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RESEARCH ARTICLE

Asplanchna-kairomone induces life history shifts in *Brachionus angularis* (Rotifera)

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Abstract – Predator-derived kairomones play an important role in ecological and evolutionary processes that enable the prey to survive predation pressure. In the presence of predatory *Asplanchna*, some *Brachionus* and *Keratella* species develop morphological and behavioral defenses, but whether rapid population growth and diapause are inducible defenses largely remains unknown. In the present study, parental *B. angularis* females cultured at 1.0×10^6 and 2.0×10^6 cells · mL^{-1} of *Scenedesmus obliquus* were indirectly exposed to 0, 40, 80 and 160 ind. L^{-1} of *A. brightwelli* using mesh enclosure, and their life-table demographic parameters, population growth rates and morphological characters were calculated and measured. The results showed that *Asplanchna*-released kairomone decreased significantly average lifespan, life expectancy at hatching, generation time and net reproduction rate, but increased the proportion of sexual offspring of parental *B. angularis* females. The threshold *Asplanchna* density required for significant effects varied with food level. Kairomone released by *Asplanchna* at 80 ind. L^{-1} increased significantly the intrinsic rate of population increase of *B. angularis* cultured at 2.0×10^6 cells · mL^{-1} of *S. obliquus*, which would offset the mortality of exposed females from predation. The accumulation of kairomone in aquatic environments enhanced the indirect effect of *Asplanchna* on the population growth of *B. angularis*. The present results indicated that rapid population growth of *B. angularis* induced by *Asplanchna* kairomone might facilitate the coexistence of preys with predators, and higher proportion of sexual offspring and then resting egg production might help the preys avoid the predator in time instead of facing the enemy through defenses.

Keywords: rotifer / predation / life table demography / population growth rate / sexual reproduction / morphometrics

1 Introduction

Predation is one of the most important factor structuring zooplankton communities (Williams, 1997). In the presence of predators, many planktonic invertebrates develop various inducible defenses that reduce the risk of predation. Defenses induced by various invertebrate or vertebrate predators have been extensively studied in *Daphnia* Straus and several genera of rotifers (reviewed in Larsson and Dodson, 1993; De Meester *et al.*, 1999; Gilbert, 1999; Tollrian and Dodson, 1999; Lass and Spaak, 2003). In *Daphnia*, the defenses may be changes in morphology (*e.g.* neckteeth formation, tail spine elongation, helmet enlargement), behavior (*e.g.* diel vertical migration, enhanced capability to escape, swarming) or life history (*e.g.* age or size at first reproduction, reproductive rate, diapause induction) (reviewed in Lass and Spaak, 2003; reviewed in Gilbert, 2013). In rotifers, the known predator-induced defenses are morphological (*e.g.* Soto and Sarma, 2009; Yin *et al.*, 2017; reviewed in Gilbert, 2017) and behavioral (Peña-Aguado *et al.*, 2008; Gilbert, 2014), but whether the life history shifts such as rapid population growth and diapause are inducible defenses largely remains unknown.

Brachionus angularis Gosse is a common rotifer species in many natural waterbodies. Different from some species of *Brachionus* Pallas and *Keratella* Bory de St. Vincent, *B. angularis* does not develop any remarkably elongated spines in response to *Asplanchna*-released kairomone. As another undefended rotifer species, *Synchaeta pectinata* Ehrenberg was speculated to develop a high population growth rate that offsets mortality from predation (Wallace *et al.*, 2006), but the experimental evidence is scarce. If undefended *S. pectinata* can develop a high population growth rate, *B. angularis* should also be able to develop a high population growth rate in response to *Asplanchna*-released kairomone. If so, what is the *Asplanchna* density resulting in the high population growth rate in this species?

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In cladocerans, diapause has been proposed as a predator avoidance strategy (Hairston, 1987). Kairomones released by fish predators induced directly diapause in a population of *D. magna* Strauss (Ślusarczyk, 1995, 1999, 2001; Pijanowska and Stolpe, 1996). In rotifers, kairomone in the medium conditioned by *A. brightwellii* Gosse at 10 and 100 ind. L^{-1} decreased the proportion of sexual offspring of *B. calyciflorus* (Yin *et al.*, 2015), but that conditioned by *A. brightwellii* at 100 ind. L^{-1} did not affect the proportion of sexual offspring of *B. angularis* (Yin *et al.*, 2017). Because the *Asplanchna* kairomone is very unstable (Gilbert, 1967; Halbach, 1970) and thus the use of *Asplanchna*-conditioned media is also problematic (reviewed in Gilbert, 2013), the effect of kairomone released directly by *Asplanchna* on the proportion of sexual offspring in rotifers needs further investigation.

The present study investigated the effect of kairomone released by different densities of *A. brightwellii* on life-table demographic parameters, population growth rates and the morphological characters of both lorica and egg of parental *B. angularis* females cultured at two algal densities, with the aim of testing the following three hypotheses: (i) *B. angularis* develops a high population growth rate in response to kairomone released by a certain density of *Asplanchna*, based on the speculation on *S. pectinata* (Wallace *et al.*, 2006); (ii) kairomone released by a certain density of *Asplanchna* shortens the generation time and thus increases the population growth rate because it decreases the reproduction rate of *B. angularis* (Yin *et al.*, 2017); and (iii) similar to the effect of fish kairomone on *D. magna* (Ślusarczyk, 1995, 1999, 2001; Pijanowska and Stolpe, 1996), higher concentrations of *Asplanchna* kairomone induce higher levels of sexual reproduction in *B. angularis*.

2 Materials and methods

2.1 Sample collection and culture

Individuals of *A. brightwellii* and *B. angularis* were collected from Lake Jinghu (31°36′11″N, 118°38′23″E) in July and September 2016, respectively, identified morphologically under a microscope, and clonally cultured in rotifer culture medium (Gilbert, 1963) at 20 ± 1 °C. *B. angularis* was fed 1.0×10^6 cells · mL^{-1} of *Scenedesmus obliquus* (Turp.) Kütz which was semi-continuously cultured in HB-4 medium (Li *et al.*, 1959). Algal cells at the exponential phase of growth were harvested by centrifugation at 3,000 rpm for 5 min, resuspended in rotifer culture medium and stored at 4 °C. The density of algal cells was determined by counting using a haemocytometer. *A. brightwellii* was maintained at a density of 5000 ind. L^{-1} in 500 mL beakers and daily fed 30 000 ind. L^{-1} of *B. angularis*. All clones of *A. brightwellii* and *B. angularis* were cultured in the laboratory for at least 6 months, and one clone of each species was randomly selected for the experiments. For mass cultures of the rotifers and all the experiments, an illumination incubator with a 16:8-h light: dark photoperiod at 130 lx at 20 ± 1 °C was used.

2.2 Life table experiments

Life table experiments of *B. angularis* subject to *Asplanchna*-released kairomone were conducted in beakers each containing 50 mL of culture medium. Prior to the life table experiments, the *B. angularis* clone was maintained at the designated food levels for more than 5 days to allow acclimation. To separate predators from preys but allow the diffusion of *Asplanchna* kairomone, a small mesh container which was prepared by covering a 25 μm pore-sized mesh at the downside end of a pipe (length: 10 cm, diameter: 1.5 cm) was hung in water column of each beaker with the upside end above the water surface. The water volume in each pipe was adjusted to 10 mL by moving the pipe up or down. For the life-table experiments, chosen number of *A. brightwellii* individuals (<12 h old) was introduced in each mesh container and 20 neonates (<12 h old) of *B. angularis* from pre-cultures were added in each beaker. To maintain the activity of *A. brightwellii*, 10 individuals of *B. angularis* was added into each mesh container (Dumont and Sarma, 1995). Based on the ranges of *A. brightwellii* density in subtropical shallow lakes such as Lake Tingtang (Xie *et al.*, 2015; Zhang *et al.*, 2017) and *S. obliquus* density suitable for the population growth of *B. angularis* (Peng *et al.*, 2016), we chose four predator densities (0, 40, 80 and 160 ind. L^{-1}) and two algal food levels (1.0×10^6 and 2.0×10^6 cells · mL^{-1}), with three replicates for each treatment. Following initiation of the experiments, every 12 h the original cohort and neonates produced in each beaker were counted; the former were returned to the medium, and the latter were removed into a new beaker and cultured to calculate proportion of sexual offspring. Every 24 h, the surviving original *B. angularis* individuals were transferred into a fresh beaker containing 50 mL of medium with the designed level of *S. obliquus*, and the predators in each mesh container were replaced by a new batch with the same age and density, thus the predation pressure could be consistent throughout the experiments. Experiments were terminated when all mother rotifers died.

The age-specific survivorship (l_x) and fecundity (m_x), life expectancy at hatching (e_0), average lifespan (*LS*), generation time (*T*), net reproduction rate (R_0), intrinsic rate of population increase (r_m) and proportion of sexual offspring (*PS*) were calculated using the following formulae (Pianka, 1988):

Net reproductive rate: $R_0 = \sum_0^\infty l_x m_x$

Generation time: $T = \frac{\sum l_x m_x x}{R_0}$

Intrinsic rate of population increase (*r*), first an approximation using: $r - \text{rough} = \ln R_0 / T$

For final calculation, we solved the equation: $\sum_{x=0}^{n} e^{-rx} l_x m_x = 1$.

2.3 Population growth experiments

The experiment design, including the predator density, the algal food level and the culture volume, was the same as the life-table experiments. 100 neonates (<12 h old) of *B. angularis* from pre-cultures were initially introduced in each beaker, and the populations were allowed to grow for 3 days (Xi *et al.*, 2007). Thereafter, the number of *B. angularis* individuals in each beaker was counted, and the rate of population growth (*r*) was calculated using the exponential equation (Poole, 1974):

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

where N_0 and N_t are the initial and final population densities (ind. L^{-1}) of *B. angularis*, respectively, and *t* is the time in days.

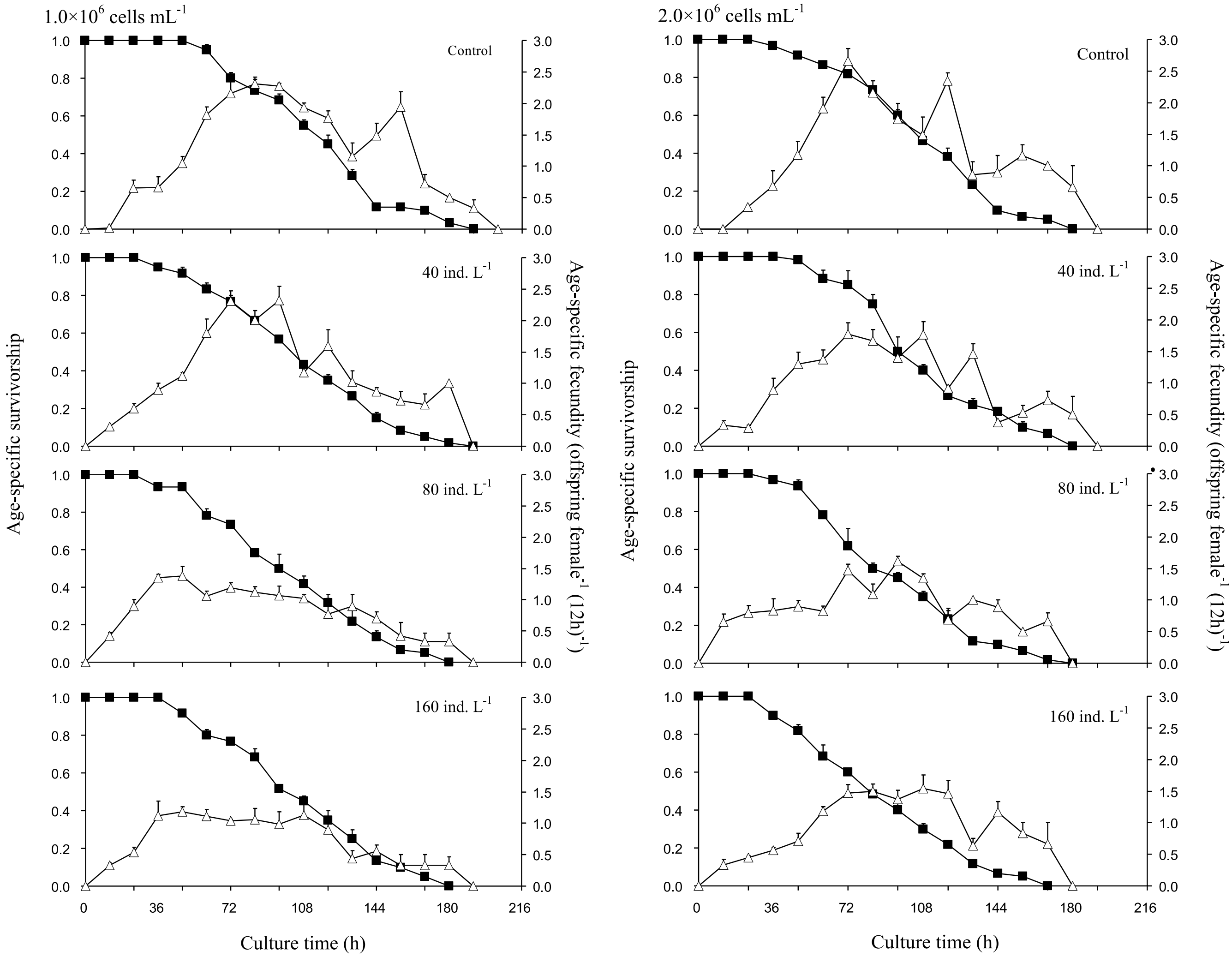

Fig. 1. Age-specific survivorship (filled square) and fecundity (unfilled triangle) of *B. angularis* exposed to kairomone concentrations released respectively by four densities of *Asplanchna* and cultured at two *S. obliquus* levels. Shown are the values mean + standard error based on three replicates.

2.4 Measurement of morphological parameters

After the 3-day population growth, 25–30 *B. angularis* individuals bearing one or two amictic eggs were sampled from each treatment. After washing in distilled water for 30 min, these animals were fixed in 4% formaldehyde solution. The length and width of lorica, and the long and short diameter of egg of each animal were measured under a microscope using the MC-D500U(E) Digital Camera (Phenix, Jiangxi, China) at 200 × magnification. Thereafter, body size (V_b) was calculated by $V_b = 0.2a^2b$, where a and b represents the lorica length and width, respectively. Egg volume (V_e) was calculated by $V_e = 3\pi(a^2b + ab^2)/4$, where a and b is the long and short diameter of egg, respectively (Zhang and Huang, 1991).

2.5 Statistical analyses

All statistical analyses were performed using SPSS 11.5. The Levene's test was performed to test the homogeneity of variances. Kaplan-Meier analyses were conducted to test for the differences in the survivorships of the rotifer cohorts among the four *Asplanchna*-released kairomone concentrations. Two-way ANOVA was conducted to analyze the significant effects of algal level, *Asplanchna*-released kairomone concentration and their interactions on each parameter, and multiple comparisons of LSD were performed to determine which groups were significantly different among the four *Asplanchna*- released kairomone concentrations at a specific food level. Paired *t*-tests were carried out to identify the differences of each variable between two algal densities. Results with P values of less than 0.05 were considered statistically significant.

3 Results

3.1 Life table demography

The age-specific survivorship of *B. angularis* was not affected by *Asplanchna*-released kairomone concentration ($P > 0.05$). Of course, limited samples ($N = 3$) may lead the statistical power to detect significant differences is quite low. The age-specific fecundity curves of *B. angularis* exposed to *Asplanchna*-released kairomone generally showed the hump-shaped sawtooth-like pattern. Compared to the controls, and at 1.0×10^6 cells · mL^{-1} of *S. obliquus*, kairomone released by *Asplanchna* at 80 and 160 ind. L^{-1} decreased the peak fecundities of *B. angularis* by 40.3% and 48.9%, respectively ($P < 0.05$). At 2.0×10^6 cells · mL^{-1} of *S. obliquus*, kairomone released by *Asplanchna* at 40–160 ind. L^{-1} decreased the peak fecundities of *B. angularis* by 33.5%, 44.7% and 42.1%, respectively ($P < 0.05$) (Fig. 1).

The main life-table demographic parameters of *B. angularis* in relation to *Asplanchna*-released kairomone concentration and food level are presented in Figure 2. At both algal levels, *Asplanchna*- released kairomone concentration affected significantly nearly all the life table demographic parameters ($P < 0.05$) except the intrinsic rate of population increase of *B. angularis* cultured at 1.0×10^6 cells · mL^{-1} of *S. obliquus* ($P > 0.05$). Compared with the controls, and at 1.0×10^6 cells · mL^{-1} of *S. obliquus*, kairomone released by *Asplanchna* at 40–160 ind. L^{-1} shortened significantly the life expectancy at hatching and the average lifespan by 8.5%, 12.8% and 8.5%, and 9.5%, 14.3% and 9.5%, respectively. Kairomone released by *Asplanchna* at 80–160 ind. L^{-1} decreased the generation time and the net reproduction rate by 21.2% and 18.2%, and 33.9% and 40.7%, but increased the proportion of sexual offspring by 126.5% and 191.2%, respectively. (Fig. 2).

The increase in algal density affected the magnitudes of effects of *Asplanchna*-released kairomone concentration on the life table demographic parameters. Compared with the controls, and at 2.0×10^6 cells · mL^{-1} of *S. obliquus*, kairomone released by *Asplanchna* at 80–160 ind. L^{-1} shortened significantly the life expectancy at hatching and the average lifespan by 13.6% and 20.5%, and 15.4% and 23.1%, respectively. Kairomone released by *Asplanchna* at 40–160 ind. L^{-1} decreased the generation time and the net reproduction rate by 18.8% and 9.4%, and 35.8% and 45.3%, respectively. Kairomone released by *Asplanchna* at 80 ind. L^{-1} increased the intrinsic rate of population increase by 15.8%, but that at 160 ind. L^{-1} decreased the intrinsic rate of population increase by 19.8%. Kairomone released by *Asplanchna* at 80–160 ind. L^{-1} increased the proportion of sexual offspring by 386.7% and 426.7%, respectively. In addition, compared to 1.0×10^6 cells · mL^{-1} of *S. obliquus*, and when *B. angularis* was exposed to kairomone released by *Asplanchna* at 160 ind. L^{-1}, 2.0×10^6 cells · mL^{-1} of *S. obliquus* decreased the life expectancy at hatching and the average lifespan by 18.6% and 21.1%, respectively. When *B. angularis* was exposed to kairomone released by *Asplanchna* at 40 and 160 ind. L^{-1}, 2.0×10^6 cells · mL^{-1} of *S. obliquus* decreased the intrinsic rate of population increase by 6.88% and 18.5%, respectively (Fig. 2).

Two-way ANOVA showed that both the life expectancy at hatching and the average lifespan of *B. angularis* were significantly affected by *Asplanchna*-released kairomone concentration, food level and their interaction. Both the generation time and the proportion of sexual offspring were affected by *Asplanchna*-released kairomone concentration. The net reproduction rate and the intrinsic rate of population increase were affected by both *Asplanchna*-released kairomone concentration and food level (Tab. 1).

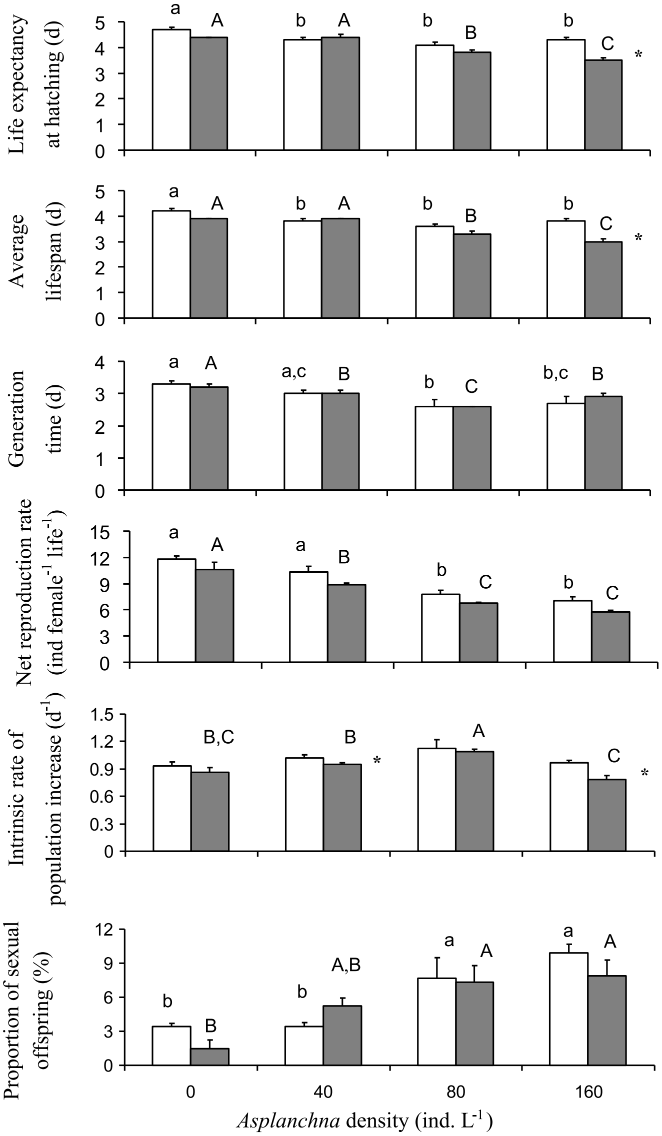

Fig. 2. Life expectancy at hatching, the average lifespan, generation time, net reproduction rate, intrinsic rate of population increase and proportion of sexual offspring of *B. angularis* exposed to kairomone concentrations released respectively by four densities of *Asplanchna* and cultured at two *S. obliquus* levels. Shown are the values mean + standard error based on three replicates. Small and capital letters indicate means that are similar (same letter) or different (different letters) for each variable among four *Asplanchna*-released kairomone concentrations when fed 1.0×10^6 (unfilled bars) and 2.0×10^6 (filled bars) cells mL^{-1} of *S. obliquus*, respectively (LSD multiple comparison), and asterisk (*) indicates means that are different for each variable between two food levels ($P < 0.05$, *t*-test).

3.2 Population growth

At both algal levels, *Asplanchna*-released kairomone concentration affected significantly the rate of population growth ($P < 0.05$), but did not influenced lorica length and width, body size and egg volume of *B. angularis* ($P > 0.05$). Compared with the controls, and at 1.0×10^6 cells · mL^{-1} of *S. obliquus*, kairomone released by *Asplanchna* at 160 ind. L^{-1}

Table 1. Results of analysis of variance (two-way ANOVA) performed for each life-table demographic parameter of *B. angularis* exposed to four *Asplanchna*-released kairomone concentrations and cultured at two *S. obliquus* levels.

Variation source	*SS*	*df*	*MS*	*F*	*P*
Life expectancy at hatching					
Kairomone concentration (A)	1.63	3	0.54	24.35	<**0.01**
Algal density (B)	0.61	1	0.61	27.37	<**0.01**
A × B	0.55	3	0.18	8.18	<**0.01**
Error	0.36	16	0.02		
Average lifespan					
Kairomone concentration (A)	1.63	3	0.54	24.52	<**0.01**
Algal density (B)	0.60	1	0.60	27.09	<**0.01**
A × B	0.56	3	0.19	8.35	<**0.01**
Error	0.36	16	0.02		
Generation time					
Kairomone concentration (A)	1.66	3	0.55	16.81	<**0.01**
Algal density (B)	0.00	1	0.00	0.06	>0.05
A × B	0.09	3	0.03	0.88	>0.05
Error	0.53	16	0.03		
Net reproductive rate					
Kairomone concentration (A)	84.77	3	28.26	45.54	<**0.01**
Algal density (B)	8.66	1	8.66	13.96	<**0.01**
A × B	0.17	3	0.06	0.09	>0.05
Error	9.93	16	0.62		
Intrinsic rate of population increase					
Kairomone concentration (A)	0.20	3	0.07	9.39	<**0.01**
Algal density (B)	0.05	1	0.05	6.43	<**0.05**
A × B	0.02	3	0.01	0.84	>0.05
Error	0.11	16	0.01		
Proportion of sexual offspring					
Kairomone concentration (A)	0.02	3	0.01	15.01	<**0.01**
Algal density (B)	0.00	1	0.00	0.69	>0.05
A × B	0.00	3	0.00	1.36	>0.05
Error	0.00	16	0.00		

decreased the rate of population growth by 26.5%. At 2.0×10^6 cells · mL^{-1} of *S. obliquus*, kairomone released by *Asplanchna* at 40 ind. L^{-1} increased the rate of population growth by 6.75%, but that at 160 ind. L^{-1} decreased it by 6.75% (Fig. 3).

Two-way ANOVA showed that the rate of population growth of *B. angularis* was significantly affected by *Asplanchna*-released kairomone concentration, food level and their interaction. Both lorica length and egg volume of *B. angularis* were affected only by the interaction between *Asplanchna*- released kairomone concentration and food level (Tab. 2).

4 Discussion

Predation is recognized as a major factor affecting the life history traits of freshwater rotifers (reviewed in Gilbert, 2013). In order to understand life history strategies of rotifers under *Asplanchna* predation, both life table approach and renewed batch culture method are usually simultaneously used. When rotifer females of basic morph (parental females) were used as subject, life table approach was used to study its survival, reproduction and population growth under *Asplanchna* predation, but most population growth experiments included multiple, overlapping generations of rotifers, which would lead to inaccurate analyses on life-history strategies, because females of basic morph were not subject to possible allocation costs related to bearing longer, induced spines during postnatal growth and throughout their lifetime, but the proportion of induced morphs in the *Asplanchna* treatments was initially zero and then would have gradually increased over time as these females reproduced (reviewed in Gilbert, 2013). Gilbert (2013) proposed that the interval for population growth experiments has to be short, probably similar to the lifespan of the rotifer. Considering the short juvenile period (1.25 d) and fast embryonic development (0.73 d) of *B. angularis* at 20 °C (Walz, 1987), the present study allowed the rotifer populations to grow for only 3 days, and then obtained the population growth rate, and morphometric characters of the parental females and their egg sizes. Three-day population growth experiment is also usually used to test the effects of environmental factors such as temperature, salinity, food level and toxicant concentration on the population growth rates of rotifers (*e.g.* Snell, 1986; Radix *et al.*, 2002; Xi and Feng, 2004; Xi *et al.*, 2007).

Survivorship and offspring production are the two key components of fitness (Case, 2000; Stelzer, 2005). The studies on females of basic morph of several rotifer species showed

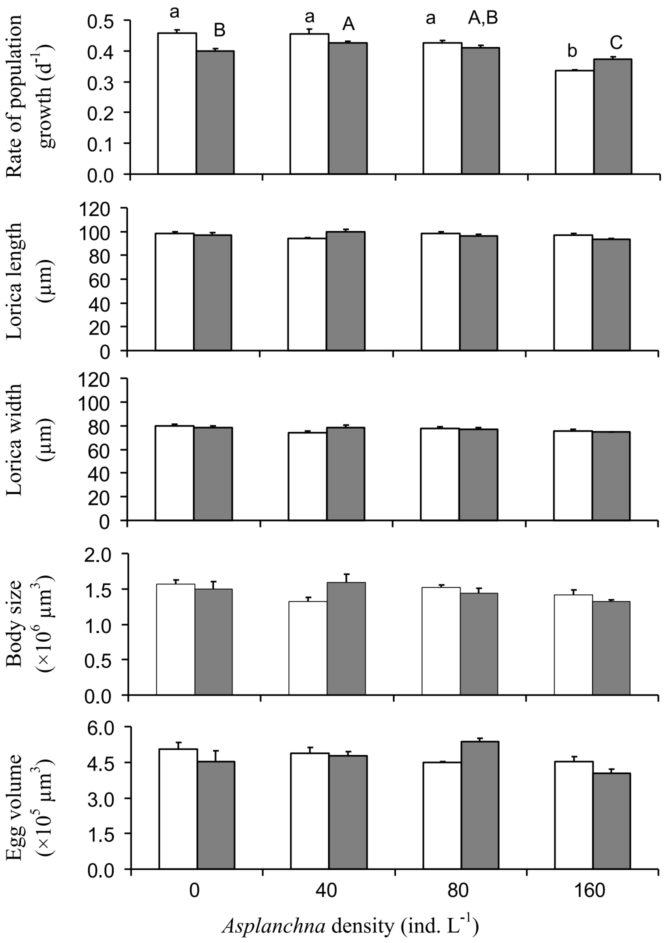

Fig. 3. Rate of population growth, lorica length and width, body size and egg volume of *B. angularis* exposed to kairomone concentrations released respectively by four densities of *Asplanchna* and cultured at two *S. obliquus* levels. Shown are the values mean + standard error based on three replicates. Small and capital letters indicate means that are similar (same letter) or different (different letters) for each variable among four *Asplanchna*-released kairomone concentrations when fed 1.0×10^6 (unfilled bars) and 2.0×10^6 (filled bars) cells mL^{-1} of *S. obliquus*, respectively (LSD multiple comparison).

that both the survival and the reproductive rate of rotifers were affected not only by temperature, food level and predator-released kairomone concentration, but also by rotifer species. At 15 °C under same food levels, both the survival and the reproductive rate of *B. havanaensis* Rousselet decreased significantly with increasing *Asplanchna*-released kairomone concentration; but at higher temperature and higher food density, they were not affected by *Asplanchna*-released kairomone concentration (Pavón-Meza *et al.*, 2008). The survival (average lifespan and life expectancy at hatching) of *B. calyciflorus* decreased in the presence of kairomone released by *A. brightwellii* at 800 ind. L^{-1}, but that of *Plationus patulus macracanthus* Daday (Segers, 2007) did not. The reproductive rate of *B. calyciflorus* decreased significantly with increasing *Asplanchna*-released kairomone concentration, and that of *P. patulus macracanthus* decreased in the presence of kairomone released by *A. brightwellii* at 800 ind. L^{-1} (Sarma *et al.*, 2011). The present study showed that at 1.0×10^6 cells · mL^{-1} of *S. obliquus*, kairomone released by *Asplanchna* at 40–160 ind. L^{-1} decreased the average lifespan and the life expectancy at hatching, and that released by *Asplanchna* at 80–160 ind. L^{-1} decreased the net reproduction rate of parental *B. angularis* females. The increase in food level decreased the effect magnitude of kairomone released by *Asplanchna* at 40 ind. L^{-1} on the average lifespan and the life expectancy at hatching, but increased that on the net reproduction rate.

Reproduction in one age class can be deleterious to parental survival to subsequent age classes. A greater investment in reproduction by rotifers often lowers survivorship (Sarma *et al.*, 2002; Ogello *et al.*, 2016). In the presence of kairomone released by salamander axolotl *Ambystoma mexicanum* Shaw & Nodder, *B. havanaensis* adopted the life history strategy of high reproduction and low survivorship; but in the presence of kairomone released by copepod *Acanthocyclops robustus* Sars, it adopted the opposite life history strategy of low reproduction and high survivorship (García *et al.*, 2007). *B. calyciflorus* exposed to *Asplanchna*-conditioned medium adopted the life history strategy of low reproduction and high survivorship (Guo *et al.*, 2011). However, in the present study, we did not find that *B. angularis* allocated energy between reproduction and survivorship, but increased investment in sexual reproduction was observed.

The kairomones released by fish (which prefer larger prey) cause an earlier reproduction, production of more but smaller eggs and overall body size reduction in *Daphnia* (Vanni, 1987; Machádek, 1991; Stibor, 1992). In the presence of kairomones released by invertebrate predators (which prefer smaller prey), individuals of some *Daphnia* clones delay their maturation and produce fewer but larger offspring (Spitze, 1991; Brett, 1992; Lüning, 1992; Pijanowska and Kowalczewski, 1997). In the present study, kairomone released by *A. brightwelli* did cause an earlier reproduction (shortened generation time) and production of fewer eggs (inferred from decreased net reproduction rate), but it did not affect body sizes of parental *B. angularis* females and their egg volumes. Therefore, whether energy expenditure in survival and reproduction of parental *B. angularis* females was saved and allocated to the hidden morphological defenses needs further investigation.

The population growth rate of rotifers generally decreased in the presence of *Asplanchna* kairomone (*e.g.* Pavón-Meza *et al.*, 2008; Aránguiz-Acuña *et al.*, 2010; Sarma *et al.*, 2011). However, the population growth rate of *B. havanaensis* increased in the presence of kairomone released by *A. mexicanum* or *A. robustus* (García *et al.*, 2007). In the present study, we found that *B. angularis* cultured at 2×10^6 cells · mL^{-1} of *S. obliquus* developed a significantly high intrinsic rate of population increase in the presence of kairomone released by *Asplanchna* at 80 ind. L^{-1} (the life table experiments) and a markedly high population growth rate in the presence of kairomone released by *Asplanchna* at 40 ind. L^{-1} (the population growth experiments), which supports the hypothesis that *B. angularis* develops a high population growth rate in response to kairomone released by a certain density of *Asplanchna*. The lower *Asplanchna* density resulting in the significantly high population growth rate of *B. angularis* might be attributed to accumulation of *Asplanchna* kairomone in the un-renewed medium during the three-day population growth experiments.

Table 2. Results of analysis of variance (two-way ANOVA) performed for rate of population growth and morphometric parameters of *B. angularis* exposed to four *Asplanchna*-released kairomone concentrations and cultured at two *S. obliquus* levels.

Variation source	*SS*	*df*	*MS*	*F*	*P*
Rate of population growth					
Kairomone concentration (A)	0.00	1	0.00	6.39	<**0.05**
Algal density (B)	0.03	3	0.01	35.86	<**0.01**
A × B	0.01	3	0.00	9.31	<**0.01**
Error	0.00	16	0.00		
Lorica length					
Kairomone concentration (A)	0.88	1	0.88	0.13	>0.05
Algal density (B)	25.55	3	8.52	1.22	>0.05
A × B	68.76	3	22.92	3.29	<**0.05**
Error	111.53	16	6.97		
Lorica width					
Kairomone concentration (A)	1.10	1	1.10	0.17	>0.05
Algal density (B)	52.07	3	17.36	2.76	>0.05
A × B	36.03	3	12.01	1.91	>0.05
Error	100.54	16	6.28		
Body size					
Kairomone concentration (A)	1.51×10^{6}	1	1.51×10^{6}	0.01	>0.05
Algal density (B)	8.66×10^{8}	3	2.89×10^{8}	1.74	>0.05
A × B	1.42×10^{9}	3	4.73×10^{8}	2.86	>0.05
Error	2.65×10^{9}	16	1.65×10^{8}		
Egg volume					
Kairomone concentration (A)	1.65×10^{6}	1	1.65×10^{6}	0.09	>0.05
Algal density (B)	1.49×10^{8}	3	4.96×10^{7}	2.64	>0.05
A × B	1.90×10^{8}	3	6.33×10^{7}	3.37	<**0.05**
Error	3.01×10^{8}	16	1.88×10^{7}		

Gilbert (2013) thought that higher *Asplanchna* densities may produce higher concentrations of excretory products which may inhibit, or promote, rotifer population growth. The results available now showed that higher densities of *A. brightwelli* promoted indirectly not only the population growth but also the lorica thickness and hardness of *B. angularis* (the resent study; Yin *et al.*, 2017). It might be difficult to conclude that all those indirect effects result from *Asplanchna* excretory products. The most ideal methodology for determining the effects of kairomone on population growth rates of rotifers would involve the use of both purified kairomone and chemostat cultures (Gilbert, 2013).

Pourriot (1986) thought that the rate at which planktonic rotifers multiply during the parthenogenetic phase, providing there is sufficient food, is due more to the short period of embryonic development and the early period of life than to the net reproduction rate. The kairomone released by copepod *A. robustus* decreased the generation time and thus increased the population growth rate of *B. havanaensis* (García *et al.*, 2007). Identical results were obtained in the present study, which supported the hypothesis that kairomone released by a certain density of *Asplanchna* shortens the generation time and thus increases the population growth rate of *B. angularis*.

As a predator avoidance strategy, diapause in *D. magna* can be induced by fish kairomones to avoid the predator in time instead of facing the enemy through defenses (Slusarczyk, 1995, 1999, 2001; Pijanowska and Stolpe, 1996). In the presence of kairomone released by *A. brightwellii* at 100 ind. L^{-1}, *B. calyciflorus* saves energy expenditure in sexual reproduction and allocates it to the production of more parthenogenetic offspring to offset predation loss, but *B. angularis* preserves the energy expenditure of sexual reproduction and maintains resting-egg production (Yin *et al.*, 2017). The present study showed that *B. angularis* exposed to the kairomone released by *A. brightwellii* at 80 and 160 ind. L^{-1} invested more energy in sexual reproduction, which supported the hypothesis that higher concentrations of *Asplanchna* kairomone induce higher levels of sexual reproduction, and verified the idea that under heavy predation pressure, with a low chance of survival for parthenogenetic females, resting egg formation may result in a higher fitness than immediate reproduction (Pijanowska and Stolpe, 1996).

5 Conclusion

Asplanchna-released kairomone decreased significantly average lifespan, life expectancy at hatching, generation time and net reproduction rate, but increased the proportion of sexual offspring of parental *B. angularis* females. The threshold *Asplanchna* density required for significant effects varied with food level. Kairomone released by *Asplanchna* at 80 ind. L^{-1} increased significantly the intrinsic rate of population increase of *B. angularis*, which would offset the mortality of exposed females from predation. The accumulation of kairomone in aquatic environments enhanced the indirect effect of *Asplanchna* on the population growth of *B. angularis*. Rapid population growth of *B. angularis* induced by

Asplanchna kairomone might facilitate the coexistence of preys with predators, and higher proportion of sexual offspring and then resting egg production might help the preys avoid the predator in time instead of facing the enemy through defenses.

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