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The effects of food level on the life history variables of the two closely related rotifer species *Keratella tropica* and *Keratella valga*

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Abstract – *Keratella tropica* and *Keratella valga* are very similar in external morphology. *K. tropica* is a warm water species, and occurs in tropical and subtropical regions. *K. valga* is a eurythermal and widespread species. In subtropical shallow lakes, *K. tropica* has a higher density than *K. valga*. In the present study, *K. tropica* and *K. valga* were collected, respectively, from Lake Tingtang and Lake Jinghu in Wuhu city, Anhui, China, and their life history variables were compared at four levels (0.5×10^6, 1.0×10^6, 2.0×10^6 and 4.0×10^6 cells.mL^{-1}) of *Scenedesmus obliquus* at 20 °C. The results showed that both rotifer species had the same response to increasing food levels as regards duration of reproductive and post-reproductive periods, average lifespan, life expectancy at hatching, generation time, net reproductive rate and intrinsic rate of population increase, but differed in their duration of pre-reproductive period. The duration of pre-reproductive period of the rotifers was significantly affected by food level, species and their interaction ($P < 0.01$), the duration of reproductive period was affected by species and the interaction between food level and species ($P < 0.05$), and the average lifespan, the life expectancy at hatching, the generation time and the net reproductive rate were all significantly affected by species ($P < 0.01$). Regardless of the effect of food level, the duration of pre-reproductive and reproductive periods, the average lifespan, the life expectancy at hatching, the generation time and the net reproductive rate of *K. tropica* were longer or higher than those of *K. valga*. The higher density of *K. tropica* in subtropical lakes might be attributed to its longer lifespan and higher reproductive rate.

Key words: Rotifer / *Keratella tropica* / *Keratella valga* / life history variable / algal food density

Introduction

Keratella tropica and *Keratella valga* are two morphologically similar rotifer species. In contrast to *K. valga*, *K. tropica* has a small half plaque after the posteromedian plaque on the dorsal lorica. *K. tropica* is a warm water species, and occurs in tropical and subtropical regions, including Afrotropical, Australian, Nearctic, Neotropical, Oriental and Palearctic regions (Segers, 2007). *K. valga* is a eurythermal and widespread species (Ehrenberg, 1834; Edmondson and Hutchinson, 1934; Wang, 1961). Both rotifer species have different responses in each of the life history parameters to increasing temperature. *K. tropica* is adapted to higher temperatures than *K. valga* (Xi *et al.*, 2013). However, the differences in their life history parameters and responses to increasing food levels remain unknown.

In Lake Jinghu, a subtropical shallow lake, *K. tropica* occurs in May and June when the average water temperature is close to 20 °C, and *K. valga* appears between February and April when the average water temperature is about 15 °C. As usual, *K. tropica* has a higher density than *K. valga* (Wen *et al.*, 2011), but the cause for their different abundances remains unknown.

Life table analysis provides a rigorous approach to studying population dynamics. From observations of reproduction and mortality of individual rotifers, population statistics can be calculated such as average lifespan, generation time, net reproductive rate and population growth rate, which can provide valuable insight into the suitability of the ambient conditions for the zooplankton (Stearns, 1976; Wallace *et al.*, 2006). The effect of food level on population dynamics of rotifers can be

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investigated by life table analysis. Up to now, however, relatively few studies have been carried out to investigate the role of food level on life history characteristics of different rotifer species (Schmid-Araya, 1991; Galindo *et al.*, 1993; Sarma *et al.*, 1996, 2007; Kirk, 1997a, 1997b; Nandini and Sarma, 2002; Sarma and Nandini, 2002; Fernández-Araiza *et al.*, 2005; Nandini *et al.*, 2007). Because the effect of food level on life history variables of rotifers differed not only with species, strain and clone (Schmid-Araya, 1991; Pérez-Legaspi and Rico-Martínez, 1998; Dong *et al.*, 2004, 2009; Wang *et al.*, 2014), but also temperature and tested range of food level (Sarma and Rao, 1991; Sarma and Nandini, 2002; Pavon-Meza *et al.*, 2005; Ning *et al.*, 2013; Pan *et al.*, 2014), it is difficult to determine the precise differences in responses to increasing food levels between rotifer species. Therefore, studies on comparative life table variables of different rotifer species in relation to food density are important.

In this study, we collected *K. tropica* and *K. valga* individuals, respectively, from Lake Tingtang and Lake Jinghu, for clonal culture in the laboratory. With three clones selected randomly from each rotifer species, we compared their life history variables at four *Scenedesmus obliquus* levels (0.5×10^6, 1.0×10^6, 2.0×10^6 and 4.0×10^6 cells.mL^{-1}) with the aim of testing the following two hypotheses: (1) the two closely related rotifer species have different responses in some life history variables to increasing food levels; and (2) *K. tropica* with a higher density in subtropical lakes has higher survival and reproductive variables.

Material and methods

Keratella tropica and *K. valga* individuals were respectively collected from Lake Tingtang and Lake Jinghu in May and February 2009, for clonal culture in our laboratory. Lake Jinghu and Lake Tingtang have an average depth of 1.3 and 2.0 m, and a water surface area of 7.9 and 13.47 ha, respectively. They are located in the center of Wuhu city (between 119°21′ longitude and 31°20′ latitude), which has an average air temperature of 15.7 °C (the highest temperature is 41 °C, and the lowest is − 15 °C) (Xi *et al.*, 2013).

Depending on the water temperature when the rotifers were collected, stock cultures of *K. tropica* and *K. valga* were respectively kept at 25 and 20 °C for about a month in illumination incubators, and were fed daily on *S. obliquus*. Algae were grown in a semi-continuous culture using HB-4 medium (Li *et al.*, 1959) renewed daily at 20%. Algae in exponential growth were centrifuged and resuspended in the rotifer medium (Gilbert, 1963).

Life table experiments for *K. tropica* and *K. valga* were conducted simultaneously but separately on cohorts of 12 individuals at 0.5×10^6, 1.0×10^6, 2.0×10^6 and 4.0×10^6 cells.mL^{-1} of *S. obliquus* and at 20 °C. For each rotifer species, the experimental design consisted of a total of 144 1.5-mL glass cups (4 food levels × 12 individuals × 3 clones), each containing 0.5 mL of rotifer medium with the corresponding density of *S. obliquus*. Thirty-six individuals (12 individuals per clone × 3 clones) were used as 36 replicates when duration of pre-reproductive, reproductive and post-reproductive periods, and average lifespan were calculated and statistically analyzed. However, three clones from each rotifer species were used as three replicates when life table demographic parameters were calculated and statistically analyzed.

Before the life table experiments commenced, all the rotifer clones were maintained at the designed food levels and at 20 °C for one week to allow for acclimation. Then, 12 neonates (< 2 h old) from each rotifer clone were individually introduced into glass cups each containing 0.5 mL of rotifer medium with the corresponding density of *S. obliquus*. Thereafter, all these cultures were observed every 12 h under a dissecting microscope, and the number of original test individuals alive and carrying the first egg, and neonates produced by each original test individual were counted. Every day, the original test individuals alive were transferred into fresh glass cups, each containing 0.5 mL of rotifer medium with the corresponding density of *S. obliquus*, and dead individuals and neonates were eliminated. The experiments were continued until the last adult individual of every cohort died.

Based on the data collected, we derived the following variables: duration of pre-reproductive, reproductive and post-reproductive periods, average lifespan, age-specific survivorship (l_x) and fecundity (m_x) (x was defined as the age interval, lx as the proportion surviving at the beginning of the age interval and m_x as the number of offspring produced per female alive at the start of the age interval by the end of that interval), life expectancy at hatching (e_0, the life expectancy of the cohort at the beginning of the age interval), net reproductive rate (R_0, net population increase rate after a generation), generation time (T, the time between parental birth and offspring birth) and intrinsic rate of population increase (r_m, a maximum value of the rate of population increase under ideal conditions). The following formulae (Pianka, 1988) were used:

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

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

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

For final calculation, we solved the equation :

$$\sum_{x=0}^{n} e^{-rx} l_x m_x = 1$$

Kaplan–Meier analyses were conducted to test for the differences in the age-specific survivorship of the two rotifer species among the four food levels. All data were tested for normality using the one-sample

Kolmogorov–Smirnov procedure. The homogeneity of variances was checked using Levene's test. Two-way analyses of variance (ANOVA) were conducted to identify significant effects of food level and species, and their interaction on each of the life history variables. Tukey HSD tests were used to determine which groups were significantly different among the four food levels for each rotifer species.

Results

The duration of the pre-reproductive, reproductive and post-reproductive periods, and the average lifespan of the two rotifer species are shown in Figure 1. Two-way ANOVA showed that the duration of pre-reproductive period of the rotifers was significantly affected by food level, species and their interaction ($P < 0.01$), the duration of reproductive period was affected by species and the interaction between food level and species ($P < 0.01$), and the average lifespan was affected by species ($P < 0.01$) (Table 1). Tukey HSD tests showed that the duration of the pre-reproductive period of *K. tropica* was shorter at 4.0×10^6 cells.mL^{-1} of *S. obliquus* than at the other three food levels. The duration of the pre-reproductive period of *K. valga* at 2.0×10^6 cells.mL^{-1} of *S. obliquus* was the shortest. The duration of the pre-reproductive period of *K. valga* at 1.0×10^6 cells.mL^{-1} of *S. obliquus* was shorter than that at 0.5×10^6 cells.mL^{-1} of *S. obliquus*, but both were similar to that at 4.0×10^6 cells.mL^{-1} of *S. obliquus* (Fig. 1).

The differences in the duration of the pre-reproductive and reproductive periods and the average lifespan between the two rotifer species varied with food level. At 0.5×10^6 cells.mL^{-1}, the duration of the reproductive period and the average lifespan of *K. tropica* were longer than those of *K. valga* ($P < 0.01$), but the durations of the pre-reproductive period were similar ($P > 0.05$). At 1.0×10^6 cells.mL^{-1}, the duration of pre-reproductive and reproductive periods and the average lifespan of *K. tropica* were longer than those of *K. valga* ($P < 0.05$). At 2.0×10^6 cells.mL^{-1}, the duration of the pre-reproductive period of *K. tropica* was longer than that of *K. valga* ($P < 0.01$), but their duration of reproductive period and average lifespan were similar ($P > 0.05$). At 4.0×10^6 cells.mL^{-1}, the duration of the pre-reproductive period of *K. tropica* was shorter than that of *K. valga* ($P < 0.01$), but the duration of the reproductive period of *K. tropica* was longer than that of *K. valga* ($P < 0.01$), and their average lifespans were similar ($P > 0.05$) (Fig. 1).

Regardless of the effect of food level, the duration of pre-reproductive and reproductive periods, and the average lifespan of *K. tropica* were longer than those of *K. valga* (Fig. 1).

Food level did not significantly affect the age-specific survivorship of the two rotifer species, and the age-specific fecundity of *K. valga* ($P > 0.05$), but affected markedly the age-specific fecundity of *K. tropica* ($P < 0.05$).

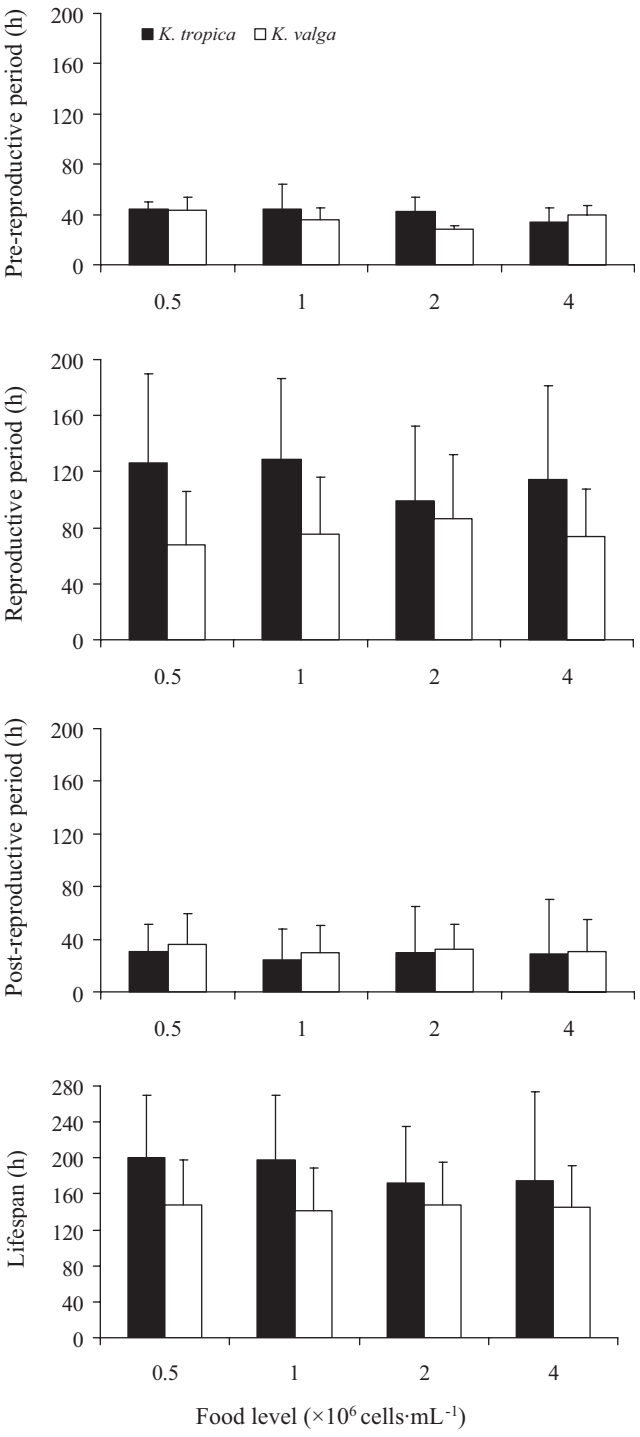

Fig. 1. Duration of principal developmental periods of *K. tropica* and *K. valga* cultured at four levels of *S. obliquus* ($\times 10^6$ cells.mL^{-1}) (Mean + SD).

At 4.0×10^6 cells.mL^{-1} of *S. obliquus*, *K. tropica* had the highest peak fecundity (Fig. 2).

The life expectancy at hatching, the generation time and the net reproductive rate of the rotifers were all significantly affected by species ($P < 0.01$), but the intrinsic rate of population increase was affected by species

Table 1. Effects of food level and species on the duration of principal developmental periods and the life table demographic parameters of *K. tropica* and *K. valga* (two-way ANOVA).

Source	Sum of squares	df	Mean square	*F*
Pre-reproductive period				
Food density (A)	2980.34	3	993.45	8.27*
Species (B)	1229.25	1	1229.25	10.23*
A × B	4125.79	3	1375.26	11.45*
Error	33 643.58	280	120.16	
Reproductive period				
Food density (A)	3530.71	3	1176.90	0.45^{ns}
Species (B)	122 430.01	1	122 430.01	46.98*
A × B	22 673.04	3	7557.68	2.90*
Error	729 626.56	280	2605.81	
Post-reproductive period				
Food density (A)	1383.00	3	461.00	0.64^{ns}
Species (B)	1200.50	1	1200.50	1.66^{ns}
A × B	164.50	3	54.83	0.08^{ns}
Error	202 978.00	280	724.92	
Average lifespan				
Food density (A)	10 831.71	3	3610.57	0.88^{ns}
Species (B)	119 764.34	1	119 764.34	29.29*
A × B	14 261.98	3	4753.99	1.16^{ns}
Error	1 144 841.47	280	4088.72	
Life expectancy at hatching				
Food density (A)	848.45	3	282.82	1.47^{ns}
Species (B)	3387.27	1	3387.27	17.65*
A × B	355.86	3	118.62	0.62^{ns}
Error	3071.28	16	191.96	
Net reproductive rate				
Food density (A)	1.46	3	0.49	0.88^{ns}
Species (B)	27.82	1	27.82	50.13*
A × B	3.07	3	1.02	1.85^{ns}
Error	8.88	16	0.56	
Generation time				
Food density (A)	848.45	3	282.82	1.47^{ns}
Species (B)	3387.27	1	3387.27	17.65*
A × B	355.86	3	118.62	0.62^{ns}
Error	3071.28	16	191.96	
Intrinsic rate of population increase				
Food density (A)	0.02	3	0.01	0.95^{ns}
Species (B)	0.02	1	0.02	2.54^{ns}
A × B	0.06	3	0.02	2.96^{ns}
Error	0.10	16	0.01	

*$P < 0.01$, ns$P > 0.05$.

($P > 0.05$), and none of these life-table demographic parameters were affected by food level and the interaction between food level and species ($P > 0.05$) (Table 1). Regardless of the effect of food level, the life expectancy at hatching, the generation time and the net reproductive rate of *K. tropica* were longer or higher than those of *K. valga* (Fig. 3).

Discussion

Previous comparative studies have shown that the effect of food level on life history variables is species-dependent. At 20 °C, the duration of the pre-reproductive period of *Brachionus plicatilis* at low (0.2×10^4 cells.mL^{-1}) and high (10.0×10^4 cells.mL^{-1} of *Brachiomonas submarina*) food levels increased, but that of *Encentrum linnhei* was not affected by food levels. The duration of the reproductive period and the average lifespan of *B. plicatilis* and *E. linnhei* were not affected by food levels (Schmid-Araya, 1991). The duration of the pre-reproductive periods of both sibling species BNA13 in *Brachionus calyciflorus* complex at low (0.5×10^6 cells.mL^{-1}) and high (4.0×10^6 cells.mL^{-1} of *S. obliquus*) food densities, and sibling species BNB3 at high food density decreased. The duration of the reproductive period and the average lifespan of both sibling species increased with increasing food levels. The duration of the post-reproductive period of sibling species BNA13 increased with increasing food levels, but that of sibling species BNB3 decreased with increasing food levels (Wang *et al.*, 2014). In the present study, *K. tropica* had a

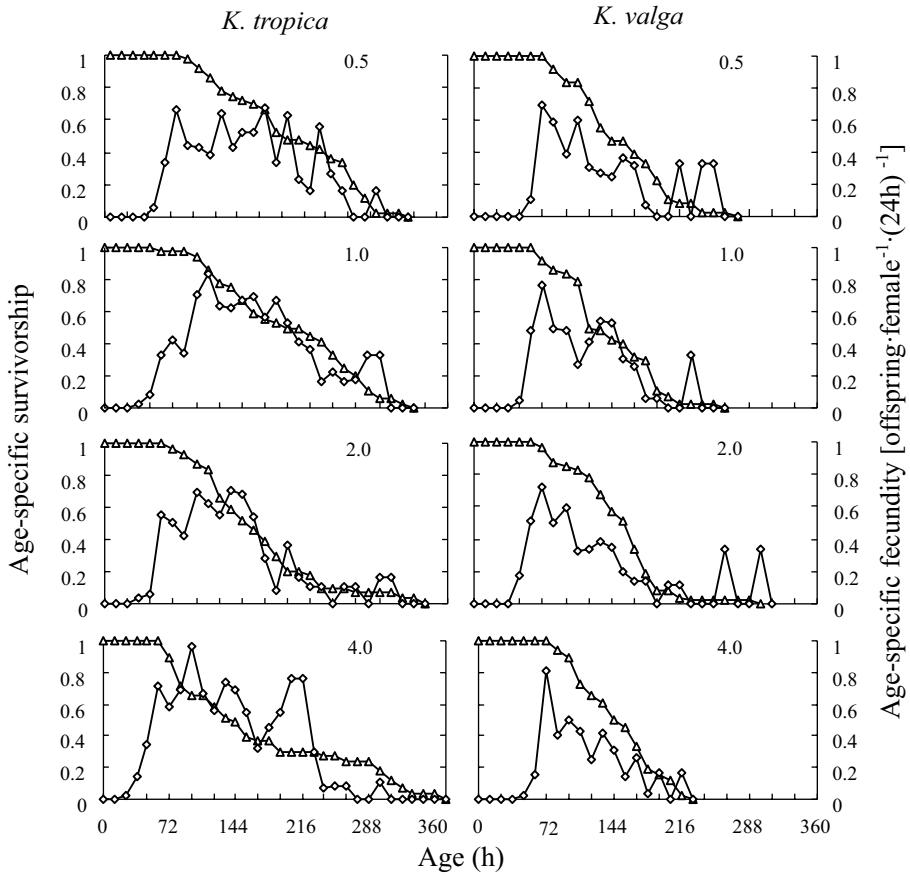

Fig. 2. Age-specific survivorship (*triangle*) and fecundity curves (*rhomb*) of *K. tropica* and *K. valga* at four levels of *S. obliquus* ($\times 10^6$ cells.mL^{-1}).

shorter pre-reproductive period at 4.0×10^6 cells.mL^{-1} of *S. obliquus* than at the other three food levels. The duration of the pre-reproductive period of *K. valga* at 2.0×10^6 cells.mL^{-1} of *S. obliquus* was the shortest. The duration of the pre-reproductive period of *K. valga* at 1.0×10^6 cells.mL^{-1} of *S. obliquus* was shorter than that at 0.5×10^6 cells.mL^{-1} of *S. obliquus*, but both were similar to that at 4.0×10^6 cells.mL^{-1} of *S. obliquus*. The duration of reproductive and post-reproductive periods, the average lifespan and the life expectancy at hatching of *K. tropica* and *K. valga* were not affected by food levels.

Food level is an important factor affecting rotifer development (Cheng *et al.*, 2011). Similar to the effect of lower food concentrations, excessive high food concentrations also decrease intake energy because of clogging of filtration apparatus. An inevitable allocation of a proportion of limited intake energy for metabolism might leave much less energy for growth and development, and thus result in a prolonged pre-reproductive period (Galindo *et al.*, 1993; Dumont *et al.*, 1995).

The generation time is the average length of time between the birth of an individual and the birth of its own offspring. As such, it reflects changes in the time required to reach sexual maturity and the embryonic development time. In the range of 1.0×10^6–10.0×10^6 cells.mL^{-1} of *Nannochloris oculata*, the generation time of both *Lecane quadridentata* and *Lecan luna* increased with increasing food levels (Pérez-Legaspi and Rico-Martínez, 1998). Similarly, in the range of 0.5×10^6–4.0×10^6 cells.mL^{-1} of *S. obliquus*, sibling species BNA13 and BNB3 in *B. calyciflorus* complex increased with increasing food levels (Wang *et al.*, 2014). However, in the range of 0.25×10^6–4.0×10^6 cells.mL^{-1} of *Chlorella valgaris*, the generation time of both *Brachionus macracanthus* and *Platyias quadricornis* decreased with increasing food levels (Sarma and Nandini, 2002). In the range of 0.5×10^6–4.0×10^6 cells.mL^{-1} of *S. obliquus*, and among four *B. calyciflorus* clones with different biochemical and genetic characteristics, the generation time of clone A was not affected by food level, the generation time of clone B at 4.0×10^6 cells.mL^{-1}, and clone D at 4.0×10^6 cells.mL^{-1} and 8.0×10^6 cells.mL^{-1}were the longest, but that of clone C at 4.0×10^6 cells.mL^{-1} of *S. obliquus* was the shortest (Dong *et al.*, 2009). In the present study, we found that food level did not affect the generation time of *K. tropica* and *K. valga*. Considering the significant effects of food levels on the duration of the pre-reproductive periods of the two rotifer species, their embryonic development time under different food levels deserves investigation.

Discussing the evolution of lifespan of planktonic organisms in the context of life history variables, King (1982) opined that the ratio of average lifespan to

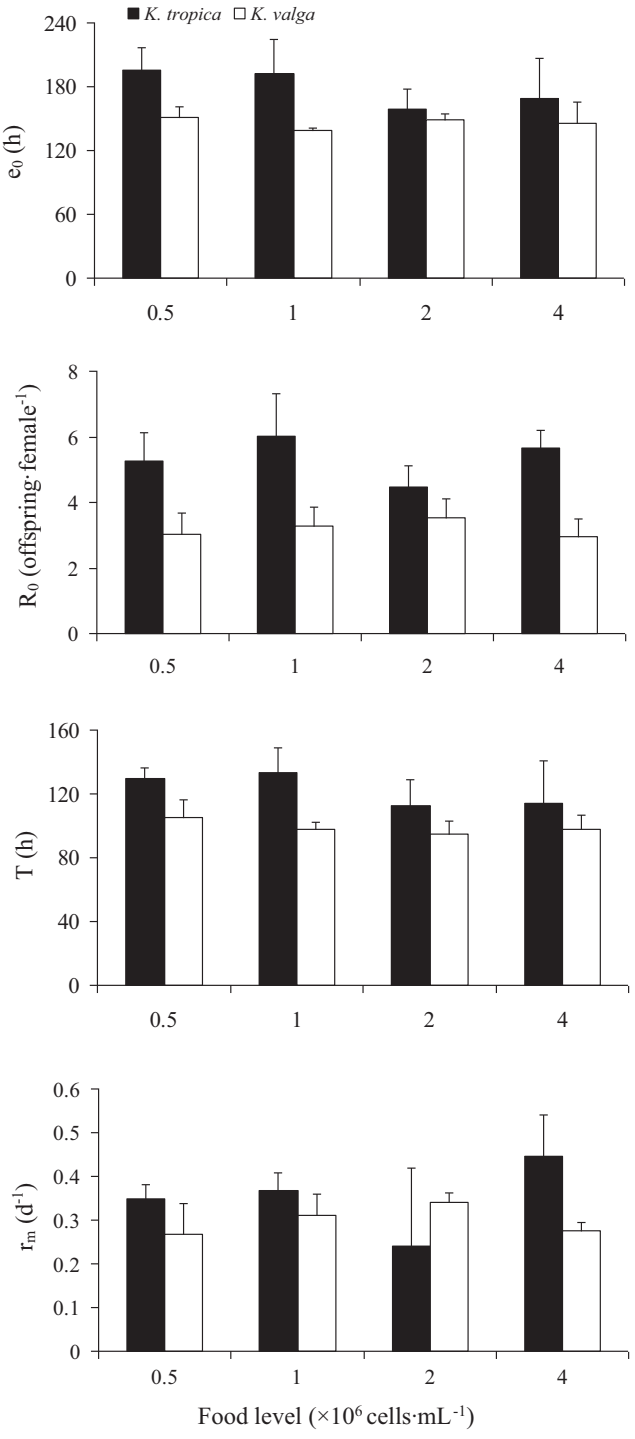

Fig. 3. Life expectancy at hatching (e_0), net reproductive rate (R_0), generation time (T) and intrinsic rate of population increase (r_m) of *K. tropica* and *K. valga* cultured at four levels of *S. obliquus* ($\times 10^6$ cells.mL^{-1}) (Mean + SD).

generation time in parthenogenetically reproducing organisms should be 2. However, this ratio varied from 1.6 to 3.9 for *Brachionus patulus* (Sarma and Rao, 1991). In the present study, this ratio ranged from 1.40 to 1.54 due to relatively longer average lifespan and shorter generation time (Table 2).

The net reproductive rate of *L. quadridentata* at the intermediate food level (5.0×10^6 cells.mL^{-1} of *Nannochloris oculata*) was the highest, but that of *L. luna* was the lowest (Pérez-Legaspi and Rico-Martínez, 1998). The net reproductive rates of *B. macracanthus*, *P. quadricornis* and sibling species BNA13 and BNB3 of *B. calyciflorus* decreased with increasing food levels (Sarma and Nandini, 2002; Wang *et al.*, 2014). The net reproductive rate of clone A of *B. calyciflorus* was not affected by food level, the net reproductive rate of clone B at 2.0×10^6 cells.mL^{-1} of *S. obliquus* was the lowest, the net reproductive rates of clone C at 1.0×10^6 cells.mL^{-1} and 8.0×10^6 cells.mL^{-1} of *S. obliquus* were the highest, but those of clone D at 4.0×10^6 and 8.0×10^6 cells.mL^{-1} of *S. obliquus* were the highest (Dong *et al.*, 2009). In the present study, we found that the net reproductive rates of *K. tropica* and *K. valga* were not affected by food levels.

At 20 °C and in the range of 2×10^3–1×10^4 cells.mL^{-1} of *Cryptomonas erosa*, *K. tropica* had r values of 0.25–0.54.d^{-1} (Gilbert, 2009, 2011, 2012); identical results were obtained in the present study. Clone A of *B. calyciflorus* at 2.0×10^6 cells.mL^{-1} of *S. obliquus*, clone B at 1.0×10^6 cells.mL^{-1} of *S. obliquus*, and clone C at the low and high food levels had the highest intrinsic rate of population increase, but clone D at 4.0×10^6 and 8.0×10^6 cells.mL^{-1} of *S. obliquus* had the highest intrinsic rate of population increase (Dong *et al.*, 2009). Sibling species BNA13 and BNB3 of *B. calyciflorus* at 4.0×10^6 cells.mL^{-1} of *S. obliquus* had the highest intrinsic rate of population increase (Wang *et al.*, 2014). *B. macracanthus* at 0.5×10^6 cells.mL^{-1} of *C. valgaris* had the highest intrinsic rate of population increase, but the intrinsic rate of population increase of *P. quadricornis* was not affected by food levels (Sarma and Nandini, 2002). In the present study, we found that the intrinsic rates of population increase of *K. tropica* and *K. valga* were not affected by food levels.

The present results showed that *K. tropica* and *K. valga* had a different response in the duration of the pre-reproductive period to increasing food levels, which were similar to the results obtained by Sarma and Nandini (2002), Dong *et al.* (2009) and Wang *et al.* (2014), and supported the hypothesis that the two rotifer species have different responses in some life history variables to increasing food levels.

Table 2. Ratios of average lifespan to generation time of *K. tropica* and *K. valga* cultured at four levels of *S. obliquus* (cells.mL^{-1}).

Rotifer species	0.5×10^6	1×10^6	2×10^6	4×10^6
K. tropica	1.54	1.48	1.52	1.53
K.valga	1.40	1.45	1.56	1.48

It is known that the difference in life history variables between rotifer species, strain or clone differed with food levels (Sarma and Rao, 1991; Pérez-Legaspi and Rico-Martínez, 1998; Sarma and Nandini, 2002; Dong *et al*., 2009; Wang *et al*., 2014) or temperature (Sarma and Rao, 1991; Pérez-Legaspi and Rico-Martínez, 1998; Hu *et al*., 2008; Tao *et al*., 2008; Li *et al*., 2009; Xi *et al*., 2013; Wang *et al*., 2014). When the effect of food level or temperature was disregarded, the significant differences in life history variables also existed between rotifer species, strain or clone. For example, regardless of the effect of temperature, *B. rubens* had a higher net reproductive rate and intrinsic rate of population increase, but shorter life expectancy at hatching and generation time than *Brachionus urceolaris* (Hu *et al*., 2008); *Brachionus caudatus* had a longer reproductive period, life expectancy at hatching and generation time than *Brachionus forcatus* (Tao *et al*., 2008), and *K. tropica* had longer life expectancy at hatching and generation time, and a higher net reproductive rate and intrinsic rate of population increase than *K. valga* (Xi *et al*., 2013). Similarly, regardless of the effect of food levels, *B. macracanthus* had a higher net reproductive rate and intrinsic rate of population increase than *P. quadricornis* (Sarma and Nandini, 2002). Among four *B. calyciflorus* clones, clone B had the longest average lifespan, life expectancy at hatching and generation time, and clone D had the lowest intrinsic rate of population increase (Dong *et al*., 2009). In the present study, regardless of the effect of food levels, the duration of pre-reproductive and reproductive periods, the average lifespan, the life expectancy at hatching, the generation time and the net reproductive rate of *K. tropica* were longer or higher than those of *K. valga*, which indicated that their differences are primarily genetically determined.

In contrast to *K. valga*, *K. tropica* had a longer lifespan and higher reproductive rate, which might lead to its higher density in subtropical lakes, such as Lake Jinghu and Lake Tingtang, and supported the hypothesis that *K. tropica* with a higher density in subtropical lakes has higher survival and reproductive variables.

Conclusion

K. tropica and *K. valga* had a different response in the duration of pre-reproductive period to increasing food levels. Regardless of the effect of food levels, the duration of pre-reproductive and reproductive periods, the average lifespan, the life expectancy at hatching, the generation time and the net reproductive rate of *K. tropica* were longer or higher than those of *K. valga*. The higher density of *K. tropica* in subtropical lakes might be attributed to its longer lifespan and higher reproductive rate.

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