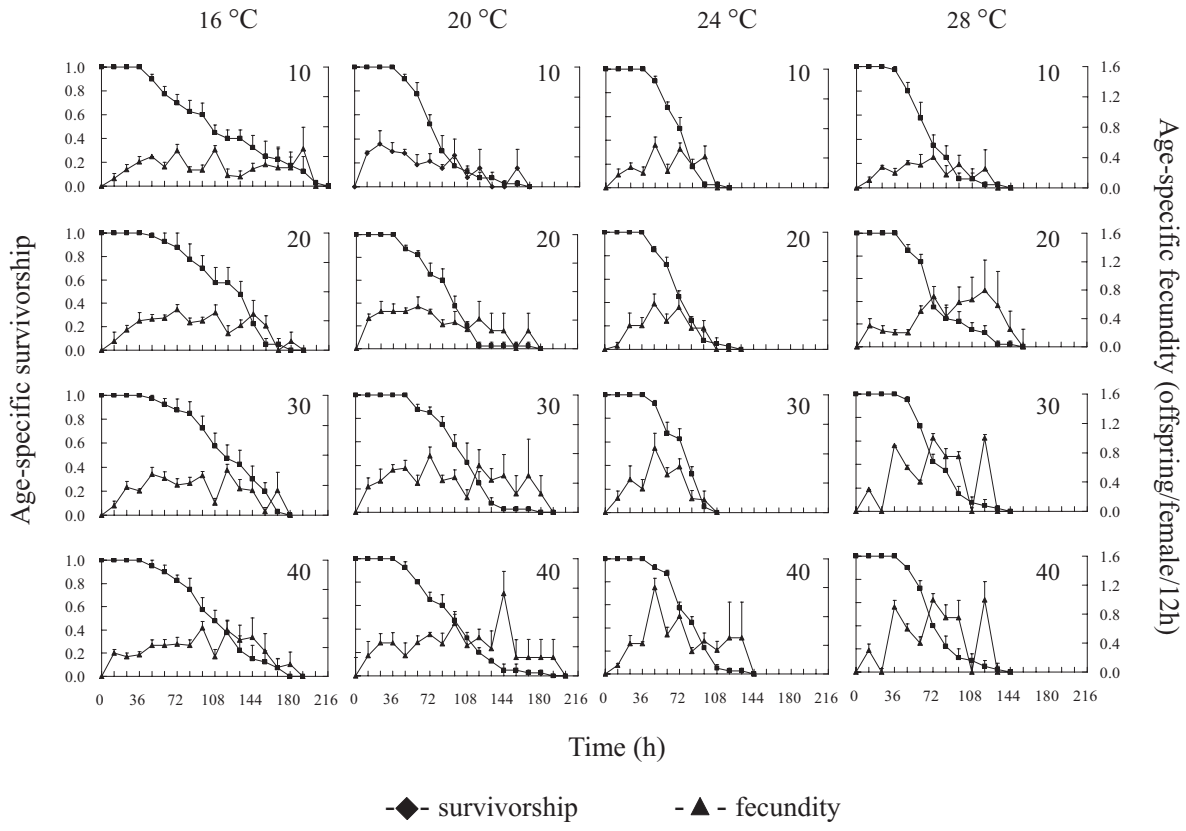

Fig. 1. Survivorship and fecundity of *Asplanchna brightwelli* cultured at four temperatures and prey (*B. angularis*, ind.mL^{-1}) densities (mean ± SE).

For population growth experiments, we used the same experimental design as used for the life-table experiments. Following initiation of the experiments, we estimated daily the density of *A. brightwelli* from each replicate using whole counts. The living individuals of *A. brightwelli* were then transferred to new beakers with the chosen quantity of medium, food density and temperature. The population growth experiments were terminated after 16 days when the predator populations in most replicates began to decline. Based on the data collected, we obtained the rate of population increase (r) using the exponential equation after appropriate curve fitting (Poole, 1974):

$$r = (\ln N_t - \ln N_0)/t$$

All data were tested for normality using the one-sample Kolmogrov–Smirnov procedure. Homogeneity of variances was checked using Levene's test. One-way analysis of variance (ANOVA) was conducted to identify the significant effect of temperature at each prey density as well as prey density at each temperature on each of the life history variables, and two-way ANOVA was conducted to identify significant effects of temperature, prey density and their interaction on each of the life history variables. Multiple comparisons were conducted using least significant difference (LSD) tests.

Results

Life table demography

The age-specific survivorship of *A. brightwelli* fed *B. angularis* in relation to prey density and temperature are presented in Figure 1. There was no mortality in the first 1.5 days but a high death in the next 2.5 days, the survivorship curves began to show steep mortality, especially at higher temperatures (24 and 28 °C). In general, regardless of prey density, the survivorships at 16 and 20 °C were significantly higher than at 24 and 28 °C ($P < 0.01$). Regardless of temperature, prey density did not significantly affect the survivorship.

The age-specific fecundity curves of *A. brightwelli* fed *B. angularis* showed the hump-shaped sawtooth-like pattern. In general, the duration of reproductive period decreased with increasing temperature, except for those at 24 °C with 10–30 ind.mL^{-1}. The age-specific fecundity increased with increasing temperature, except for that at 28 °C with 10 ind.mL^{-1} (Fig. 1).

The main life-table demographic parameters of *A. brightwelli* fed *B. angularis* in relation to prey density and temperature are presented in Table 1. Temperature affected significantly both the average lifespan and the life expectancy at hatching ($P < 0.01$, two-way ANOVA; Table 2), but prey density and the interaction between

Table 1. Effects of prey density (*B. angularis*, ind.mL^{-1}) on life-table demography and population growth of *A. brightwelli* cultured at four temperatures (mean ± SE).

Parameters	Prey density	Temperature			
		16 °C	20 °C	24 °C	28 °C
Life-table demography					
Average lifespan (h)	10	101.7 ± 12.6^{A}	66.0 ± 4.6^{aB}	57.6 ± 2.8^{aB}	55.8 ± 5.8^{B}
	20	104.4 ± 10.8^{A}	73.8 ± 4.9^{aB}	59.1 ± 1.6^{aB}	63.6 ± 3.7^{B}
	30	106.2 ± 9.5^{A}	88.5 ± 3.3^{bB}	61.2 ± 2.9^{abC}	63.0 ± 2.7^{C}
	40	95.1 ± 7.0^{A}	77.1 ± 1.6^{abB}	67.8 ± 1.9^{bBC}	60.6 ± 3.5^{C}
Life expectancy at hatching (h)	10	94.8 ± 10.5^{A}	65.0 ± 3.8^{aB}	58.0 ± 2.3^{aB}	56.5 ± 4.9^{B}
	20	97.0 ± 9.0^{A}	71.5 ± 4.1^{acB}	59.3 ± 1.3^{aB}	63.0 ± 3.1^{B}
	30	98.5 ± 7.9^{A}	83.8 ± 2.8^{bB}	61.0 ± 2.4^{abC}	62.5 ± 2.3^{C}
	40	89.3 ± 5.8^{A}	77.5 ± 4.0^{bcAB}	66.5 ± 1.6^{bBC}	60.5 ± 2.9^{C}
Generation time (h)	10	70.7 ± 3.3^{A}	41.5 ± 2.0^{aB}	45.7 ± 3.3^{aB}	45.7 ± 4.8^{B}
	20	69.5 ± 3.1^{A}	49.4 ± 3.1^{abBC}	48.4 ± 2.9^{aC}	60.7 ± 5.7^{AB}
	30	70.2 ± 4.1^{A}	60.9 ± 4.5^{bcAB}	46.4 ± 3.6^{aC}	52.0 ± 2.5^{BC}
	40	67.5 ± 3.9^{A}	62.4 ± 5.3^{cAB}	52.2 ± 1.5^{aBC}	50.1 ± 3.5^{C}
Net reproductive rate	10	2.3 ± 0.2^{A}	2.5 ± 0.3^{A}	1.7 ± 0.2^{aB}	1.2 ± 0.1^{aB}
	20	3.3 ± 0.5^{A}	3.3 ± 0.4^{A}	1.8 ± 0.2^{abB}	2.2 ± 0.2^{bB}
	30	3.6 ± 0.3^{AC}	4.0 ± 0.3^{AD}	2.6 ± 0.3^{bcB}	2.8 ± 0.2^{bBC}
	40	3.4 ± 0.5	3.1 ± 0.4	3.4 ± 0.3^{c}	2.3 ± 0.3^{b}
Intrinsic rate of population increase (day^{-1})	10	0.336 ± 0.048^{B}	0.648 ± 0.096^{A}	0.288 ± 0.072^{aBC}	0.096 ± 0.024^{aC}
	20	0.480 ± 0.096^{AB}	0.720 ± 0.096^{A}	0.312 ± 0.096^{abB}	0.360 ± 0.048^{bB}
	30	0.528 ± 0.048	0.720 ± 0.096	0.552 ± 0.096^{bc}	0.528 ± 0.048^{c}
	40	0.521 ± 0.050	0.552 ± 0.096	0.624 ± 0.072^{c}	0.408 ± 0.072^{bc}
Population growth					
Rate of population increase (day^{-1})	10	0.057 ± 0.066	0.207 ± 0.039	0.054 ± 0.034^{a}	0.049 ± 0.021^{a}
	20	0.269 ± 0.053^{A}	0.309 ± 0.043^{A}	0.125 ± 0.037^{aB}	0.092 ± 0.023^{aB}
	30	0.155 ± 0.017^{BC}	0.226 ± 0.032^{B}	0.325 ± 0.030^{bA}	0.135 ± 0.016^{abC}
	40	0.185 ± 0.050	0.264 ± 0.028	0.273 ± 0.054^{b}	0.185 ± 0.045^{b}

*Lowercase and capital letters indicate sample means that are similar (same letter) or different (different letter) for each variable among the four prey densities and temperatures, respectively (LSD multiple comparison test).

temperature and prey density did not affect them ($P > 0.05$). Both the average lifespan and the life expectancy at hatching was the longest at 16 °C and the shortest at 24 and 28 °C (Table 1).

Both temperature and prey density, and their interaction had significant effects on the generation time ($P < 0.05$, Table 2). The generation times were longer at lower temperatures (16 and 20 °C) and higher prey densities (30 and 40 ind.mL^{-1}) (Table 1).

Both temperature and prey density had significant effects on the net reproductive rate and the intrinsic rate of population increase ($P < 0.01$, Table 2), but their interaction did not affect them ($P > 0.05$). The net reproductive rates were significantly higher at lower temperatures (16 and 20 °C) than at higher temperatures (24 and 28 °C). The intrinsic rate of population increase was the highest at 20 °C. The intrinsic rate of population increase was higher at 16 °C than at 28 °C, but both of them were similar to that at 24 °C. Both the net reproductive rate and the intrinsic rate of population increase increased with prey density increasing from 10 to 30 ind.mL^{-1}, but those at 40 ind.mL^{-1} were similar to those at 20 and 30 ind.mL^{-1} (Table 1).

Population growth

At all the four temperatures, the maximum density of *A. brightwelli* increased with increasing availability of *B. angularis* in the medium (Fig. 2). Both temperature and prey density, and their interaction had significant effects on the population growth rate of *A. brightwelli* ($P < 0.05$, Table 2). At 20 °C and 20–40 ind.mL^{-1}of *B. angularis*, *A. brightwelli* had higher population growth rates (Table 1).

Discussion

The effect of prey density on survival and development of *Asplanchna* species depended on prey species. The survival of *A. girodi* De Guerne was not significantly affected by the density of both *B. havanaensis* Rousselet (densities ranged from 1 to 8 ind.mL^{-1}) and *Anuraeopsis fissa* Gosse (250–2000 ind.mL^{-1}), but the average lifespan of *A. girodi* fed *B. calyciflorus* Pallas at 1 ind.mL^{-1} was longer than that at 2–8 ind.mL^{-1}. The generation time of *A. girodi* decreased with increasing prey (*B. havanaensis* or *B. calyciflorus*) density, but increased with increasing *A. fissa* density (Dumont and Sarma, 1995; Sarma *et al.*, 2003). In the present study, we found that the effect of prey density on survival and development of *A. brightwelli* also depended on temperature. At 16 and 28 °C, and 16, 24 and 28 °C, the average lifespan and the life expectancy at hatching, and the generation time of *A. brightwelli* were not affected by *B. angularis* density, respectively. However, at 20 °C, both the average lifespan and the life expectancy

Table 2. Results of two-way ANOVA performed for different life-table demographic and population growth parameters of *A. brightwelli* cultured at four temperatures and prey (*B. angularis*) densities.

Parameters and sources	*MS*	*SS*	d.f.	*F*
Life-table demography				
Average lifespan				
Temperature	5920.12	17760.35	3	42.12**
Prey density	238.34	715.01	3	1.70ns
Temperature × prey density	112.19	1009.73	9	0.80ns
Error	140.56	6746.67	48	
Life expectancy at hatching				
Temperature	4123.02	12369.06	3	40.74**
Prey density	168.56	505.69	3	1.67ns
Temperature × prey density	82.24	740.19	9	0.81ns
Error	101.21	4858.00	48	
Generation time				
Temperature	1404.39	4213.17	3	25.16**
Prey density	176.75	530.26	3	3.17*
Temperature × prey density	139.94	1259.49	9	2.51*
Error	55.81	2679.07	48	
Net reproductive rate				
Temperature	5.15	15.45	3	13.11**
Prey density	5.35	16.04	3	13.60**
Temperature × prey density	0.49	4.44	9	1.26ns
Error	0.39	18.86	48	
Intrinsic rate of population increase				
Temperature	0.00	0.001	3	12.11**
Prey density	0.00	0.001	3	7.99**
Temperature × prey density	7.20×10^{-5}	0.001	9	1.91ns
Error	3.78×10^{-5}	0.002	48	
Population growth				
Population growth rate				
Temperature	0.051	0.154	3	8.330**
Prey density	0.060	0.179	3	9.655**
Temperature × prey density	0.019	0.169	9	3.040**
Error	0.01	0.30	48	

MS, mean square; SS, sum of squares; d.f., degrees of freedom; *F*, *F* ratio.
*, Significant ($P < 0.05$), **, very significant ($P < 0.01$), ns, non-significant ($P > 0.05$).

at hatching of *A. brightwelli* fed *B. angularis* at 30 ind.mL^{-1} tended to be the longest, and the generation time increased with increasing *B. angularis* density. At 24 °C, both the average lifespan and the life expectancy at hatching increased with increasing prey density (Table 1).

Although it is the general trend that survival and developmental time of rotifers decreased with increasing temperature, the present results showed that the temperature effect on survival and developmental time of *A. brightwelli* depended on prey density. At 40 ind.mL^{-1} of *B. angularis*, both the average lifespan and the life expectancy at hatching of *A. brightwelli* did decrease with increasing temperature. However, at 10 and 20 ind.mL^{-1} of *B. angularis*, both the average lifespan and the life expectancy at hatching of *A. brightwelli* at 20, 24 and 28 °C were similar. At 30 ind.mL^{-1} of *B. angularis*, both the average lifespan and the life expectancy at hatching of *A. brightwelli* at 24 and 28 °C were also similar. At all the four *B. angularis* densities, the generation time of *A. brightwelli* did not decrease with increasing temperature (Table 1). All those results stated above did not support the hypothesis that at all the tested prey levels, both the survival and the generation time of *A. brightwelli* decrease with increasing temperature, and might be attributed to the significant interaction between temperature and prey density.

The net reproductive rate of *A. girodi* fed *B. calyciflorus* at 2 ind.mL^{-1} or *B. havanaensis* at 1 ind.mL^{-1} was the lowest (Sarma *et al.*, 2003), but that of *A. girodi* fed *A. fissa* increased with increasing prey density (Dumont and Sarma, 1995). In the present study, we found that the effect of prey density on the net reproductive rate of *A. brightwelli* depended on temperature. At 16 and 20 °C, *B. angularis* density did not affect the net reproductive rate of *A. brightwelli*. But at 24 °C, the net reproductive rate of *A. brightwelli* fed *B. angularis* at 40 ind.mL^{-1} was higher than that at 10 and 20 ind.mL^{-1}. At 28 °C, the net reproductive rate of *A. brightwelli* fed *B. angularis* at 10 ind.mL^{-1} was the lowest (Table 1). The results stated above supported hypothesis that whether a prey level is suitable for the reproduction of *A. brightwelli* depends on temperature, and the negative effect of the unsuitable food level becomes greater with increasing temperature. In addition, the effect of temperature on the net reproductive rate of *A. brightwelli* also depended on prey density.

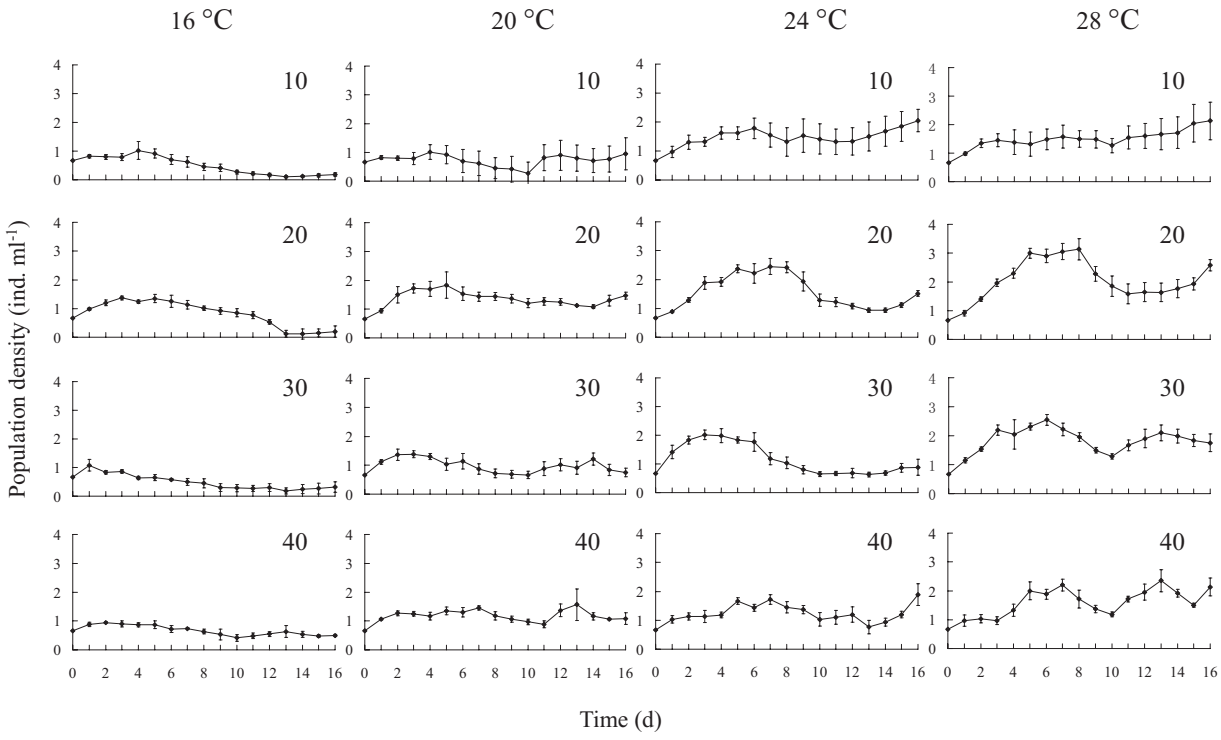

Fig. 2. Population growth curves of *Asplanchna brightwelli* cultured at four temperatures and prey (*B. angularis*, ind.mL^{-1}) densities (mean ± SE).

At 10 and 20 ind.mL^{-1} of *B. angularis*, the net reproductive rate of *A. brightwelli* was higher at 16 and 20 °C than at 24 and 28 °C. At 30 ind.mL^{-1} of *B. angularis*, the net reproductive rate of *A. brightwelli* was higher at 16 and 20 °C than at 24 °C, and that at 28 °C was not significantly different from that at 16 and 24 °C. The further increase in *B. angularis* density made the significant effect of temperature on the net reproductive rate disappeared (Table 1).

An organism usually utilizes its intake energy for survival, growth and reproduction. Because of the differences in the energetic costs of metabolism at different temperatures, the demand for intake energy for survival, growth and reproduction was lower at lower temperatures than at higher ones, which might be the reason for that at 20 °C, *A. brightwelli* fed 30 ind.mL^{-1} of *B. angularis* tended to have the longest lifespan and the highest reproductive rate; but at 24 °C, only 40 ind.mL^{-1} of *B. angularis* maximized the lifespan and the reproductive rate of *A. brightwelli*.

The data of net reproductive rate of *A. brightwelli* obtained in the present study were much lower than those reported for *Asplanchna* (*e.g.*, 9–15 offspring female^{-1} lifespan^{-1} for *A. girodi*; Dumont and Sarma, 1995), which might be attributed to the much lower prey biomass used here.

The intrinsic rate of population increase of *A. girodi* obtained from life-table demography increased with increasing prey (*B. havanaensis* or *B. calyciflorus*) availability in the medium (Sarma *et al.*, 2003), but that of *A. girodi* was not significantly affected by *A. fissa* density (Dumont and Sarma, 1995). Similarly, in the present study, at 16 and 20 °C, *B. angularis* density did not affect the intrinsic rate of population increase of *A. brightwelli*. At 24 °C, however, the intrinsic rate of population increase of *A. brightwelli* fed *B. angularis* at 40 ind.mL^{-1} was higher than that at 10 ind.mL^{-1}. At 28 °C, the intrinsic rate of population increase of *A. brightwelli* fed *B. angularis* at 10 ind.mL^{-1} was the lowest. In addition, the present results showed that at 10 and 20 ind.mL^{-1} of *B. angularis*, the intrinsic rate of population increase of *A. brightwelli* at 20 °C was the highest. At 30 and 40 ind.mL^{-1} of *B. angularis*, the intrinsic rate of population increase of *A. brightwelli* was not affected by temperature (Table 1).

The *r* values in population growth studies of *A. sieboldi* Leydig fed *B. havanaensis*, *B. rubens* Ehrenberg, *B. patulus* Muller, *B. macracanthus* Jakubski or *B. calyciflorus* and *A. brightwelli* fed *B. calyciflorus* or *A. fissa* increased with increasing prey density (Sarma *et al.*, 1998, 2002b; Nandini *et al.*, 2003). Similarly, in the present study, at 28 °C, the population growth rate of *A. brightwelli* increased with increasing *B. angularis* density. However, at 24 °C, the population growth rate of *A. brightwelli* fed *B. angularis* at 30 and 40 ind.mL^{-1} was higher than that at 10 and 20 ind.mL^{-1}. At 16 and 20 °C, the population growth rate of *A. brightwelli* was not affected by *B. angularis* density. In addition, the present results showed that at 10 and 40 ind.mL^{-1} of *B. angularis*, the population growth rate of *A. brightwelli* was not affected by temperature. At 20 ind.mL^{-1} of *B. angularis*, the population growth rate of *A. brightwelli* was higher at 16 and 20 °C than at 24 and 28 °C. At 30 ind.mL^{-1} of *B. angularis*, the population

growth rate of *A. brightwelli* was the highest at 24 °C (Table 1).

Generally, rotifers are opportunistic which own high population growth rates (Allan, 1976). Most herbivorous rotifers usually have *r* values about 0.5 day^{-1} (Sarma *et al.*, 2001), but carnivorous genus may have *r* values higher than 0.5 up to 1.5 day^{-1}. The *r* values of *A. girodi* ranged from 0.09 to 1.51 day^{-1} (Dumont and Sarma, 1995; Sarma *et al.*, 2003), and those of *A. sieboldi* ranged from 0.07 to 0.43 day^{-1} (Sarma *et al.*, 2002a; Nandini *et al.*, 2003). *A. brightwelli* had *r* values of 0.22–1.01 day^{-1} (Sarma *et al.*, 1998). In the present study, the *r* values of *A. brightwelli* ranged from 0.05 to 0.33 day^{-1}, and are in agreement with the range stated above for those *Asplanchna* species.

The *r* values in population growth studies are generally smaller than those from life-table demography (Dumont and Sarma, 1995; Sarma *et al.*, 2003). Identical results were obtained in the present study. Intrinsic rate of population increase is defined as the rate of increase per animal under specified physical conditions, in an unlimited environment where the effects of increasing density do not need to be considered (Birch, 1948), which might be the reason for that disparity between the two types of *r* values.

In natural water bodies, the dynamics patterns of *A. brightwelli* population will be changed by climate changes, which will lead to community reorganizations and imply consequences for the functioning of ecosystems.

Conclusion

Temperature affected significantly all the life-table demographic parameters and the population growth rate obtained from the population growth study, prey density affected the generation time, the net reproductive rate, the intrinsic rate of population increase and the population growth rate, and the interaction between temperature and prey density affected the generation time and the population growth rate. At 20 °C under 20–40 $ind.mL^{-1}$ of *B. angularis*, *A. brightwelli* had higher population growth rates.

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