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RESEARCH ARTICLE

Interspecific effects of the cladoceran- (*Moina macrocopa*) and the rotifer- (*Brachionus calyciflorus*) conditioned medium on main life history variables in relation to temperature and algal density

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Abstract – Current research on the effects of cladoceran allelochemicals on rotifers has been inconclusive and the allelopathic effects of rotifers on cladocerans are unknown. We sought to fill this knowledge gap with life table demography experiments assessing the interspecific effects of *Moina macrocopa*-conditioned mediums (MCM) and *Brachionus calyciflorus*-conditioned mediums (CCM) on the main life history variables under different temperatures and algal densities. Our results demonstrate that, when compared to the allelopathic effects of *M. macrocopa* on *B. calyciflorus*, *M. macrocopa* had higher sensitivity to the allelochemicals from *B. calyciflorus*. When compared to the controls, the chemically-mediated effects of *M. macrocopa* on the net reproductive rate (R_0), intrinsic rate of population growth (r_m) and total number of offspring (NO) of *B. calyciflorus* were non-significant in many cases while in a few the impacts were stimulatory or inhibitory under different concentrations of MCM, temperatures, and food densities. However, when compared to the controls, the allelopathic effects of *B. calyciflorus* on the R_0, r_m and NO of *M. macrocopa* were stimulatory in many cases; some impacts were inhibitory or non-significant under different concentrations of CCM, temperatures, and food densities. In addition, life expectancy at birth (e_0), generation time (T), and average lifespan (LS) of *B. calyciflorus* and *M. macrocopa* cultured in the conditioned medium nearly did not differ significantly from the controls. Our results suggest that the interspecific allelopathic effects of *B. calyciflorus* and *M. macrocopa* are dependent on the origin and concentration of the allelochemical, life history variable, temperature, and food (algal) density. Additionally, the underlying mechanisms should be further investigated.

Keywords: *Moina macrocopa* / *Brachionus calyciflorus* / allelopathic interaction / conditioned medium / life table demography

1 Introduction

Competition is a major biotic interaction regulating zooplankton population dynamics and community structure (*e.g.*, Rothhaupt, 1990; Chase *et al.*, 2002; Huang *et al.*, 2014). Rotifers and cladocerans are two common constituents and dominant groups of freshwater zooplankton communities (Dumont and Negrea, 2002; Wallace *et al.*, 2015). They overlap in their feeding niche (Dodson, 1974) and often compete for limited food resources. Cladocerans generally outcompete rotifers, due to a stronger exploitative and/or mechanical interference. They can also damage vulnerable rotifers to the extent of eliminating them from their natural ecosystem or culture medium in the laboratory (Gilbert, 1988). Natural planktonic structure is influenced by secondary metabolites from other aquatic organisms, which often act as allelochemicals (Sarma and Nandini, 2018). Many studies have focused on understanding the allelopathic effects of rotifer predators on their prey (*e.g.*, Pavón-Meza *et al.*, 2008; Peña-Aguado *et al.*, 2008; Guo *et al.*, 2011; Sarma *et al.*, 2011; Nandini *et al.*, 2014; Pan *et al.*, 2017, 2018), between cladocerans and algal foods (*e.g.*, Lampert *et al.*, 1994; Lürling and Van Donk, 1996; Ha *et al.*, 2001; Lürling, 2003; Yang *et al.*, 2007), and between rotifers and algal foods (*e.g.*, Yang *et al.*, 2005, 2008; Verschoor *et al.*, 2007; Ma *et al.*, 2018). Prey mainly adapts to and alleviates allelopathic stress through changes in behavior, morphology or life-history strategies (Lass and Spaak, 2003). These allelochemicals are generally species-specific secondary metabolites, whose effect may

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differ among zooplankton. Hence, these allelochemicals are potentially important in controlling the population dynamics of competing species and structuring the plankton community (Vet, 1999; Mitchell and Carvalho, 2002).

Zooplankton release their chemicals, not only into the water column, but also on the surface of their algal food and other animals (Guo *et al.*, 2011), resulting in phytoplanktivorous rotifers and cladocerans absorbing allelochemicals from both the water and their food (algae). The allelopathic interactions (*e.g.*, amount released) of rotifers and cladocerans are regulated by environmental factors, such as food density and temperature (Verschoor *et al.*, 2007; Pavón-Meza *et al.*, 2008). Different conditions influence the amount of allelopathic substances produced, and temperature increases can result in possible degradation of the allelopathic substances.

In subtropical and tropical water bodies, small cladocerans (*e.g.*, the genera *Moina*) can coexist with some rotifer species (*e.g.*, the genera *Brachionus*) (Nogrady *et al.*, 1993; Dumont *et al.*, 1994; Lampert and Sommer, 1997; Wen *et al.*, 2017). Their allelopathic interactions contribute to their coexistence, which may be regulated by allelopathic substances released by other small zooplankton. Hence, experiments assessing allelopathic interactions occurring within populations of one rotifer species and one cladoceran species will further the general understanding of the relationship among multiple rotifer and cladoceran species. Allelopathic effects of cladocerans on rotifers have been previously quantified (Conde-Porcuna, 1998; Guo *et al.*, 2011; Gama-Flores *et al.*, 2018). Conde-Porcuna (1998) found that allelochemicals from a cladoceran, *Daphnia longispina*, inhibit the reproduction and population growth of a rotifer, *Keratella cochlearis.* Conversely, allelochemicals secreted by a cladoceran, *D. similis*, stimulate the reproduction and population growth of a rotifer, *B. calyciflorus* (Guo *et al.*, 2011). Gama-Flores *et al.* (2018) focused on the effects of a cladoceran-conditioned medium on the demography of brachionid rotifers. This study found that among the three rotifer species, *B. havanaensis* was the most sensitive in regard to the life history variable response to allelopathic substances from cladocerans, especially *M. macrocopa*. Conversely, *B. calyciflorus* hardly responded to the cladoceran allelochemicals. Moreover, the effects (*i.e.*, stimulatory, inhibitory, or no response) of allelochemicals from the three cladoceran species on the population growth rates of the three rotifer species were not identical. These findings suggest that the effects of cladoceran allelochemicals on rotifers are inconclusive and depend on the rotifer species, rotifer life history variable, and origin of the allelochemical. Moreover, it remains unknown how rotifer-mediated allelochemicals affect the survivorship- or reproductive variables of cladocerans.

Our previous study focused on the outcomes of competition between *B. calyciflorus* and *M. macrocopa*, under different temperatures and food densities. We found that under each temperature condition, *M. macrocopa* outcompeted *B. calyciflorus* under low algal density conditions (0.5×10^6 cells/mL). The population growth rates of *B. calyciflorus* cultured with *M. macrocopa* were lower than the control growth rates. Meanwhile, the population growth rates of *M. macrocopa* cultured with *B. calyciflorus* were higher in the control growth rates, except under the highest temperature condition (Huang *et al.*, 2014). These results suggest that *B. calyciflorus* allelochemicals stimulated the population growth of *M. macrocopa*. Conversely, *B. calyciflorus* outcompeted *M. macrocopa* under higher algal density conditions (1.0 and 3.0×10^6 cells/mL). The population growth rates of *B. calyciflorus* cultured with *M. macrocopa* were lower than the control growth rates. However, the growth rates were higher under the combination of the two higher temperature conditions and the highest algal density (Huang *et al.*, 2014). This suggests that the *M. macrocopa* allelochemicals stimulated the population growth of *B. calyciflorus*. Based on these results, we speculated that allelopathic stimulation might exist in the competitive process of *M. macrocopa* and *B. calyciflorus*, which depends on the origin of allelochemicals, stage of the competitive process (*i.e.*, the relative density of *M. macrocopa* and *B. calyciflorus* equal with the relative concentration of allelochemicals from *M. macrocopa* and *B. calyciflorus*), temperature, and algal density.

Allelopathic substances released by zooplankton are poorly understood and their extraction, purification, composition, chemical structure, and function remain unclear (Kalacheva *et al.*, 2000; Ferland-Raymond *et al.*, 2010; Guo *et al.*, 2011; Sarma *et al.*, 2018). Therefore, many scholars rely on zooplankton-conditioned mediums to replace the naturally secreted allelochemicals to conduct relative studies (*e.g.*, Conde-Porcuna, 1998; Yang *et al.*, 2005, 2007, 2008; Verschoor *et al.*, 2007; Rodríguez *et al.*, 2010; Guo *et al.*, 2011; Gama-Flores *et al.*, 2018; Sarma *et al.*, 2018). Therefore, we also used plankton-conditioned mediums to replace the allelochemicals in our study.

We performed life table experiments to examine the interspecific effects of different concentrations of allelochemicals in *M. macrocopa*- and *B. calyciflorus*-conditioned medium on the main life history variables under different temperature and *S. obliquus* (algal) densities. These experiments tested the following hypotheses: (1) allelopathic stimulation exists in the competitive process between *M. macrocopa* and *B. calyciflorus*; (2) the allelopathy is stimulatory, inhibitory, or nearly invalid, depending on the origin and concentration of allelochemicals, life history variable, temperature, and algal density.

2 Materials and methods

2.1 Experimental organisms

B. calyciflorus was isolated from Lake Jiuliantang (31°33' N, 118° × 37' E, Wuhu city, China), and *M. macrocopa* was supplied by the Laboratory of Aquaculture Biology, Nagasaki University of Japan. Both species were clonally cultured from one amictic female for more than 1 year at 25 ± 1 °C under natural illumination *via* an incubator, using EPA medium (pH 7.4–7.8; prepared by dissolving 96 mg $NaHCO_3$, 60 mg $CaSO_4$, 60 mg $MgSO_4$ and 4 mg KCl in 1 L distilled water; USEPA, 1985) and *S. obliquus* ($1.0-2.0 \times 10^6$ cells/mL) as the exclusive food. Prior to experimentation, the two zooplanktons were fed on 0.5, 1.0, and 3.0×10^6 cells/mL *S. obliquus* at 20 ± 1, 25 ± 1, and 30 ± 1 °C for at least one week, respectively. During the period, the two zooplankton populations were kept in log-phase growth. *S. obliquus* were grown in a semicontinuous culture using HB-4 medium (Li *et al.*, 1959) refreshed daily at 40%. Algae in exponential growth were centrifuged at 3000 rpm for 5 min, resuspended in the EPA medium, then stored at 4 °C. Stock algae density was determined using a hemocytometer, and subsequently diluted to the desired experimental density.

2.2 Conditioned medium (CM)

Zooplankton- (*e.g.*, rotifer and cladoceran) conditioned medium usually contains the allelochemicals released by zooplankton in the culture process as well as the allelochemicals secreted by algae, providing food for the zooplankton. Verschoor *et al.* (2007) showed that the chemicals from *S. obliquus* have a strong stimulating effect on the feeding rate of *B. calyciflorus*. The findings suggested that the algae's allelochemicals may influence the feeding and reproduction rates of *M. macrocopa*. In this study, like the method of Conde-Porcuna (1998), we also used *S. obliquus*-conditioned mediums as controls under corresponding temperature and algae density to exclude any possible influence of *S. obliquus* allelochemicals on the reproduction and population growth of *M. macrocopa* and *B. calyciflorus*.

The *S. obliquus*-conditioned medium, *M. macrocopa*-conditioned medium (MCM), and *B. calyciflorus*-conditioned medium (CCM) were obtained separately with equivalent biomasses (Mitchell and Carvalho, 2002) every day. *S. obliquus*, *M. macrocopa* (< 24 h old), and *B. calyciflorus* (random age) were respectively placed in 200 mL of EPA medium in 250 mL glass beakers. After 24 h, the planktons were separated using a plankton mesh (pore size 20 μm). CMs were filtered using Millipore 0.22 μm filters (GSTF04700) to ensure that most of the present allelochemicals in the CM would not be degraded by microbial action (Loose *et al.*, 1993).

2.3 Life-table experiments

We conducted cohort life table tests for *B. calyciflorus* exposed separately to MCM at 0.5 and 1.0 ind./mL of *M. macrocopa* (MCM-1 and MCM-2, respectively) and individual life table tests for *M. macrocopa* exposed separately to CCM at 5.0 and 10.0 ind./mL of *B. calyciflorus* (CCM-1 and CCM-2, respectively) to test the allelopathic interactions between *B. calyciflorus* and *M. macrocopa* relative to the concentration of allelochemical, temperature, and algal density. The *S. obliquus*- (stored in EPA medium for 24 h) conditioned medium was the control to avoid the likely effects of *S. obliquus*' allelochemicals in MCM or CCM on *B. calyciflorus* or *M. macrocopa* (Conde-Porcuna, 1998; Verschoor *et al.*, 2007).

Tests were conducted in 5 mL mediums with algal densities of 0.5, 1.0, and 3.0×10^6 cells/mL *S. obliquus* in 8 mL transparent jars in a dark incubator at 20 ± 1, 25 ± 1, and 30 ± 1 °C, respectively. For the *B. calyciflorus* life table experiments, we used 81 test jars (3 temperatures × 3 algal densities × 3 treatments (MCM-1, MCM-2 plus 1 control) × 3 replicates) and each jar received 5 neonates (< 4 h old). For the *M. macrocopa* life table experiments, we used 405–540 test jars (3 temperatures × 3 algal densities × 3 treatments (CCM-1, CCM-2 plus 1 control) × 15–20 replicates) and each jar received 1 neonate (< 12 h old) of the third generation produced by parthenogenetic reproduction of *M. macrocopa*. Following inoculation, the surviving test individuals were counted every 12 h and transferred to a new jar containing corresponding algal densities (0.5, 1.0, and 3.0×10^6 cells/mL *S. obliquus*) and MCM or CCM under different temperatures (20 ± 1, 25 ± 1, and 30 ± 1 °C). Dead individuals and neonates, if any, were enumerated and removed. Both experiments were continued until the last adult individual in each replicate died.

The main life history variables including life expectancy at birth (e_0), net reproductive rate (R_0), generation time (T), intrinsic rate of population growth (r_m), average lifespan (LS), total number of offspring (NO) of *B. calyciflorus* and *M. macrocopa* were calculated using the following formulas (Pianka, 1988):

Life expectancy at birth (start of age $x = 0$) $e_x = \frac{T_x}{n_x}$,

where T_x is the cumulative number of individuals from age x to maximum age, n_x = number of living individuals at the beginning of age x.

Net reproductive rate $(R_0) = \sum_0^\infty 1_x \cdot m_x$,

where l_x (age-specific survival rate) is proportion of living individuals at the beginning of age x, m_x (age-specific fecundity) is number of offspring produced per female at age x.

Generation time $(T) = \frac{\sum_0^\infty 1_x \cdot m_x \cdot x}{R_0}$.

Intrinsic rate of population growth (r_m) was firstly estimated as r-rough $= \frac{\ln R_0}{T}$.

For final calculation, we solved the equation: $\sum_{x=0}^{n} e^{-rx} \cdot 1_x \cdot m_x = 1$, where n is the age at maturity.

Total number of offspring (NO) is number of offspring produced per *M. macrocopa* or *B. calyciflorus* female during whole lifetime.

2.4 Statistical analysis

Analysis-of-variance (ANOVA) and multiple comparison tests were performed with SPSS 16.0 to quantify significant differences in the life expectancy at birth (e_0), net reproductive rate (R_0), generation time (T), intrinsic rate of population growth (r_m), average lifespan (LS), and total number of offspring (NO) of *B. calyciflorus* and *M. macrocopa* between the zooplankton-conditioned medium and control under different temperatures and algal densities. Data were first tested for homoscedasticity (Levene's test for ANOVA) and normality (Kolmogorov-Smirnoff test). Data that were non-normal or heteroscedastic were then analyzed using the Kruskal-Wallis tests.

3 Results

3.1 Effect of MCM concentration on *B. calyciflorus*

The three-way ANOVA results on the effects of temperature, algal density, and MCM concentration and their interactions on the main life history variables (*i.e.*, e_0, R_0, T, r_m, LS, and NO) of *B. calyciflorus* are presented in Table 1. Temperature, algal density and interactions of temperature × algal density, algal density × MCM and temperature × algal

Table 1. Results of the three-way ANOVA testing the effects of temperature, algal density, competitor-conditioned medium concentration and their interactions on the selected life history variables of *B. calyciflorus* and *M. macrocopa*.

Source of variation	DF	SS	MS	*F*
B. calyciflorus				
Life expectancy at birth (e_0)				
Temperature	2	18351.81	9175.91	313.43 ***
Algal density	2	181.39	90.69	3.10 *
MCM	2	2.73	1.37	0.05 ns
Temperature × Algal density	4	570.13	142.53	4.87 **
Temperature × MCM	4	191.84	47.96	1.64 ns
Algal density × MCM	4	297.28	74.32	2.54 *
Temperature × Algal density × MCM	8	196.47	24.56	0.84 ns
Error	54	1580.91	29.28	
Net reproductive rate (R_0)				
Temperature	2	28.16	14.08	125.76 ***
Algal density	2	7.46	3.73	33.34 ***
MCM	2	0.09	0.04	0.38 ns
Temperature × Algal density	4	10.74	2.69	23.98 ***
Temperature × MCM	4	0.40	0.10	0.88 ns
Algal density × MCM	4	1.65	0.41	3.68 **
Temperature × Algal density × MCM	8	1.99	0.25	2.22 *
Error	54	6.05	0.11	
Generation time (T)				
Temperature	2	7925.84	3962.92	115.74 ***
Algal density	2	118.02	59.01	1.72 ns
MCM	2	99.51	49.76	1.45 ns
Temperature × Algal density	4	1031.47	257.87	7.53 ***
Temperature × MCM	4	421.81	105.45	3.08 *
Algal density × MCM	4	536.89	134.22	3.92 **
Temperature × Algal density × MCM	8	193.26	24.16	0.71 ns
Error	54	1848.90	34.24	
Intrinsic rate of population growth (r_m)				
Temperature	2	1.86	0.93	60.79 ***
Algal density	2	0.22	0.11	7.08 **
MCM	2	0.05	0.02	1.53 ns
Temperature × Algal density	4	0.23	0.06	3.83 **
Temperature × MCM	4	0.09	0.02	1.52 ns
Algal density × MCM	4	0.08	0.02	1.38 ns
Temperature × Algal density × MCM	8	0.06	0.01	0.50 ns
Error	54	0.82	0.02	
Average lifespan (LS)				
Temperature	2	38056.47	19028.23	860.40 ***
Algal density	2	168.41	84.20	3.81 *
MCM	2	0.59	0.29	0.01 ns
Temperature × Algal density	4	443.67	110.92	5.02 **
Temperature × MCM	4	133.48	33.37	1.51 ns
Algal density × MCM	4	239.82	59.96	2.71 *
Temperature × Algal density × MCM	8	176.66	22.08	1.00 ns
Error	54	1194.24	22.12	
Total number of offspring (NO)				
Temperature	2	37.75	18.87	148.00 ***
Algal density	2	9.88	4.94	38.74 ***
MCM	2	0.26	0.13	1.02 ns
Temperature × Algal density	4	13.09	3.27	25.66 ***
Temperature × MCM	4	0.36	0.09	0.70 ns
Algal density × MCM	4	1.41	0.35	2.76 *
Temperature × Algal density × MCM	8	1.89	0.24	1.85 ns

Table 1. (continued).

Source of variation	DF	SS	MS	*F*
Error	54	6.89	0.13	
M. macrocopa				
Life expectancy at birth (e_0)				
Temperature	2	972.87	486.44	433.61 ***
Algal density	2	29.25	14.63	13.04 ***
CCM	2	0.48	0.24	0.21 ns
Temperature × Algal density	4	17.06	4.27	3.80 *
Temperature × CCM	4	12.73	3.18	2.84 *
Algal density × CCM	4	0.81	0.20	0.18 ns
Temperature × Algal density × CCM	8	14.38	1.80	1.60 ns
Error	54	60.58	1.12	
Net reproductive rate (R_0)				
Temperature	2	2336.31	1168.16	43.58 ***
Algal density	2	2785.49	1392.75	51.96 ***
CCM	2	7074.58	3537.29	131.96 ***
Temperature × Algal density	4	1926.10	481.52	17.96 ***
Temperature × CCM	4	1382.06	345.52	12.89 ***
Algal density × CCM	4	1722.26	430.57	16.06 ***
Temperature × Algal density × CCM	8	1185.94	148.24	5.53 ***
Error	54	1447.56	26.81	
Generation time (T)				
Temperature	2	522.58	261.29	2044.00 ***
Algal density	2	0.47	0.24	1.84 ns
CCM	2	1.22	0.61	4.77 *
Temperature × Algal density	4	4.07	1.02	7.95 ***
Temperature × CCM	4	3.59	0.90	7.02 ***
Algal density × CCM	4	1.80	0.45	3.51 *
Temperature × Algal density × CCM	8	0.89	0.11	0.87 ns
Error	54	6.90	0.13	
Intrinsic rate of population growth (r_m)				
Temperature	2	4.22	2.11	2494.00 ***
Algal density	2	0.02	0.01	8.89 ***
CCM	2	0.24	0.12	140.24 ***
Temperature × Algal density	4	0.02	0.01	6.63 ***
Temperature × CCM	4	0.13	0.03	39.63 ***
Algal density × CCM	4	0.11	0.03	33.78 ***
Temperature × Algal density × CCM	8	0.06	0.01	8.19 ***
Error	54	0.05	0.00	
Average lifespan (LS)				
Temperature	2	6975.07	3487.53	422.33 ***
Algal density	2	204.11	102.05	12.36 ***
CCM	2	3.48	1.74	0.21 ns
Temperature × Algal density	4	112.92	28.23	3.42 **
Temperature × CCM	4	75.87	18.97	2.30 *
Algal density × CCM	4	7.84	1.96	0.24 ns
Temperature × Algal density × CCM	8	109.20	13.65	1.65 ns
Error	555	4583.11	8.26	
Total number of offspring (NO)				
Temperature	2	20845.13	10422.57	41.61 ***
Algal density	2	19628.62	9814.31	39.18 ***
CCM	2	41237.25	20618.63	82.31 ***
Temperature × Algal density	4	12119.60	3029.90	12.10 ***
Temperature × CCM	4	9331.13	2332.78	9.31 ***
Algal density × CCM	4	10472.76	2618.19	10.45 ***

Table 1. (continued).

Source of variation	DF	SS	MS	*F*
Temperature × Algal density × CCM	8	8752.73	1094.09	4.37 ***
Error	555	139026.10	250.50	

MCM: *M. macrocopa*-conditioned medium; CCM: *B. calyciflorus*-conditioned medium.
DF: degrees of freedom; SS: sum of squares; MS: mean square; *F*: *F*-ratio.
ns: non-significant ($P > 0.05$).
* Significant ($P < 0.05$).
** Highly significant ($P < 0.01$).
*** Very highly significant ($P < 0.001$).

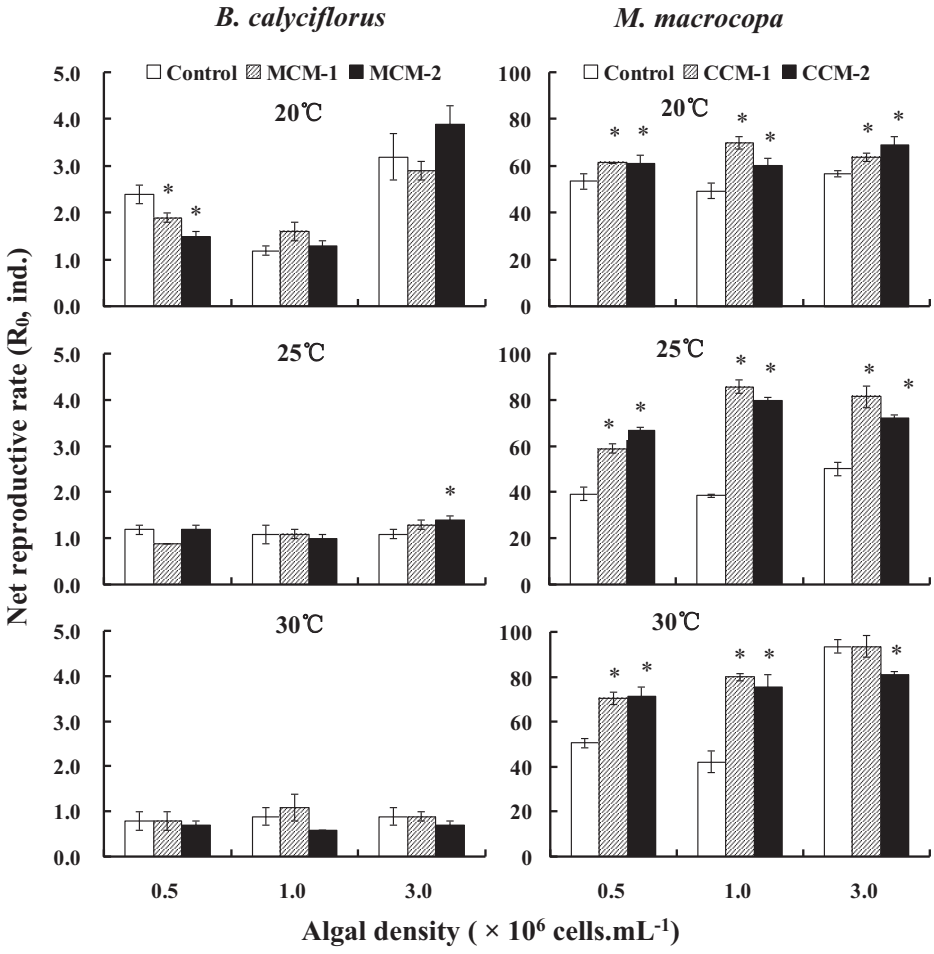

Fig. 1. Effects of two concentrations of competitor-conditioned medium on the net reproductive rate (R_0) of *B. calyciflorus* and *M. macrocopa* under different temperatures and algal densities (mean ± SE). Control, MCM-1, MCM-2, CCM-1, CCM-2 and * are same with Figure 4.

density × MCM had significant effects on the R_0 of *B. calyciflorus* ($P < 0.05$, Tab. 1). Temperature, algal density, and their interaction also had significant effects on the r_m of *B. calyciflorus* ($P < 0.01$, Tab. 1). Compared to the controls, both the R_0 and r_m of *B. calyciflorus* in MCM were significantly reduced under the combination of 20 °C and 0.5×10^6 cells/mL algal density ($P < 0.05$, Figs. 1 and 2). However, the R_0 and r_m of *B. calyciflorus* in MCM were significantly elevated in MCM-2 under the combination of 25 °C and 3.0×10^6 cells/mL algal density ($P < 0.05$, Figs. 1 and 2). The both variables had no significant difference under the other combinations of temperature and algal density ($P > 0.05$, Figs. 1 and 2).

Temperature, algal density and interactions of temperature × algal density and algal density × MCM also had significant effects on the NO of *B. calyciflorus* ($P < 0.05$, Tab. 1). Compared to the controls, the NO of *B. calyciflorus* in MCM were significantly decreased under the combination of 20 °C and 0.5×10^6 cells/mL algal density ($P < 0.05$, Fig. 3). The

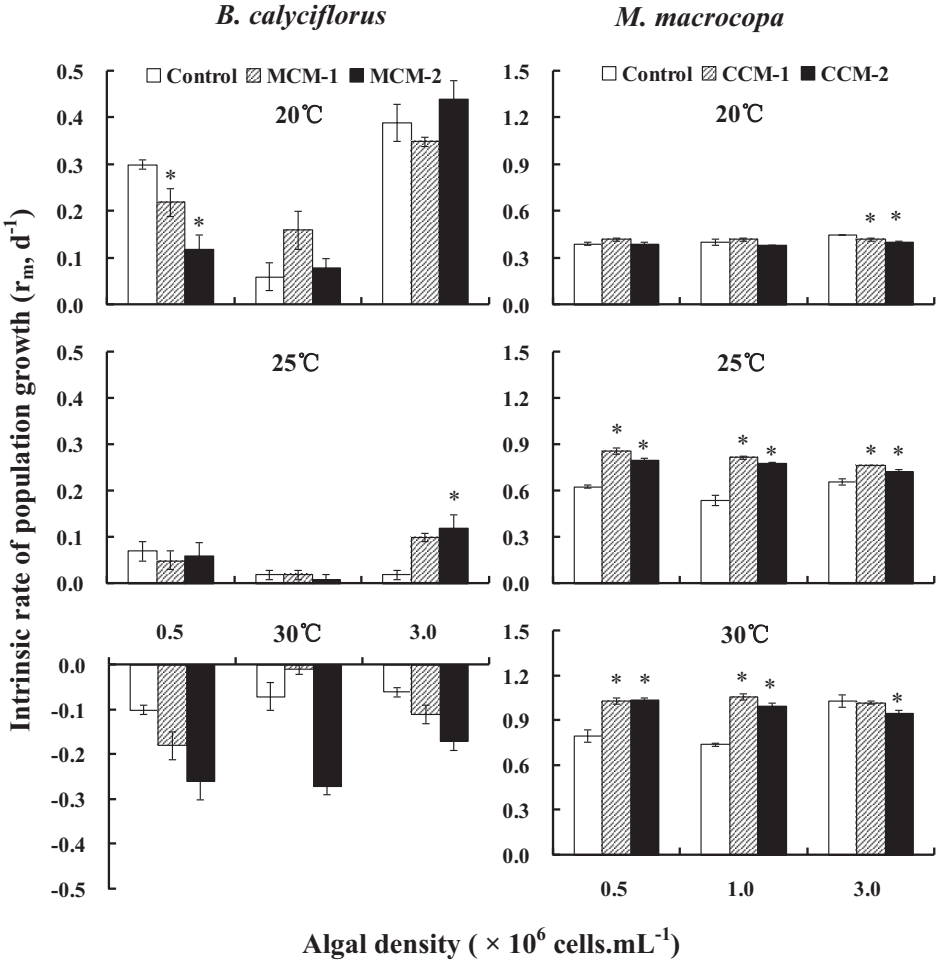

Fig. 2. Effects of two concentrations of competitor-conditioned medium on the intrinsic rate of population growth (r_m) of *B. calyciflorus* and *M. macrocopa* under different temperatures and algal densities (mean ± SE). Control, MCM-1, MCM-2, CCM-1, CCM-2 and * are same with Figure 4.

variable had no significant difference under the other combinations of temperature and algal density ($P > 0.05$, Fig. 3).

Temperature, algal density, and the temperature × algal density and algal density × MCM interactions had significant effects on the e_0 and LS of *B. calyciflorus* ($P < 0.05$, Tab. 1). Compared to the controls, neither the e_0 or LS of *B. calyciflorus* in MCM had significant changes ($P > 0.05$, Figs. 4 and 5), except that they were significantly prolonged under the combination of 25 °C and 1.0×10^6 cells/mL algal density ($P < 0.05$, Figs. 4 and 5). Regardless of temperature and algal density, compared to the controls, MCM had no significant effects on the T of *B. calyciflorus* ($P > 0.05$, Fig. 6).

3.2 Effect of CCM concentration on *M. macrocopa*

The three-way ANOVA results on the effects of temperature, algal density, CCM concentration, and their interactions on the main life history variables (*i.e.*, e_0, R_0, T, r_m, LS, and NO) of *M. macrocopa* are presented in Table 1. Temperature, algal density, CCM, and their interactions all had significant effects on the R_0, r_m and NO of *M. macrocopa* ($P < 0.001$, Tab. 1). The R_0, r_m and *NO* of *M. macrocopa* cultured in CCM were significantly higher than in controls at all temperatures and algal densities ($P < 0.05$, Figs. 1–3), expect under a few conditions. Compared to the controls, R_0, r_m and NO were significantly lower under the combination of 30 °C, 3.0×10^6 cells/mL algal density and CCM-2. The T was also prolonged under the combination of 20 °C and 3.0×10^6 cells/mL algal density ($P < 0.05$, Figs. 1–3 and 6). The r_m of *M. macrocopa* was not significantly affected under the combination of 20 °C and 0.5 and 1.0×10^6 cells/mL algal density ($P > 0.05$, Fig. 2).

Temperature, algal density, and the temperature × algal density and temperature × CCM interactions had significant effects on the e_0 and LS of *M. macrocopa* ($P < 0.05$, Tab. 1). Both the e_0 and LS of *M. macrocopa* cultured in CCM-1 were significantly shorter than in the controls under the combination of 20 °C and 3.0×10^6 cells/mL algal density ($P < 0.05$, Figs. 4 and 5). The e_0 and LS of *M. macrocopa* cultured in CCM-1 were, however, significantly longer than in the controls under the combination of 25 °C and 3.0×10^6 cells/mL algal density ($P < 0.05$, Figs. 4 and 5). The both variables were not significantly affected under the other combinations of temperature and algal density compared to the controls ($P > 0.05$, Figs. 4 and 5). Regardless of temperature and algal

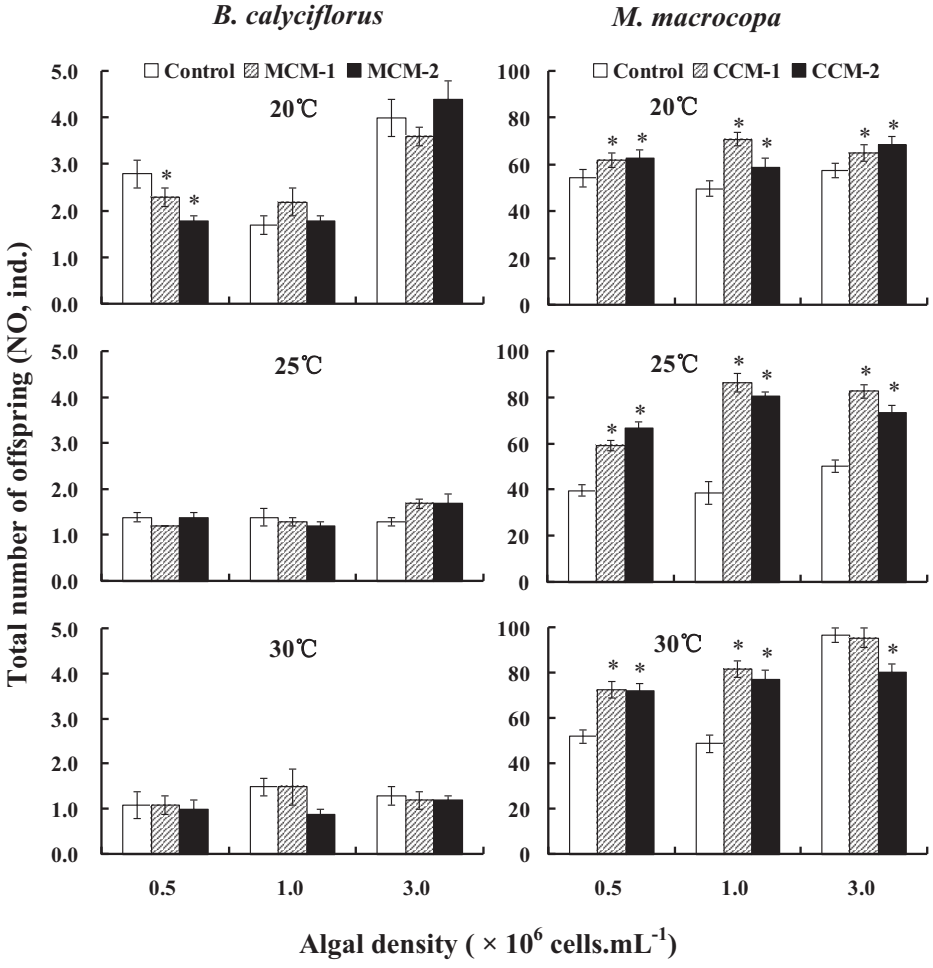

Fig. 3. Effects of two concentrations of competitor-conditioned medium on the total number of offspring (NO) of *B. calyciflorus* and *M. macrocopa* under different temperatures and algal densities (mean ± SE). Control, MCM-1, MCM-2, CCM-1, CCM-2 and * are same with Figure 4.

density, compared to the controls, CCM had no significant effects on the *T* of *M. macrocopa* ($P > 0.05$, Fig. 6), except in CCM-2 under the combination of 20 °C and 3.0×10^6 cells/mL algal density ($P > 0.05$, Fig. 6).

4 Discussion

Many field observations and laboratory studies have shown that cladocerans inhibit the population growth of rotifers through exploitative competition and mechanical interference competition (Gilbert, 1985, 1988; Burns and Gilbert, 1986a, b). The relative importance of the two competitive mechanisms is debatable (Gilbert, 1985; Fussmann, 1996). Chemical interference through allelopathy has been documented for some zooplankton species and many respond to this stress (Tollrian and Harvell, 1999; Brönmark and Hansson, 2012). Only three cases of the allelopathic effects of cladocerans on rotifers have been reported to date (Conde-Porcuna, 1998; Guo *et al.*, 2011; Gama-Flores *et al.*, 2018). *D. longispina* allelochemicals inhibit the population growth rate of *K. cochlearis* (Conde-Porcuna, 1998). Contrarily, *D. similis* allelochemicals stimulate the population growth rate of *B. calyciflorus* (Guo *et al.*, 2011). Gama-Flores *et al.* (2018) found that, compared to *B. calyciflorus* and *Plationus patulus*, *B. havanaensis* is more sensitive to the allelochemicals from *Ceriodaphnia dubia* and *D. pulex*, and especially to *M. macrocopa*. Inconsistent effects of allelochemicals from the three cladocerans on the population growth rates of the three rotifers were also detected. The effects of allelochemicals from cladoceran species on different rotifer species were either inconclusive, stimulating or inhibiting, or almost invalid, suggesting that the interaction depends on the origin of the allelochemical as well as the rotifer type. In fact, allelochemical concentrations in cladoceran-conditioned mediums accompanied with algae are higher than that in the controls without algae in the pre-culture experiments (Guo *et al.*, 2011; Gama-Flores *et al.*, 2018). Together, with the results that *S. obliquus* chemicals have a strong stimulating effect on the feeding rate of *B. calyciflorus* (Verschoor *et al.*, 2007), allelochemicals from algae (*i.e.*, food sources) may be responsible for the stimulatory effects of allelochemicals in cladoceran-conditioned medium on the population growth rates of the rotifers. The allelochemicals released by various algae that universally stimulated the feeding rates of different rotifers deserves further investigation.

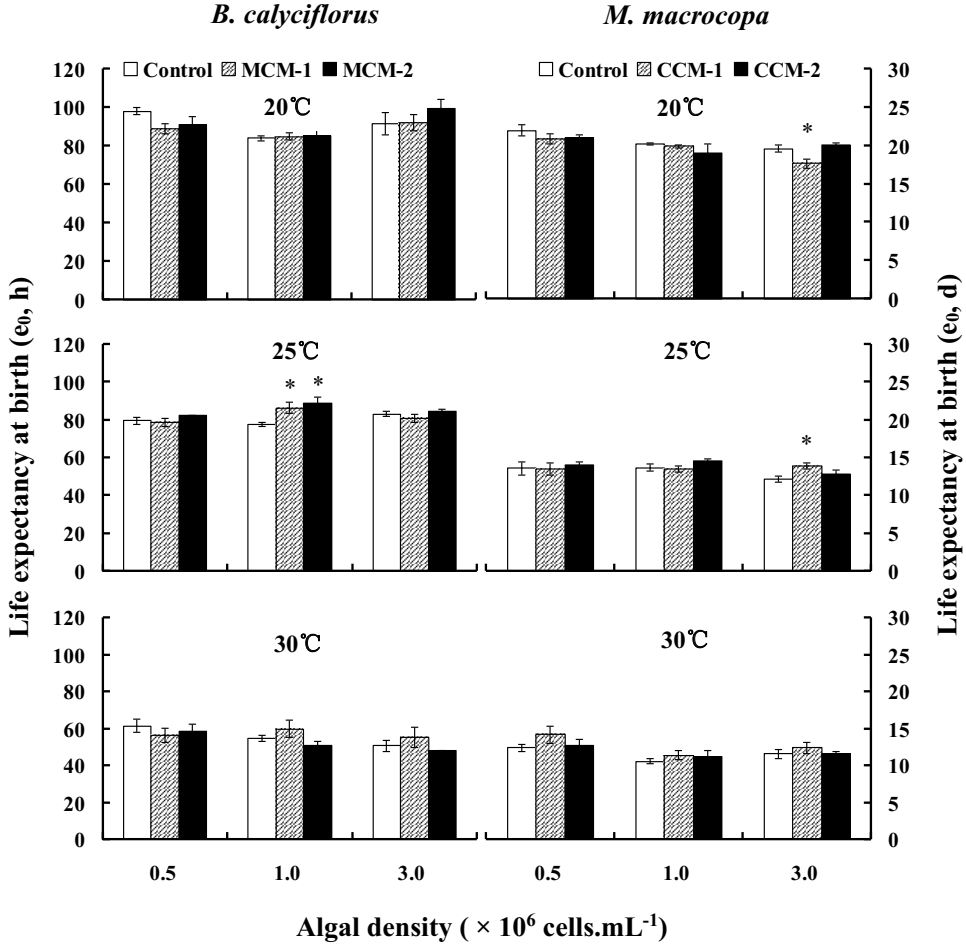

Fig. 4. Effects of two concentrations of competitor-conditioned medium on the life expectancy at birth (e_0) of *B. calyciflorus* and *M. macrocopa* under different temperatures and algal densities (mean ± SE). Control: *S. obliquus*-conditioned medium; MCM-1 and MCM-2: conditioned medium at 0.5 and 1.0 ind./mL^{-1} of *M. macrocopa* respectively; CCM-1 and CCM-2: conditioned medium at 5.0 and 10.0 ind./mL^{-1} of *B. calyciflorus* respectively; * $P < 0.05$.

Using the Conde-Porcuna (1998) method, *S. obliquus*-conditioned medium served as the control to exclude the effects of allelochemicals secreted by *S. obliquus* on the feeding rate of *B. calyciflorus*. Both R_0 and r_m of *B. calyciflorus* in MCM were inhibited under the combination of 20 °C and 0.5×10^6 cells/mL algal density, as consistent with the findings of Conde-Porcuna (1998). Our previous study found that under the same temperature and density of *S. obliquus*, competition of *M. macrocopa* inhibited the population growth rates of *B. calyciflorus*, which resulted in the elimination of *B. calyciflorus* (Huang *et al.*, 2014). These results indicated that the allelopathic inhibition of *M. macrocopa* on *B. calyciflorus* likely played a positive role in the competitive rejection of *B. calyciflorus*.

In the present study, both R_0 and r_m of *B. calyciflorus* were stimulated in MCM-2 under the combination of 25 °C and 3.0×10^6 cells/mL *S. obliquus*, which supported our first hypothesis and Guo *et al.*'s (2011) conclusions. Under the same temperature and *S. obliquus* density conditions, the results of Huang *et al.* (2014) found that *M. macrocopa*'s competition pressure stimulated the *B. calyciflorus*' population growth rate, and finally eliminated *M. macrocopa.* The allelopathic promotion of *M. macrocopa* on *B. calyciflorus* also likely aided the competitive rejection of *M. macrocopa*. Additionally, in our present study, the *B. calyciflorus*' NO in MCM was higher than that in controls under the combination of 20 °C and 0.5×10^6 cells/mL *S. obliquus*, while under the other combinations of temperature and algal density did not differ from the controls.

The present study found that the chemically-mediated effects of *M. macrocopa* on the R_0, r_m and NO of *B. calyciflorus* were non-significant in many cases. The impacts were stimulatory or even inhibitory in a few cases that were dependent on temperature, food density, concentration of *M. macrocopa* allelochemical, and type of life history variables of *B. calyciflorus.* These results support our two hypotheses: (1) allelopathic stimulation exists in the competitive process between *M. macrocopa* and *B. calyciflorus*; (2) the allelopathy is stimulatory, inhibitory, or nearly invalid, depending on the origin and concentration of allelochemicals, life history variable, temperature, and algal density. However, more research should be performed to distinguish the relative importance of chemical interference, exploitative, and mechanical interference competitions in interspecific interactions of *M. macrocopa* and *B. calyciflorus.*

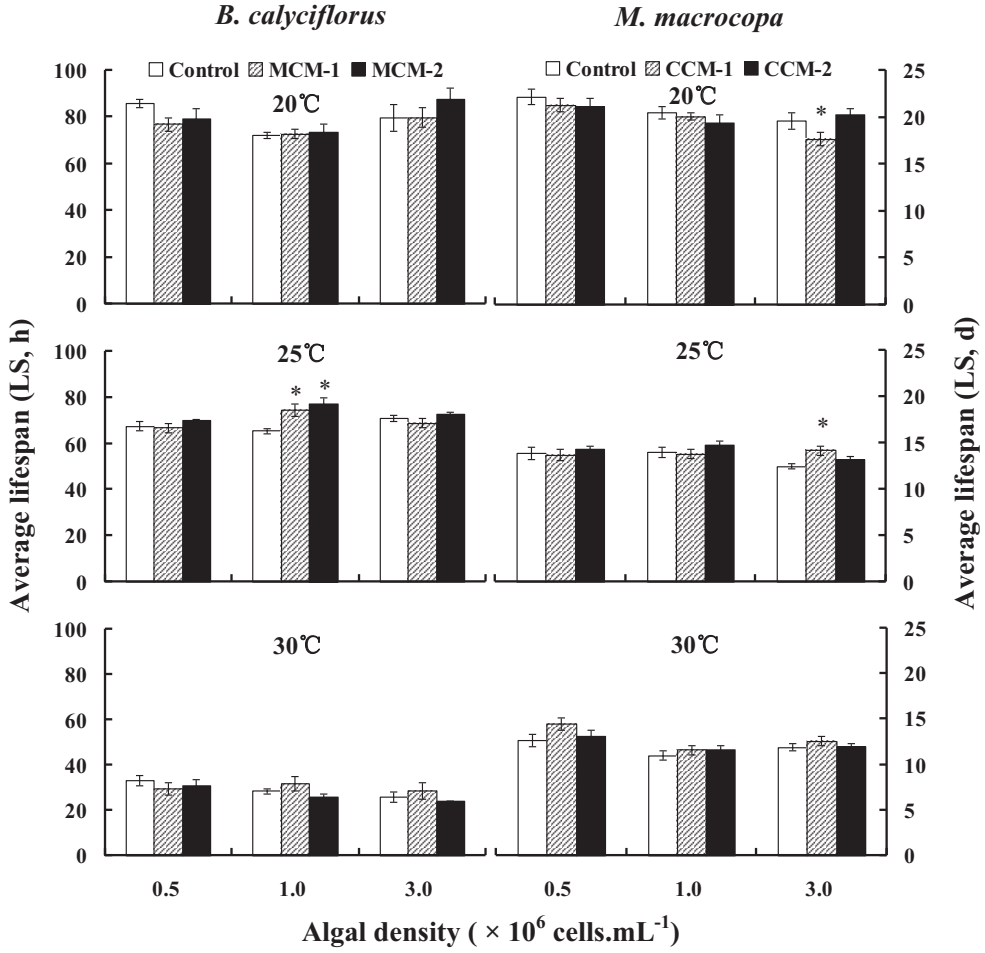

Fig. 5. Effects of two concentrations of competitor-conditioned medium on the average lifespan (LS) of *B. calyciflorus* and *M. macrocopa* under different temperatures and algal densities (mean ± SE). Control, MCM-1, MCM-2, CCM-1, CCM-2 and * are same with Figure 4.

Allelopathic effects of rotifers on cladocerans have not been reported until now. Our previous study (Huang *et al.*, 2014) found that, regardless of temperature, *M. macrocopa* outcompeted *B. calyciflorus* at 0.5×10^6 cells/mL *S. obliquus*, but the competition pressure of *B. calyciflorus* promoted the population growth rate of *M. macrocopa*. This implies that the chemical interference competitive stimulatory effects of *B. calyciflorus* on *M. macrocopa* are responsible for the increase in *M. Macrocopa*'s population growth rate. In the present study, regardless of temperature, the R_0, r_m and NO of *M. macrocopa* cultured in CCM were significantly higher than those in the controls at 0.5×10^6 cells/mL *S. obliquus*, with a few exceptions. These results support our previous study's implied results and our first hypothesis. These results also prove that allelopathic promotion of *B. calyciflorus* on *M. macrocopa* aids the competitive rejection of *B. calyciflorus*.

The *M. macrocopa*'s r_m cultured in CCM did not significantly differ from that in the controls under the combination of 20 °C and 0.5×10^6 cells/mL *S. obliquus*. This indicates that the allelopathic promotion of *B. calyciflorus* on *M. macrocopa* decreased under the lower temperature. Thus, the allelopathic stimulatory effects of *B. calyciflorus* on *M. macrocopa* were dependent on temperature. Regardless of temperature, Huang *et al.* (2014) proved that the population growth rates of *M. macrocopa* cultured with *B. calyciflorus* were higher than that in the controls (except under the highest temperature). Furthermore, the population densities increased after an initial decrease compared to that in the controls with higher densities of *S. obliquus* (1.0 and 3.0×10^6 cells/mL). Huang *et al.* (2014) also implied that the chemical interference competitive stimulatory effects of *B. calyciflorus* on *M. macrocopa* were responsible for the higher population growth rates and population densities of *M. macrocopa* cultured with *B. calyciflorus*. In the present study, regardless of temperature, the R_0, r_m and NO of the *M. macrocopa* cultured in CCM were almost all significantly higher than in the controls with higher densities of *S. obliquus* (1.0 and 3.0×10^6 cells/mL). These findings support our 2014 (Huang *et al.*) implied findings and further supports our first hypothesis.

However, *B. calyciflorus* excluded *M. macrocopa* under the same temperatures and densities of *S. obliquus* (Huang *et al.*, 2014), which indicated that the allelopathic promotion was lower than the exploitative inhibition of *B. calyciflorus* on *M. macrocopa*, and that the exploitative interference was more important. Meanwhile, compared to the controls, the R_0, r_m, and NO of *M. macrocopa* cultured in CCM were significantly lower under the combination of 30 °C, 3.0×10^6 cells/mL algal density and CCM-2. The r_m was significantly lower, likely due

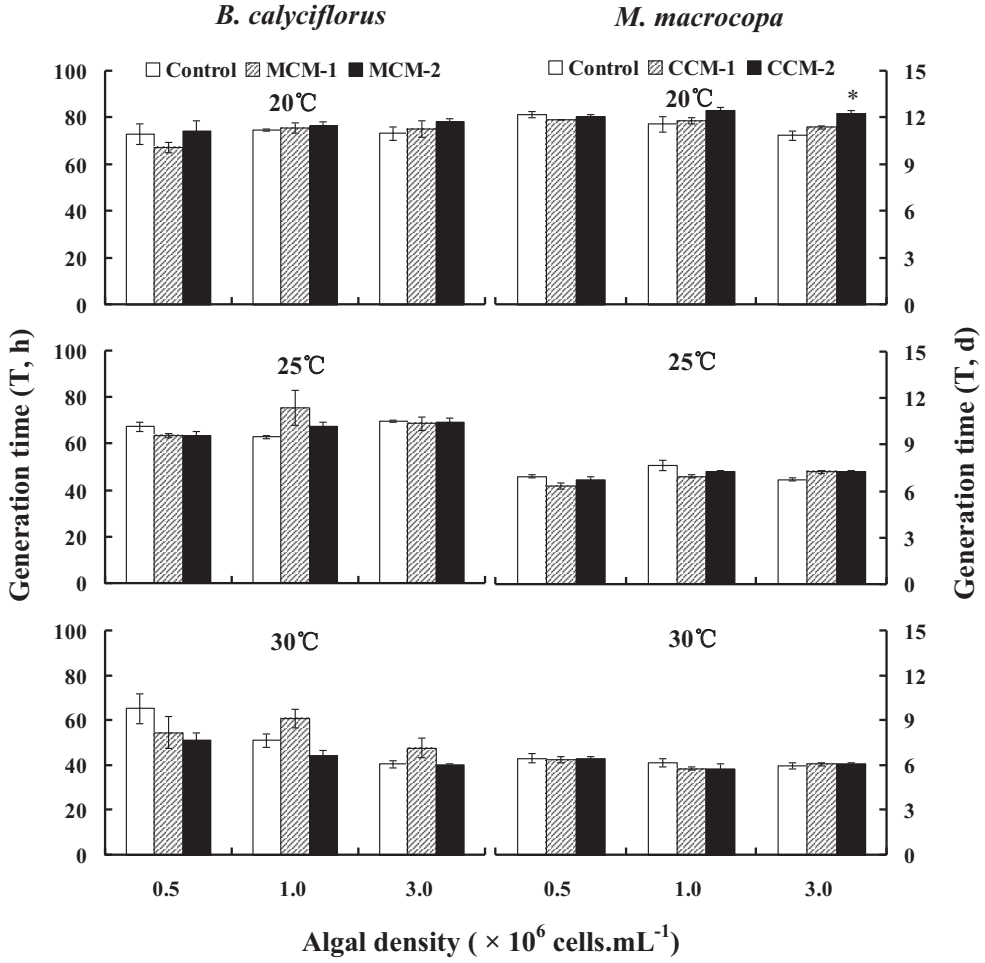

Fig. 6. Effects of two concentrations of competitor-conditioned medium on the generation time (*T*) of *B. calyciflorus* and *M. macrocopa* under different temperatures and algal densities (mean ± SE). Control, MCM-1, MCM-2, CCM-1, CCM-2 and * are same with Figure 4.

to the prolongation of the *T* under the combination of 20 °C and 3.0×10^6 cells/mL algal density. This indicates that the allelopathic inhibition of *B. calyciflorus* on *M. macrocopa* aided the competitive rejection of *M. macrocopa*. Additionally, the r_m of *M. macrocopa* cultured in CCM was not significantly affected under the combination of 20 °C and 1.0×10^6 cells/mL algal density. Based on these results, we found that the allelopathic effects of *B. calyciflorus* on the R_0, r_m, and NO of *M. macrocopa* were stimulatory in many cases, were inhibitory in a few cases, or were non-significant. The effects were dependent on temperature, food density, *M. macrocopa* life history variable, and the concentration of *B. calyciflorus* allelochemicals.

Our study found that the e_0, *T*, and LS of *B. calyciflorus* were significantly affected in only few cases due to MCM at all temperatures and algal densities. These findings are similar to the effects of CCM on the three life history variables of *M. macrocopa.* Similar results were observed in Gama-Flores *et al.* (2018). Based on the e_0, *T*, and LS, the interspecific effects of *B. calyciflorus*- and *M. macrocopa*-mediated allelochemicals are almost all invalid, indicating that the allelopathic effects between *B. calyciflorus* and *M. macrocopa* were dependent on the life history variable.

Our results found that the allelopathic substances from *M. macrocopa* and *B. calyciflorus* affected their life history variables in varying degrees. The allelopathic substances are, however, likely different in composition, amount, and activity. Prior to the present study, the information on the chemical nature of substances secreted by crustaceans and rotifers was almost completely lacking (Zadereev and Lopatina, 2015). The main difficulties in isolating and identifying these substances are related to their low concentrations in the medium, potential synergistic effects, and absence of easy and effective methods for determining the target components (Pohnert *et al.*, 2007). Extraction, isolation, structure identification, and function studies of rotifer and cladoceran allelochemicals should be addressed in future work. These findings would be of crucial importance for understanding the interspecific competitive mechanism of zooplankton, especially rotifers and cladocerans, and their co-evolution under competitive pressure.

5 Conclusions

Compared to the allelopathic effects of *M. macrocopa* on *B. calyciflorus*, *M. macrocopa* had higher sensitivity to the *B.*

calyciflorus allelochemicals. The chemically mediated effects of *M. macrocopa* on the main life history variables of *B. calyciflorus* are non-significant in many cases and stimulatory or inhibitory in a few cases. However, the allelopathic effects of *B. calyciflorus* on the main life history variables of *M. macrocopa* are stimulatory in many cases, but inhibitory and non-significant in a few cases. The underlying mechanisms for both chemically mediated effects should be further investigated. Overall, the interspecific allelopathic effects of *B. calyciflorus* and *M. macrocopa* were dependent on the origin and concentration of allelochemical, life history variable, temperature, and algal (food) density.

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