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Combined Effects of Temperature and the Microcystin MC-LR on the Feeding Behavior of the Rotifer *Brachionus calyciflorus*

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Abstract The aim of this study was to investigate the responses in filtration and grazing rates of five rotifer strains of the species *Brachionus calyciflorus* under different temperatures and MC-LR concentrations. The results showed that strain identity, MC-LR concentration, temperature, and the interactions of these factors significantly affected both response variables, with the exception of the interaction of strain and MC-LR on the grazing rates. At low MC-LR concentrations and for the control group, the filtration and grazing rates increased with increasing temperature. The filtering and grazing rates of *B. calyciflorus* exposed to higher MC-LR concentrations, however, showed no evident enhancement with increasing of temperature. At high temperatures, the filtration and grazing rates of all rotifer strains decreased significantly with increasing concentration of MC-LR, however *B. calyciflorus* exhibited a refractory stability in the presence of increased MC-LR levels at lower temperatures.

Keywords Rotifer · *Brachionus calyciflorus* · Temperature · Microcystin · Feeding behavior

Bloom proliferation and the spread of cyanobacteria are well-known phenomena in both fresh and brackish water systems around the world (Codd et al. 2005; Frazão et al. 2010). Owing to the production of cyanotoxins, most cyanobacteria strains of the genus *Microcystis* are considered to be of serious health risks (Carmichael et al. 1990). Out of 80 variants, *Microcystis aeruginosa* is usually the dominant species and the largest producer of microcystins which are the most common and abundant cyanotoxins, particularly the variant microcystin-LR (MC-LR) (Barrios et al. 2015). Following the collapse of blooms, microcystin concentrations in water sources vary from trace levels up to 1.8 (mg/L) or higher (Chorus and Bartram 1999). These toxins may affect local organisms (Whitton and Potts 2000) and pose a threat to humans, the tertiary consumers of aquatic organisms, due to the potential for bioaccumulation (Falconer 2005; Berry and Lind 2010).

Aquatic animals, particularly zooplankton, are often used as test organisms to assess for potential adverse effects of chemicals. This is supported by their rapid growth, high reproductive rate, short generation time, and general sensitivity to toxic substances, making them excellent bioindicators of water quality (Snell and Janssen 1995; Landsberg 2002; Sarma and Nandini 2006; Kostopoulou et al. 2012). Cyanobacterial toxins, mainly microcystins, have been suggested to cause rapid mortality of herbivorous zooplankton, as well as long-term chronic effects on zooplankton growth and reproduction (Paerl et al. 2001; Lürling 2003; Zhang and Geng 2012). In addition, these toxic compounds may act as feeding deterrents and as such inhibit feeding of grazers especially cladocerans, copepods, and rotifers (Ostrofsky et al. 1983; Burns et al. 1989; Shaw et al. 1997). The effects of cyanotoxins are often determined by extracting the active compounds from cyanobacteria cultured under laboratory conditions or directly exposing the test organisms to cyanobacterial cells (Barrios et al. 2015). These bacteria have, however, been well documented to simultaneously produce more than one cyanotoxin as well as secondary metabolites

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that may also be toxic (Jungmann 1992). It is therefore not clear whether all of the observed toxicological effects found in zooplankton exposed to cyanobacterial cells or their crude extracts are attributable to any particular intracellular toxin or other toxins or even substances attached to the cyanobacterial cell wall (Ghadouani et al. 2004). The use of purified toxins could provide direct evidence of the effects of individual cyanotoxins in organisms.

Besides cyanotoxins, temperature has, moreover, a major impact on zooplankton physiology, ecology, and behavior by changing metabolic rates and activity level (Claska and Gilbert 1998). High temperatures can also trigger outbreaks of toxic algal blooms, cyanotoxin production (Jang et al. 2003; El-Shehawy et al. 2012), and therefore play a vital role in modifying the responses of zooplankton to toxic cyanobacteria (Gilbert 1996; Montagnes et al. 2001). Nevertheless, very little information on combined effects of purified MC-LR and temperature on rotifer feeding behavior is available.

In addition to exogenous variables, the identity of the rotifers' strain is one of the most significant endogenous factor determining their feeding strategy under changing environmental conditions (Awaiss and Kestemont 1992; Hu and Xi 2008; Snell 2014). Different strains tend to be characterized by different traits, allowing them to adapt to their ecological niches. An increasing number of studies has documented the effects of environmental factors on demographic traits and population growth among different rotifer strains (Halbach 1973; Awaïss and Kestemont 1992; Xi et al. 2005; Gama-Flores et al. 2014). Nevertheless, the effects of such hidden differentiations among strains are usually overlooked in studies focusing on the feeding behavior and responses to cyanotoxin exposure. Accordingly, the current study aimed to quantify the filtration and grazing rates of the five *Brachionus calyciflorus* rotifer strains when exposed to purified MC-LR at different temperatures.

Materials and Methods

Zooplankton samples were collected using a 30-μm vertical plankton net towed in lentic water bodies from four cities; XN2 was from Xi'ning (36°39′N, 101°42′E), LZC1 and LZB1 were from Lanzhou (36°05′N, 103°45′E), KMC23 was from Kunming (25°03′N, 102°42′E), and BNB3 was

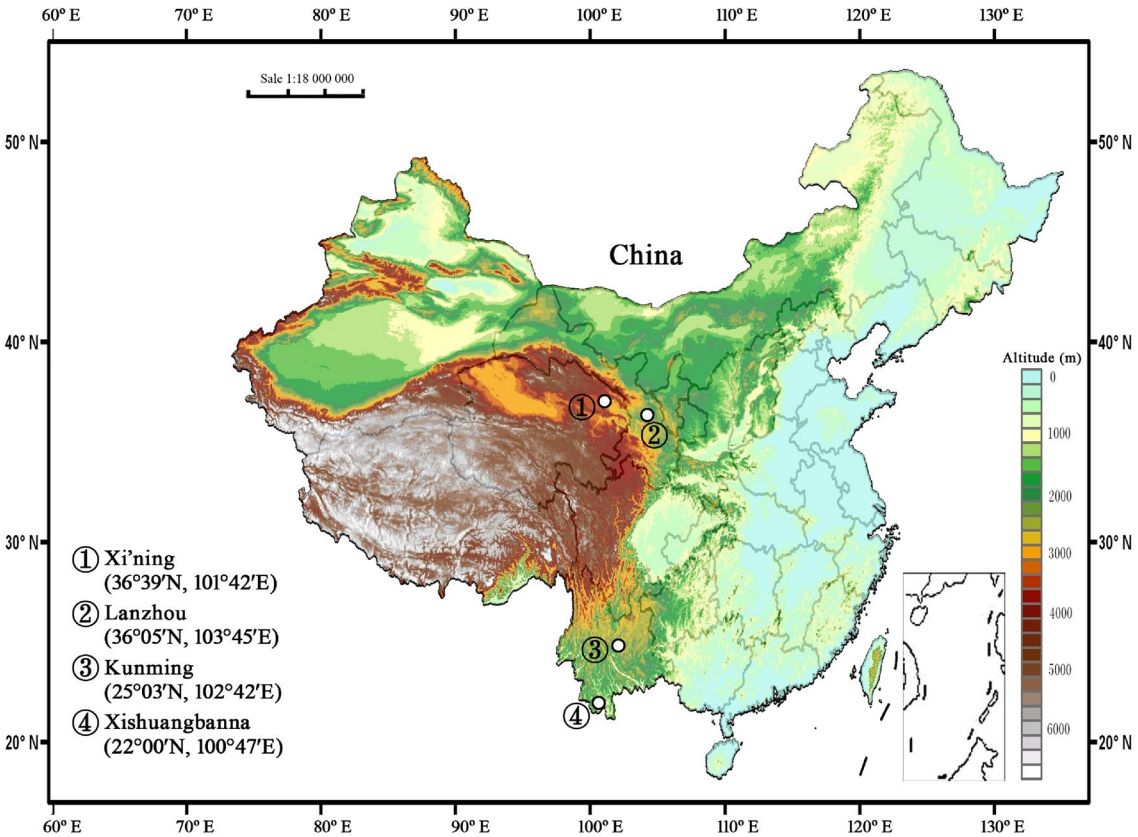

Fig. 1 Sampling locations of *Brachionus calyciflorus* strains in China

from Xishuangbanna (22°00′N, 100°47′E). These cities were located in four different climate zones, namely mountain plateau zones, temperate, subtropical and tropical zones in China (Fig. 1). Observations under microscope revealed *B. calyciflorus* samples to be free of the other zooplankters, and that the clonal populations for each *B. calyciflorus* strain were established from a single parthenogenetic female, in order to reduce variation within strains.

Rotifers were cultured in a fluorescent illumination incubator at a temperature of 24 ± 1°C on a 14:10 h light:dark photoperiod under 130 lx for over 6 months. During the routine culture and pre-culture before experiment, all animals were fed daily with *Scenedesmus obliquus* at 1.0×10^6 cells/mL, and maintained using EPA medium (prepared by dissolving 96 mg $NaHCO_3$, 60 mg $CaSO_4$, 60 mg $MgSO_4$, and 4 mg KCl in 1 L of distilled water) (Peltier and Weber 1985). *Scenedesmus obliquus* was grown semi-continuously in HB-4 medium (Li et al. 1959), which was replenished daily at 20% with a 16:8 light:dark photoperiod under a 3000 lx fluorescent light. In the exponential phase, fresh algae were harvested and stored at 4°C for use within two days. The density of the *S. obliquus* suspension was ascertained using a haemocytometer.

The MC-LR (95% purity) used in this study was purchased from Express Technology Co., Ltd. (Beijing, China), split charging from the certified MC-LR standard (Microcystin-LR, MCYL1GAM004, Taiwan Algal Science Inc.). According to the range of dissolved MCs in natural waters worldwide and the climate features (especially temperature) in the four sampled climate zones, the MC-LR concentrations were set at 0.0, 2.0, 4.0, and 6.0 mg/L and tested at 16, 20, 24, and 28°C. Before the experiment, microcystin-LR was dissolved in distilled water to achieve a stock solution of 50 µg/mL, and serially diluted to reach nominal concentrations using EPA medium for the experiments. The exposure concentrations were verified by high performance liquid chromatography (HPLC) in each of three replicates collected immediately prior to the addition of the rotifers.

In the experiment, 30 neonates (<4 h old), non-fed but active, were introduced into 8-ml glass beakers containing 3 ml test solution with 1.0×10^6 cells/ml *S. obliquus*, after which the beakers were covered with plastic boards to prevent the evaporation of water from the test medium, and then placed on shakers set at 80 rpm in complete darkness at four different temperatures to prevent the algae from settling and growth, respectively. All the experiments were conducted for 20 h with three replicates per treatment, so that there were 240 total units (4 concentrations × 4 temperatures × 5 strains × 3 replicates). After feeding, the density of unconsumed algae cells in each beaker was quantified using a haemocytometer. The EPA medium, containing algae *S. obliquus* at 1.0×10^6 cells/mL (but no *B. calyciflorus*), served as reference.

Grazing rates were calculated as the quantity of particles gathered from a food suspension in a specified period of time, while filtration rates showed the volume of medium passing through the filter to gather food. The filtering rate (F), i.e., the average volume of liquid filtered by each *B. calyciflorus* per unit time (ml ind^{-1} h^{-1}), the grazing rate (G), i.e., the average number of algae cells ingested by each *B. calyciflorus* per unit time (cell ind^{-1} h^{-1}), were calculated according to the following equations given by Frost (1972).

$$F = \frac{V}{n} \times \frac{\ln C_t - \ln C_{tf}}{t} \quad (1)$$

$$G = \frac{V}{n} \times \frac{\ln C_t - \ln C_{tf}}{t} \times \frac{C_{tf} - C_0}{\ln C_{tf} - \ln C_0} \quad (2)$$

where V is the solution volume (ml); t is the experimental time (h); n is the number of rotifers in each replicate; C_0 and C_{tf} are the initial and final densities of a given microalgae; and C_t is the final microalgal density of the control group in which no rotifer is present and the algae *S. obliquus* is cultured synchronously with the test groups.

Data on the grazing (G) and filtration (F) rates were statistically tested using SPSS 19.0 to quantify the differences among the treatments. All data were tested for normality using the one-sample Kolmogorov–Smirnov procedure. The homogeneity of variances was checked using Levene's test. In order to evaluate the effect of MC-LR concentrations on G and F, one-way ANOVAs were performed for each temperature and strain separately. The combined effects of MC-LR concentrations, temperature and their interactions on G and F were conducted using the two-way ANOVA for each strain separately. Finally, the three-way ANOVA was used to assess the effects of strain, MC-LR concentration, temperature and their interactions. Multiple comparisons were performed using SNK-q method to determine which groups were significantly different among groups. $p < 0.05$ was considered to be statistically significant.

Results and Discussion

The analysis of the chemical concentrations at the beginning of the exposure period revealed that the nominal and actual exposure levels were similar for all treatments. Control levels were found to be below the detection limit (0.05 µg/L LOD) in all cases. The nominal MC-LR concentrations in EPA medium were 2.0, 4.0, and 6.0 mg/L, and the exposure concentrations were 1.95 ± 0.07, 3.93 ± 0.09, and 5.83 ± 0.12 mg/L, respectively. As difference between measured and nominal concentrations are marginal the present study was based on the latter.

Table 1 Results of the three-way ANOVA performed on the grazing rates (*G*) and filtration rates (*F*) of five *B. calyciflorus* rotifer strains (S) subjected to three MC-LR concentrations (M) and four temperatures (T)

Source of variation	Filtration rate					Grazing rate				
	DF	SS[a]	MS[a]	F	*p*	DF	SS[a]	MS[a]	F	*p*
Strain (S)	4	1.5E−5	3.8E−6	19.4	<0.001	4	1.3E+6	3.3E+5	14.3	<0.001
MC-LR (M)	3	6.7E−5	2.2E−5	113.1	<0.001	3	5.6E+6	1.9E+6	81.2	<0.001
Temperature (T)	3	1.0E−3	0.0E+0	1382.4	<0.001	3	1.1E+8	3.6E+7	1597.1	<0.001
S×M	12	4.6E−6	4.3E−6	2.0	0.032	12	4.2E+5	3.5E+4	1.5	0.121
S×T	12	5.1E−5	4.3E−6	21.6	<0.001	12	5.6E+6	4.7E+5	20.4	<0.001
M×T	9	3.7E−5	4.2E−6	21.0	<0.001	9	2.3E+6	2.5E+5	11.1	<0.001
S×M×T	36	1.1E−5	3.0E−7	1.5	0.045	36	1.3E+6	3.5E+4	1.5	0.040
Error	160	3.2E−5	4.2E−6			160	3.7E+6	2.3E+4		

DF degrees of freedom, *SS* sum of squares, *MS* mean square, *F* F-ratio

[a]scientific notation

The results of the three-way ANOVA exploring the feeding behavior depending on strains, MC-LR concentrations, and temperatures are presented in Table 1. The interaction of strain × temperature and MC-LR × temperature were significant for both the filtration and grazing rates ($p < 0.001$). Similarly, the interaction of strain × MC-LR × temperature was significant for filtration and grazing rates ($p < 0.05$). It is noteworthy that the strain × MC-LR interaction was not significant for the grazing rate ($p > 0.05$), but did affect the filtration rate ($p < 0.05$) (Table 1). The significant interactions of exogenous and endogenous factors are complex: Rotifer sensitivity can be increased by increasing temperature or by using a more sensitive strain (Snell et al. 1991).

Temperature had a significant effect on the filtration and grazing rates of all five *B. calyciflorus* strains ($p < 0.001$, Table 1). Increasing temperature caused an increase in all filtration and grazing rates in the control and the low MC-LR concentration group (2.0 mg/L). Except for the BNB3 and LZC1 strains, the filtration and grazing rates of *B. calyciflorus* at 28°C were the highest among all four temperatures in the controls and the three treatment groups (Fig. 2). Increasing temperature may directly influence the grazing rate by increasing the metabolism, for instance, by altering enzyme kinetics. Indirect implications could be seen by increasing toxicant solubility or reducing membrane and water viscosity, thereby increasing diffusion levels (Cossins and Bowler 1987).

The two-way ANOVA also indicated that both the filtration and grazing rates of all *B. calyciflorus* strains were significantly affected by temperature and MC-LR ($p < 0.05$, Table 2). The interaction of MC-LR × temperature was significant for the filtration rates of all rotifer strains ($p < 0.05$, Table 2). Except for the LZB1 strain ($p > 0.05$), the grazing rates of all strains showed a significant MC-LR × temperature interaction ($p < 0.05$, Table 2). In general, the effects of MC-LR increased significantly with increasing temperature. Bloom frequency is known to generally increase with rising global temperatures, which accelerates the growth of toxic *Microcystis* compared to its non-toxic strains (Paerl et al. 2011; El-Shehawy et al. 2012; Liu et al. 2014). Huang et al. (2012) found that the population growth and reproduction of *B. calyciflorus* was markedly affected by MC-LR with the concentrations of 0.001–200 μg/L at 30°C, but not at 20 or 25°C. In this study, we observed a similar response for this rotifer species, and the significant effects of MC-LR on the feeding behavior of the five *B. calyciflorus* strains were detected at the highest temperature (28°C).

The different rotifer strains from distinct climatic zones have adapted to local environmental fluctuation. As a result, feeding activity is finely tuned to these conditions. In this study, the filtration and grazing rates in rotifers responded diversely to changes in MC-LR concentration and temperature among different *B. calyciflorus* strains ($p < 0.001$, Table 1). At a high temperature (28°C), the feeding behavior of the KMC23 strain from subtropics was the most active among all strains, regardless of MC-LR concentration. At a low temperature, however, LZC1 from temperate zone was the most active strain compared to the other four in relation to filtration and grazing rates (Fig. 2). The key reason could be attributed to their different life history strategies and the long-term adaptation of their feeding activity to specialized temperature regimes.

The results of one-way ANOVA with SNK-q method indicated that MC-LR significantly depressed the filtration and grazing rates of all five *B. calyciflorus* strains at 28°C, as well as those of four of the strains (KMC23, XN2, LZB1, and LZC1) at 24°C ($p < 0.05$), but had no influence on BNB3 at 24°C ($p > 0.05$) (Fig. 2). At 24 and 28°C, the presence of MC-LR at higher concentrations (4.0 and 6.0 mg/L) inhibited the filtration and grazing rates of the five *B. calyciflorus* strains. However we detected no significant differences between the treatments and the controls for any rotifer strain

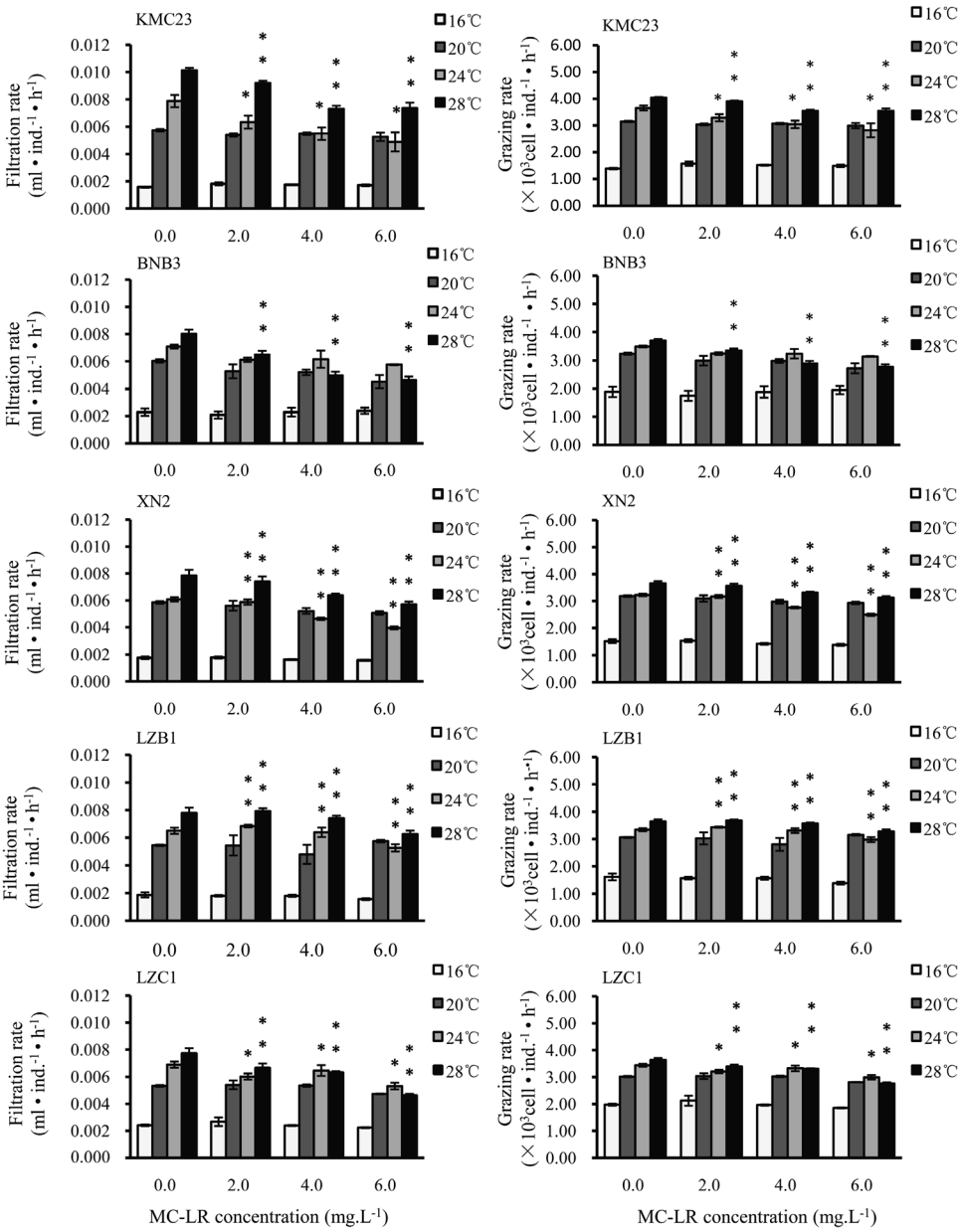

Fig. 2 The average filtration and grazing rates in the five *B. calyciflorus* strains at three MC-LR concentrations and four temperatures. *Asterisk* indicates that there are significant differences in the filtration and grazing rates between the MC-LR treatments and the control at the same temperature (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$). The error bars represent standard error calculated based on three replicates

at 16 and 20°C (Fig. 2). Previous studies have shown that MCs inhibited feeding, reduced growth, and increased mortality in cladocera and copepods with increasing concentration (Lürling and van der Grinten 2003; Ghadouani et al. 2004; Wilson et al. 2006). The 24-h LC50 in *B. plicatilis* for MC-LR was 124.87 mg/L, and the survival and reproductive rates and population growth parameter of *B. plicatilis* were lower at each test group than those at the controls (Chen et al. 2002). In the present study, the results showed that MC-LR significantly depressed the filtration and grazing rates of *B. calyciflorus* at higher temperatures, especially in treatments with higher concentrations of MC-LR (4.0 and 6.0 mg/L) at 24°C and 28°C, except for the tropical strain BNB3.

In summary, strain, MC-LR concentration, temperature, and the interactions among these factors significantly affected the filtration and grazing rates of the five *B. calyciflorus* strains, except that no significant effect was found for the strain × MC-LR interaction on rotifer grazing rates. Increasing temperatures stimulated the feeding behavior of *B. calyciflorus* in the control and low MC-LR concentration groups, and the filtration and grazing rates of all rotifer strains were significantly inhibited at different concentrations of MC-LR at 28°C. The feeding activities of the

Table 2 Results of the two-way ANOVA performed on filtration and grazing rates of five *B. calyciflorus* strains subjected to three MC-LR concentrations and four temperatures

Strains	Source of variation	Filtration rate (*F*)					Grazing rate (*G*)				
		DF	SS[a]	MS[a]	F	*p*	DF	SS[a]	MS[a]	F	*p*
KMC23	MC-LR (M)	3	1.7E−5	5.8E−6	20.3	<0.001	3	8.6E+5	2.9E+5	10.4	<0.001
	Temperature (T)	3	0.0E+0	9.5E−5	335.6	<0.001	3	3.4E+7	1.1E+7	410.6	<0.001
	M×T	9	1.6E−5	1.8E−6	6.2	<0.001	9	9.5E+5	1.1E+5	3.8	0.002
	Error	32	9.1E−6	2.8E−7			32	8.8E+5	2.8E+4		
BNB3	MC-LR (M)	3	1.6E−5	5.2E−6	17.4	<0.001	3	1.2E+6	4.1E+5	8.7	<0.001
	Temperature (T)	3	0.0E+0	4.1E−5	138.3	<0.001	3	1.5E+7	5.1E+6	108.3	<0.001
	M×T	9	1.3E−5	1.4E−6	4.7	0.001	9	1.1E+6	1.2E+5	2.6	0.023
	Error	32	9.6E−6	3.0E−7			32	1.5E+6	4.7E+4		
XN2	MC-LR (M)	3	1.3E−5	4.5E−6	34.5	<0.001	3	1.4E+6	4.5E+5	30.0	<0.001
	Temperature (T)	3	0.0E+0	5.7E−5	442.4	<0.001	3	2.6E+7	8.7E+6	769.9	<0.001
	M×T	9	5.7E−6	6.3E−7	4.9	<0.001	9	4.4E+5	4.9E+4	4.4	0.001
	Error	32	4.2E−6	1.3E−7			32	3.6E+5	1.1E+4		
LZB1	MC-LR (M)	3	4.6E−6	1.5E−6	5.1	0.005	3	4.0E+5	1.3E+5	4.4	0.011
	Temperature (T)	3	0.0E+0	7.0E−5	236.0	<0.001	3	2.9E+7	9.7E+6	317.8	<0.001
	M×T	9	6.4E−6	7.2E−7	2.4	0.033	9	5.3E+5	5.9E+4	2.0	0.080
	Error	32	9.5E−6	3.0E−7			32	9.7E+5	3.0E+4		
LZC1	MC-LR (M)	3	1.2E−5	4.0E−6	27.2	<0.001	3	1.2E+6	3.9E+5	23.4	<0.001
	Temperature (T)	3	0.0E+0	3.9E−5	267.6	<0.001	3	1.3E+7	4.4E+6	267.1	<0.001
	M×T	9	8.3E−6	9.2E−7	6.3	<0.001	9	5.9E+5	6.6E+4	3.9	0.002
	Error	32	4.7E−6	1.5E−7			32	5.3E+5	1.7E+4		

DF degrees of freedom, *SS* sum of squares, *MS* mean square, *F* F-ratio

[a]scientific notation

Kunming (KM) and Lanzhou (LZ) strains were the most active at high and low temperatures, respectively, regardless of MC-LR concentration, which could be attributed to the long-term adaptation of their feeding behavior to specialized local temperature regimes.

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