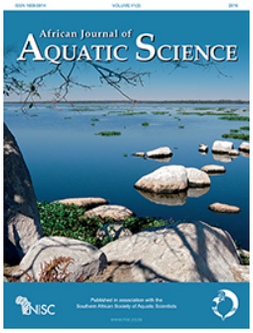

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Lifetable demography and population growth of the rotifer *Brachionus angularis* in Kenya: influence of temperature and food density

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Lifetable demography and reproductive traits of a Kenyan strain of the rotifer *Brachionus angularis* were investigated using individual and small batch culture approaches. The rotifer was identified morphologically before conducting studies at 20, 25 and 30 °C, using *Chlorella vulgaris* at 2.5 × 10^5 to 2.5 × 10^7 cells ml^{-1}. The rotifers were highly fecund, producing 2.11 ± 0.07 offspring $female^{-1}$ day^{-1} and reproductive, producing 8.43 ± 0.24 offspring $female^{-1}$ at 25 °C with 2.5 × 10^6 algal cells ml^{-1}. The highest intrinsic rate of natural increase (0.74 ± 0.02 d^{-1}), specific population growth rate (0.49 ± 0.01), longest life expectancy at hatching (12.41 ± 0.28 d) and shortest generation time (2.87 ± 0.03 d) also occurred at 25 °C with 2.5 × 10^6 algal cells ml^{-1}. The duration of hatching to first spawning was shortest (2.86 ± 0.21 h) at 30 °C with 2.5 × 10^7 algal cells ml^{-1} and longest (8.83 ± 0.39 h) at 20 °C with 2.5 × 10^5 algal cells ml^{-1}. The highest population density (255.7 ± 12.6 ind. ml^{-1}) was realised at 25 °C with 2.5 × 10^6 cells ml^{-1} on Day 8, whereas the lowest population density (122.0 ± 3.6 ind. ml^{-1}) was realised at 20 °C with 2.5 × 10^5 cells ml^{-1} on Day 8. The lorica length and width of the Kenyan strain of *B. angularis* are 85.6 ± 3.1 µm and 75.4 ± 3.6 µm, respectively. The rotifer optimally reproduces at 25 °C when fed with 2.5 × 10^6 algal cells ml^{-1}.

Keywords: alga, fecundity, generation time, lifetable parameters, population growth, Rotifera

Introduction

A lifetable is an informative tool commonly used to understand the demographic characteristics of zooplankton communities in their environments (Sarma and Nandini 2001; Xi et al. 2005; Ma et al. 2010). Lifetable demography provides information, such as age-specific survivorship, fecundity, average lifespan, generation time, population growth rate and intrinsic rate of natural increase (Galkovskaja 1987; Walz 1987; Sarma and Nandini 2002). This information is current to understanding rotifer biological behaviour under dynamic environmental conditions not only in their natural habitats (Edmondson 1964, 1965), but also in controlled culture facilities (Hagiwara 2007).

The relationship between rotifer reproduction and ambient environmental factors is well-documented (Edmondson 1965; Espinosa-Rodríguez et al. 2014). Ecologically, salinity and temperature (Snell 1986; Awaïss and Kestemont 1992), food quality and quantity (Xi and Huang 1999; Sarma and Nandini 2001, 2002) are among the most important factors influencing the growth (Yúfera 2001), lifespan (King and Miracle 1980) and reproduction (Lubzens et al. 1985) of rotifers. For example, an increase in food density enhances egg production, but reduces their lifespan (King and Miracle 1980). In their natural populations, the egg production rates of rotifers depend on both the current (Dumont et al. 1995) and the previous status of food supply (Edmondson 1965). However, if the environmental temperature varies, then the reproductive rate at any given food amount may also vary, perhaps because of the interaction of food and temperature (Edmondson 1964; Martinez et al. 1998). Temperature affects many parameters that may, individually or in combination, affect rotifer life histories (Edmondson 1965; Walz 1995).

Studies have shown that increasing temperature accelerates the rate of egg hatching, reduces the lifespan and age at first reproduction of rotifers (Galkovskaja 1987; Stelzer 1998). Similarly, geographical location and other intrinsic factors may influence rotifer growth and reproductive responses (Sarma and Nandini 2001, 2002). Ma et al. (2010) reported significant effects of the interactions of temperature, food concentration and geographic location on the life expectancy at hatching, generation time, net reproductive rate and intrinsic rate of population increase of the freshwater rotifer *Brachionus calyciflorus*. Various life-history parameters of rotifer strains in their geographical sites suggest ecological adaptations to local niches (Hu et al. 2003; Hu and Xi 2008).

Despite numerous studies on rotifer species across the world (e.g. Dumont and De Ridder 1987; Hagiwara et al. 1995; Sharma 2000; Ma et al. 2010; Ogata et al. 2011), there is a dearth of information regarding the identity and reproductive characteristics of African freshwater rotifers. Most studies in Africa have focused on the general abundance and diversity of rotifers (Murray 1911; De Ridder 1987; Sutherland et al. 2013; Akindele and Adeniyi 2013) without specification of the individual lifetable demographics under changing environmental stressors. Consequently,

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their ecological stability and/or suitability for aquaculture are largely unknown. The aims of the current study were to: (1) morphologically identify the Kenyan rotifer strain and (2) investigate its reproductive and growth characteristics at various temperatures and food densities, using individual lifetable and small-scale batch culture approaches.

Material and methods

Rotifers and algal supply

Resting eggs of *Brachionus angularis* were collected from sediments of freshwater ponds at Kisii, Kenya (00°42′ S, 34°47′ E) and transported to the Laboratory of Aquaculture Biology, Nagasaki University, Japan, for further study. The eggs were hatched in a 45-mm Petri dish under constant illumination (115.5 µmol^{-1} m^{-2}) and were acclimatised for one month at 25 ± 1 °C with daily feeding at an *ad libitum* amount of *C. vulgaris*. The pond water culture medium was GF/C filtered (Whatman) and autoclave-sterilised at 121 °C for 15 min. The liquid *Chlorella vulgaris* paste (cell diameter 3–8 µm; Super Fresh *Chlorella* V-12®) was regularly supplied by a company in Fukuoka, Japan, and stored at 4 °C.

Morphological identification

From the hatched rotifers a single amictic female was isolated and cultured for about one month with daily feeding at an *ad libitum* amount of *C. vulgaris* at 25 ± 1 °C to produce clones. From this population 20 individuals with visible and identifiable features were randomly isolated and subjected to further morphological analysis according to Shiel (1995). The rotifers were fixed with 10% formalin before analysing their morphological characteristics under a Zeiss Axioskop compound microscope at ×40 magnification. Photographs were taken and the lorica length and width were measured using an ocular micrometer.

Experimental design

Lifetable demography

The lifetable demography of the rotifers was investigated at 20, 25 and 30 °C and *C. vulgaris* food densities of 2.5 × 10^5, 2.5 × 10^6 and 2.5 × 10^7 cells ml^{-1}. To initiate individual culture of the rotifers, an amictic female from the stock culture was isolated and cultured at 25 ± 1 °C with daily feeding of *C. vulgaris* at *ad libitum* amount to establish a clonal population. From this culture about 250 amictic eggs were collected (at logarithmic growth phase) from the bottom of the culture container and incubated in an experimental 45-mm Petri dish under the same conditions as the stock cultures. Hatchlings (F_1) (<6 h) were employed in the study.

An F_1 individual was introduced into each well of a 24-well polystyrene microplate (Iwaki, Japan) containing 1 ml of each food suspension at 2.5 × 10^5, 2.5 × 10^6 and 2.5 × 10^7 algal cells ml^{-1}. The rotifer cultures at each food concentration were incubated at 20, 25 and 30 °C under complete darkness in 24 replicates. The rotifers were observed every 6 h under stereomicroscope at ×25 magnification to assess survival of parental females and the neonate number. The numbers of the parental females alive and neonates were recorded before the parental females were transferred into a new well of the microplate containing fresh culture medium with appropriate food concentration. Dead individuals, if any, were enumerated and removed. This process was continued until the last parental female died. Based on the data collected, age-specific survivorship and fecundity, life expectancy (days) at hatching (e_0), duration (hours) of first egg spawning (D_j), net reproductive rate (R_0) (offspring female^{-1}), generation time (T) (days) and intrinsic rate of natural population increase (r) were estimated using the following formulae (Lotka 1913):

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

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

where x = time interval, l_x = the probability of surviving to age x, m_x = the number of female offspring per female of age x born during the interval. The jackknife equation was used to calculate the intrinsic rate of population increase (r) as described by Meyer et al. (1986).

$$r = \frac{1}{n}\sum_{i=1}^{n} \bar{r} \pm \left(\sqrt{s_{\bar{r}}^2 / n}\right)$$

where $S^2\bar{r}$ = variance of the n jackknife pseudovalues, $\bar{r}_1, \bar{r}_2 .... \bar{r}_n$.

Population growth experiment

About 20 rotifers were selected and cultured for one week using fresh *C. vulgaris* at *ad libitum* amount. From this population, rotifers were selected and batch-cultured in 50 ml of fresh culture medium at an initial density of 5 ind. ml^{-1} in 300-ml glass jars under complete darkness without water exchange or aeration. The same food concentrations and temperature levels were tested in three replicates. The respective amounts of *C. vulgaris* suspension were added to each jar daily. The population density of rotifers was defined by counting live rotifers in 1 ml from each replicate jar daily using a counting plate with 10% Lugol's fixation. The experiments were terminated after 14 days.

The specific population growth rate (r) was calculated during the exponential growth phase using the formula:

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

where N_0 = initial population density, N_t = population density after the time (t) and t = time (8 days).

Data analysis

The data were analysed using R statistical software (version 3.2.1 of the R Foundation for Statistical Computing Platform © 2015). The Bartlett test of homogeneity of variances was used to test for the normality of the data. A two-way ANOVA was used to identify significant effects of temperature and food density on the lifetable variables and population density. Tukey's HSD *post hoc* test was performed to determine where the differences were situated. The log-rank test for groups was performed to explore the differences in age-specific survivorship among the treatments. Probability value of $p < 0.05$ was used to test for the level of significance.

Results

Morphologically, the Kenyan rotifer strain has two median occipital spines embedded on a pot-shaped lorica. The rotifer has an annulated foot and submedian spines are either reduced or lacking in some individuals (Figure 1). The lorica length and width of the Kenyan rotifer strain were 85.6 ± 3.1 µm and 75.4 ± 3.6 µm, respectively. These measurements were compared with those of other known *B. angularis* strains (Table 1.)

Lifetable demography

The age-specific survivorship and fecundity curves in relation to food density and temperature are presented in Figure 2. The age-specific survivorship was not affected by temperature ($\chi^2 = 4.60$, df = 2, $p = 0.10$) or food density ($\chi^2 = 0.40$, df = 2, $p = 0.83$), whereas the fecundity was affected by temperature ($F = 11.38$, $p < 0.001$), but not by food density ($F = 2.03$, $p = 0.13$). The highest age-specific fecundity (2.11 ± 0.07 offspring female^{-1} day^{-1}) was obtained at 25 °C with 2.5 × 10^6 algal cells ml^{-1}. Rotifers older than eight days continued to propagate at 25 °C, but not at 20 or 30 °C. The age-specific fecundity peaked on Day 4 at both 20 and 25 °C, but earlier (Day 3) at 30 °C regardless of food density (Figure 2).

The effects of temperature and food density on the lifetable demographic parameters are presented in Table 2, whereas values of the life demographic parameters in relation to different food densities and temperatures are summarised in Table 3. Life expectancy at hatching (e_0) was affected by temperature, but not by food density. The longest e_0 (12.41 ± 0.28 days) was realised at 25 °C with 2.5 × 10^6 algal cells ml^{-1}, whereas the shortest e_0 (8.91 ± 1.28 days) was obtained at 30 °C with 2.5 × 10^7 algal cells ml^{-1}. There

Figure 1: Images (40× magnification) of live (image 1) and dead (image 2) adult *Brachionus angularis* isolated from the Kisii ponds; a – lorica length, b – lorica width. Median occipital spines (c, inset in image 2) are shown in the coronal area of the dead adult rotifer

Table 1: Comparison of lorica length and width in the Kenyan strain of *Brachionus angularis* with those of five other *B. angularis* strains. Values are mean ± SD µm for (*n*) samples (in parentheses)

Strain origin	Lorica length (µm)	Lorica width (µm)	Reference
Kenya	85.6 ± 3.1 (20)	75.4 ± 3.6 (20)	Current study
Laos	86.0 ± 4.9 (20)	75.6 ± 5.7 (20)	Ogata et al. 2011
China	130 ± 7.0	115 ± 7.0	Yin and Niu 2008
Germany	120–140	–	Leutbecher 2000
New Zealand	122	–	Gilbert and Burns 1999
France	127.8 ± 5.9	–	Pourriot and Rougier 1997

was no significant difference in e_0 between 20 and 25 °C (p = 0.402). The duration of hatching to first egg spawning (D_j) decreased with increasing temperature and food density. The longest D_j was 8.83 ± 0.39 h at 20 °C with 2.5 × 10^5 algal cells ml^{-1}, whereas the shortest D_j was 2.86 ± 0.21 h at 30 °C with 2.5 × 10^7 algal cells ml^{-1}. The highest net reproductive rate (R_0) (8.43 ± 0.24 offspring female^{-1}) was obtained at 25 °C with 2.5 × 10^6 algal cells ml^{-1}, whereas the lowest R_o (3.01 ± 0.05 offspring female^{-1}) was recorded at 30 °C with 2.5 × 10^5 cells ml^{-1} of the algae (Table 3). The generation time (T) was longer at 20 and 30 °C than at 25 °C. The shortest T (2.87 ± 0.03 d) was observed at 25 °C with 2.5 × 10^6 algal cells ml^{-1}, whereas the longest T (4.96 ± 0.11 d) was realised at 30 °C with 2.5 × 10^5 algal cells ml^{-1}. The highest intrinsic rate of natural population increase (r) (0.74 ± 0.02 d^{-1}) was obtained at 25 °C with 2.5 × 10^6 algal cells ml^{-1}, whereas the lowest r (0.22 ± 0.00 d^{-1}) was recorded at 30 °C with 2.5 × 10^5 algal cells ml^{-1}.

Population growth in the batch cultures

The population growth curves in relation to different temperatures and food densities are presented in Figure 3. The rotifer population density was significantly affected by temperature (F = 5.28, p = 0.005) and food density (F = 5.89, p = 0.003), but not the interaction between them (F = 1.40, p = 0.23). Regardless of temperature, there was an earlier peak in the rotifer population densities at 2.5 × 10^7 algal cells ml^{-1}, but with lower population densities compared to the rest (Figure 3a, b, c). The highest population density (255.6 ± 12.6 ind. ml^{-1}) was obtained at 25 °C with 2.5 × 10^6 algal cells ml^{-1} (Figure 3d). The specific population growth rate (r) was significantly influenced by temperature (F = 76.134, p < 0.001) and food density (F = 109.02, p < 0.001), as well as the interaction between them (F = 26.323, p < 0.001). The highest (0.49 ± 0.01 d^{-1}) and the least (0.39 ± 0.01 d^{-1}) r values were obtained at 25 °C with 2.5 × 10^6 algal cells ml^{-1} and at 20 °C with 2.5 × 10^5 algal cells ml^{-1}, respectively (Figure 4).

Discussion

Environmental factors, such as changing food density and temperature and their interaction can influence the biological structures of zooplankton communities (Edmondson 1965; Pejler 1995; Sarma et al. 2002; Ma et al. 2010). However, the influence of these factors on the lifetable demography of *B. angularis* from African freshwater ecosystems has not been reported in the literature.

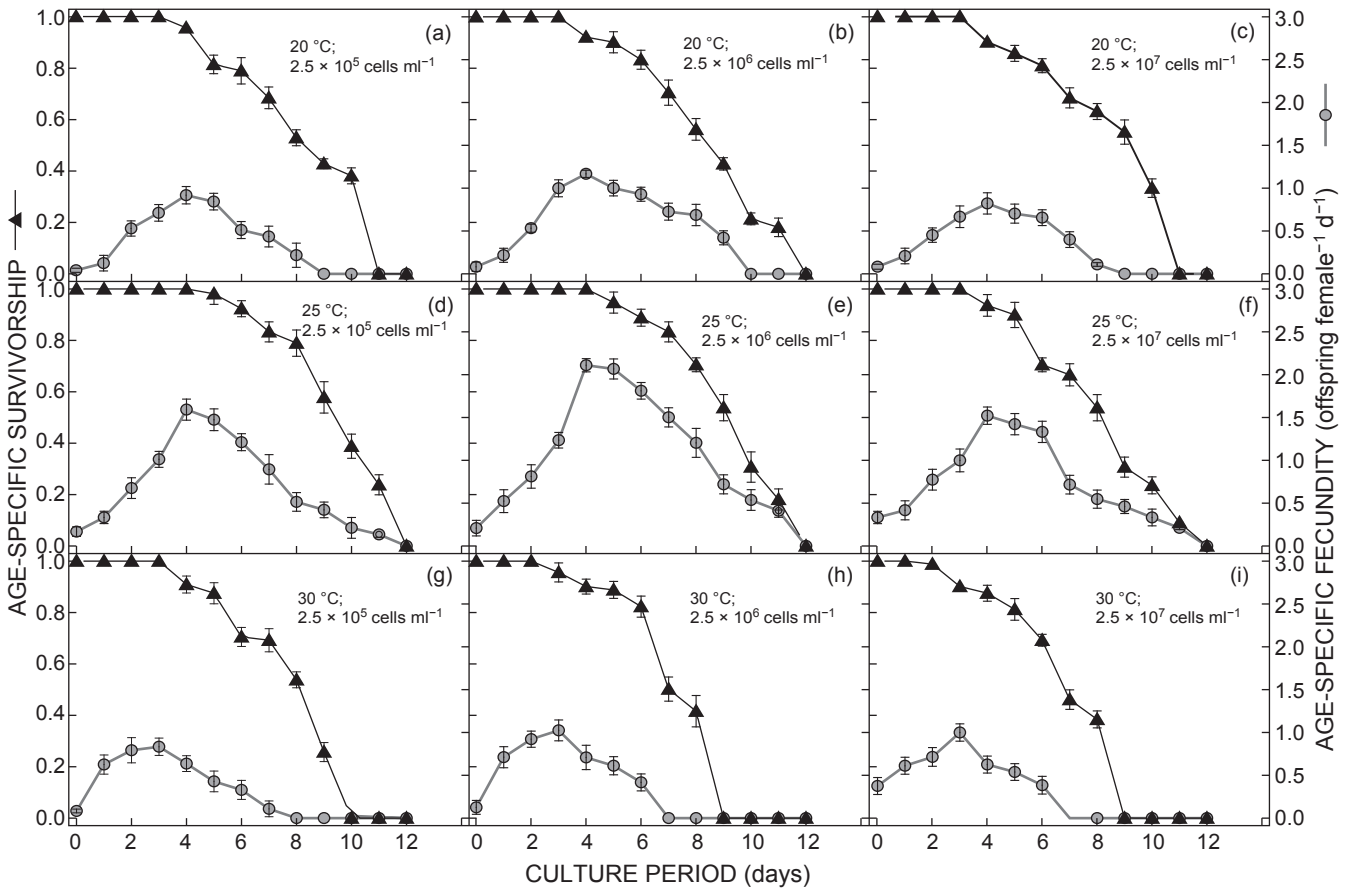

Figure 2: Age-specific survivorships and fecundities of populations of *Brachionus angularis* cultured at three different temperatures and algal densities. Values represent mean ± SD based on 24 replicate recordings. (a) 20 °C, 2.5 × 10^5; (b) 20 °C, 2.5 × 10^6; (c) 20 °C, 2.5 × 10^7; (d) 25 °C, 2.5 × 10^5; (e) 25 °C, 2.5 × 10^6; (f) 25 °C, 2.5 × 10^7; (g) 30 °C, 2.5 × 10^5; (h) 30 °C, 2.5 × 10^6; (i) 30 °C, 2.5 × 10^7 cells ml^{-1} of *Chlorella vulgaris*

The current study identified a Kenyan rotifer sample as *B. angularis* and showed the effects of changing temperature and food density on its lifetable demography and growth characteristics. The morphological observations (e.g. two median occipital spines, with either reduced or lacking submedian spines) are consistent with descriptions of *B. angularis* as reported by Shiel (1995). This study has shown that the Kenyan rotifer strain has a smaller body size (Table 1) compared to other known strains of *B. angularis*, such as the Laos strain, which is considered suitable food for small-mouthed freshwater fish larvae (Ogata et al. 2011).

Table 2: Results of a two-way ANOVA to evaluate the effect of temperature and food density on the lifetable demography of the Kenyan strain of *Brachionus angularis*. df: degrees of freedom, SS: sum of squares, MS: mean square, *F*: *F*-ratio

Demographic parameter	df	SS	MS	*F*	*p*
Life expectancy at hatching					
Food density (cells ml^{-1}) (A)	2	1.764	0.882	2.609	0.101
Temperature (B)	2	38.181	19.090	56.486	0.000*
Interaction (A × B)	4	1.639	0.409	1.212	0.340
Residuals	18	6.083	0.338		
Duration of first spawning					
Food density (cells ml^{-1}) (A)	2	8.967	4.483	12.768	0.000*
Temperature (B)	2	70.325	35.162	100.136	0.000*
Interaction (A × B)	4	3.015	0.754	2.146	0.116
Residuals	18	6.321	0.351		
Generation time					
Food density (cells ml^{-1}) (A)	2	4.245	2.122	549.684	0.000*
Temperature (B)	2	10.617	5.308	767.542	0.000*
Interaction (A × B)	4	1.507	0.376	39.014	0.000*
Residuals	18	0.173	0.009		
Net reproduction rate					
Food density (cells ml^{-1}) (A)	2	19.008	9.504	645.949	0.000*
Temperature (B)	2	79.024	39.512	2 685.5	0.000*
Interaction (A × B)	4	3.247	0.812	55.175	0.000*
Residuals	18	0.265	0.015		
Intrinsic rate of population growth					
Food density (cells ml^{-1}) (A)	2	0.190	0.095	1 022.1	0.000*
Temperature (B)	2	0.715	0.357	3 830.6	0.000*
Interaction (A × B)	4	0.046	0.115	123.73	0.000*
Residuals	18	0.001	0.000		

* = significant difference at $p < 0.05$

Based on the morphometric measurements, the Kenyan strain may qualify as an appropriate live food for larval small-mouthed freshwater fish. The suitability of small rotifers for aquaculture has been extensively discussed (Hagiwara et al. 1995; Wullur et al. 2009; Yoshimatsu and Hossain 2014). Other studies have reported that rotifer size variation could be linked to the ecological adaptations to their local geographical niches (Hu et al. 2003; Hu and Xi 2008).

The temperature and food density variations did not affect the age-specific survivorship, suggesting that rotifer survival was affected by aging. The longer life expectancy at lower temperatures (20 and 25 °C) could have been because of a decreased metabolic rate (Hagiwara et al. 1988), whereas the shorter life expectancy at 30 °C could have been because of the accumulated thermo-physiological stress. Sarma and Rao (1990) observed a decrease in life expectancy of brachionid rotifers under both increased temperature and food density. At 20 and 30 °C, rotifers older than eight days were not fecund (Figure 2), explaining their low fecundity under such conditions. Other studies have reported that the fecundity of rotifers can be affected by the ciliate epibiont-zooplankton interactions that occur in the cultures (Gilbert and Schroder 2003). Even although this parameter was not determined in the current study, it is probable that such interactions could have occurred. Further studies are necessary to unravel the role of epibiont–*B. angularis* interactions at specific temperatures. This study recorded higher age-specific fecundity at 25 °C, which was also reported for the Laos's strain of *B. angularis* by Ogata et al. (2011).

The duration of first egg spawning at 20 °C might have been delayed by slower ontogenic phases necessary to hasten reproduction (Galkovskaja 1987; Walz 1987), whereas faster ontogenetic development phases under high temperature (Athibai and Sanoamuang 2008) could explain the shorter duration of first egg spawning, as observed in our study at 30 °C. Other studies have reported longer prereproductive phases at 20 °C for rotifers (Ogata et al. 2011) and shorter duration of embryonic development at warmer temperatures of 25 and 30 °C (Walz 1987; Hu et al. 2003; Hu and Xi 2008). Baker (1979) reported 8 to 12 h as the duration of first egg spawning for the freshwater rotifers *B. angularis* and *B. calyciflorus*

Table 3: Lifetable demography of the Kenyan strain of *B. angularis* in relation to various food densities and temperatures. Life expectancy at hatching (e_0), duration of first spawning (D_j), net reproductive rate (R_0), generation time (T) and intrinsic rate of natural increase (r). Values are mean ± SD based on 24 replicates. Different superscripts in the same column indicate significant differences. Two-way ANOVA; Tukey's HSD test, $p < 0.05$, $n = 27$

Temperature (°C)	Food density (cells ml^{-1})	Lifetable demography parameter				
		e_0 (days)	D_j (hours)	R_0 (offspring female^{-1})	T (days)	r
20	2.5×10^5	11.33 ± 0.57^{a}	8.83 ± 0.39^{a}	3.71 ± 0.01^{g}	4.80 ± 0.15^{abc}	0.27 ± 0.09^{g}
	2.5×10^6	12.08 ± 0.14^{a}	6.90 ± 0.10^{a}	6.25 ± 0.04^{d}	3.49 ± 0.02^{fg}	0.52 ± 0.05^{d}
	2.5×10^7	11.08 ± 0.14^{a}	6.69 ± 0.94^{a}	3.87 ± 0.05^{fg}	4.49 ± 0.05^{d}	0.30 ± 0.01^{f}
25	2.5×10^5	11.33 ± 0.57^{a}	5.21 ± 0.99^{b}	7.80 ± 0.09^{b}	2.91 ± 0.05^{hi}	0.70 ± 0.01^{b}
	2.5×10^6	12.41 ± 0.28^{a}	5.04 ± 0.54^{b}	8.43 ± 0.24^{a}	2.87 ± 0.03^{i}	0.74 ± 0.02^{a}
	2.5×10^7	12.08 ± 0.14^{a}	4.44 ± 0.82^{b}	6.71 ± 0.06^{c}	3.42 ± 0.03^{g}	0.55 ± 0.01^{c}
30	2.5×10^5	9.33 ± 0.57^{b}	4.16 ± 0.28^{c}	3.01 ± 0.05^{i}	4.96 ± 0.11^{ac}	0.22 ± 0.00^{i}
	2.5×10^6	9.33 ± 0.57^{b}	3.75 ± 0.07^{c}	4.73 ± 0.05^{e}	3.78 ± 0.07^{e}	0.41 ± 0.01^{e}
	2.5×10^7	8.91 ± 1.28^{b}	2.86 ± 0.21^{c}	3.15 ± 0.21^{hi}	4.76 ± 0.18^{cd}	0.24 ± 0.01^{hi}

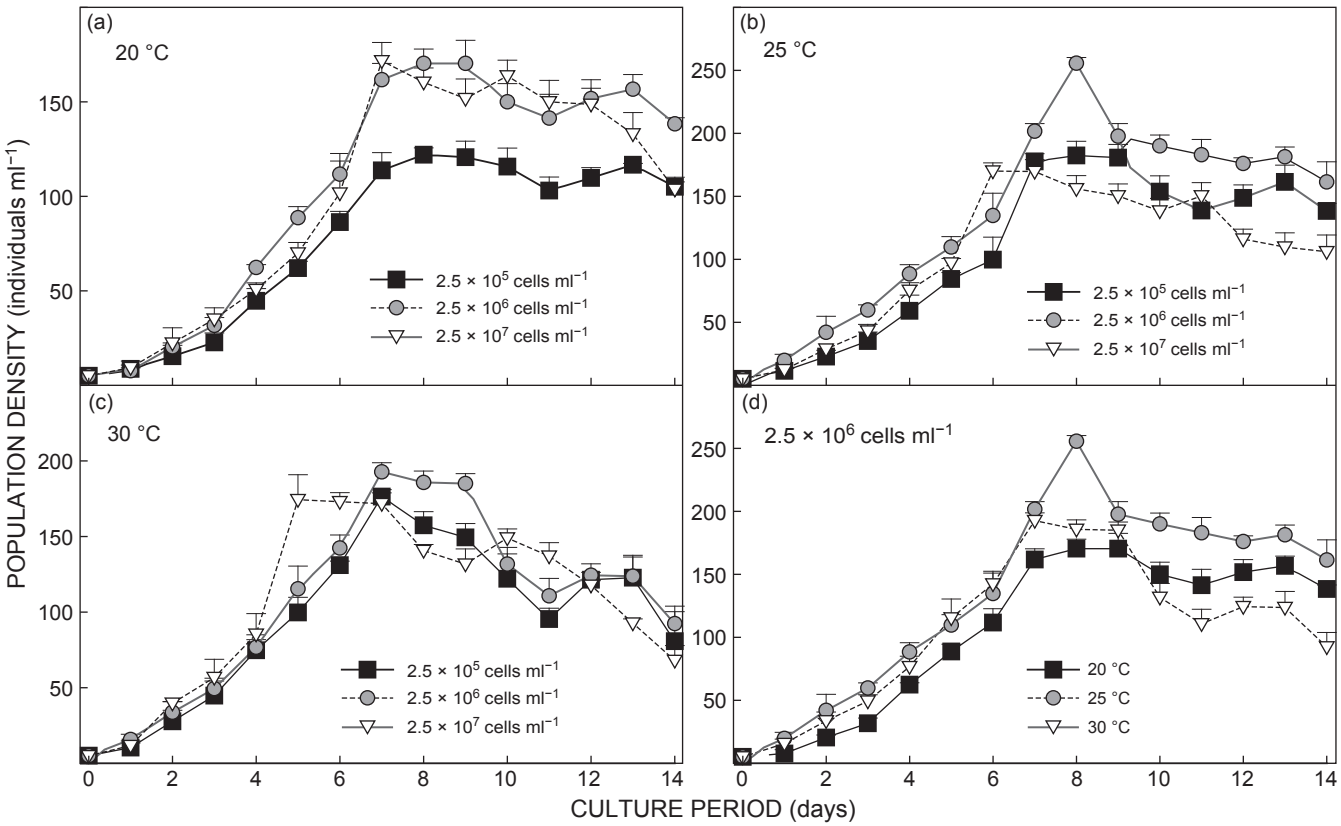

Figure 3: Population density growth curves of *Brachionus angularis* in relation to different temperatures and *Chlorella vulgaris* densities. Values are means ± SD based on 3 replicates. Two-way ANOVA, Tukey's HSD test, $p < 0.05$, $n = 378$

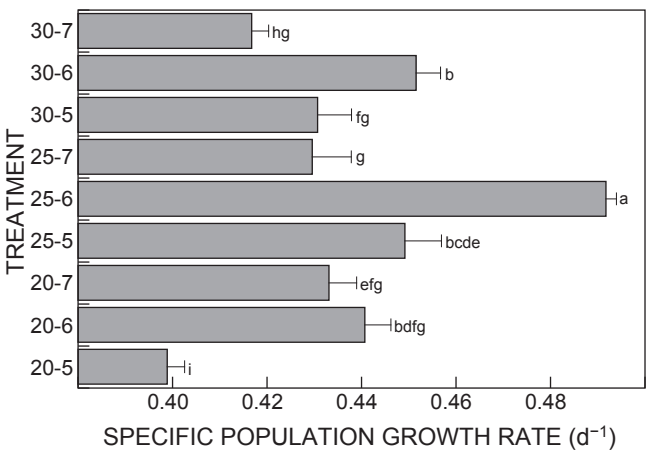

Figure 4: Specific population growth rate day^{-1} for Kenyan *Brachionus angularis* in relation to temperature and food densities. Means ± SD based on three replicate recordings two-way ANOVA, Tukey's HSD test, $p < 0.05$, $n = 27$. Different letters indicate significant differences (a>b>c>d>e>f>g>h>i). Treatments: 20, 25 and 30 °C with 5 = 2.5 × 10^5, 6 = 2.5 × 10^6 and 7 = 2.5 ×10^7 algal cells ml^{-1}

cultured at 20 °C, which is comparable to the findings of the current study.

The higher net reproductive rate at 25 °C with 2.5 × 10^6 algal cells ml^{-1} could have been because of the continuous reproduction of the older rotifers, unlike under the other culture conditions. The findings resembled those of Ma et al. (2010), who found a range of net reproductive rates of up to 5 to 23 offspring female^{-1} for freshwater *B. calyciflorus* cultured between 18 and 28 °C in different geographic populations. According to Edmondson (1964, 1965), the interactions of temperature and food densities affect the reproductive rate of rotifers even in their natural habitats. Pourriot and Rougier (1997) reported that ecological adaptations may cause different reproductive rates among species.

The prolonged generation time at 20 °C could have been caused by the longer duration of fist egg spawning. There was longer generation time at 30 °C, perhaps because of the preference of survival over reproduction. According to Chen and Cuijuan (2015), a trade-off exists between the energy required for maintenance and that for reproduction and growth. Sarma and Nandini (2002) also reported that generation time of rotifers decreases with increased food density and temperature. The findings of the current study are comparable to those of Galkovskaja (1987) and Ma et al. (2010), who reported generation times of 2 to 3 days for *B. calyciflorus* cultured at 27 °C with 3.0 × 10^6 algal cells ml^{-1} of *C. vulgaris*. The higher intrinsic rate of population increase at 25 °C with 2.5 × 10^6 algal cells ml^{-1} could be attributed to higher reproductive rates and shorter generation time of rotifers at that condition. Warmer temperatures cause shorter periods of embryonic development and therefore enhance intrinsic rate of population increase

at optimal food conditions (Hu and Xi 2008). Studies by Gilbert (2003) and Ma et al. (2010) suggested that genetic adaptations to local environmental pressures could affect the rotifer intrinsic rate of increase. In general, temperature affects many parameters, such as dissolved oxygen and biochemical reactions, which may, individually or in combination, affect rotifer life histories in any habitat (Edmondson 1965; Walz 1995).

The highest population density observed on Day 8 at 25 °C with 2.5×10^6 algal cells ml^{-1} of *C. vulgaris* (Figure 3b) suggested an occurrence of simultaneous reproduction of the old and new rotifer cohorts. The earlier peaks noted at 30 °C (Figure 3c) were probably thermal-regulated and could have been because of the shift of the reproduction maxima to the earliest stages of maturity and the shorter duration of first egg spawning. This coincided with earlier peaks observed in the individual culture experiments under similar conditions. The population density quickly declined at 30 °C, suggesting that the rotifers may have switched to a mixis phase under this stressing condition. Mixis investment is likely to reduce the short-term fitness of rotifer clones (Chen and Cuijuan 2015) as more energy is used to fertilise a mictic female to lay a resting egg than for an amictic female to produce a daughter (Sarma et al. 2002; Gilbert 2010). In such situations life expectancy and fecundity are usually reduced (Snell and King 1977), hence lowering population density. Faster deterioration of the culture medium under this condition may also have contributed to the observed results, because there was no regular water exchange.

The higher rate of specific population growth at 25 °C with 2.5×10^6 algal cells ml^{-1} was attributed to the high reproductive rate, longer life expectancy, shorter duration of the juvenile phase and the shorter generation time. Even though warmer temperatures with optimal food conditions enhance rotifer growth rates, an exceeded thermal tolerance can cause a rotifer culture crash (Stelzer 1998). Generally, the growth rate of the rotifers in the current study could have been limited by poor water quality, because there was no water exchange during the experiment. Nonetheless, the growth rates for most brachionid rotifers range from 0.2 to 2.0 d^{-1} (Sarma and Nandini 2001). Our specific growth rate values of 0.39–0.49 d^{-1} (Figure 4) were within the known range reported in the literature.

The Kenyan rotifer strain of *B. angularis* has a smaller size (lorica length: 85.6 ± 3.1 µm, width 75.4 ± 3.6 µm), making it convenient for rearing freshwater fish larvae, especially those with small mouths. The rotifer reproduces optimally at 25 °C with 2.5×10^6 algal cells ml^{-1} of *C. vulgaris*. The results of this study are relevant to the improvement of freshwater aquaculture, especially for the larvae ornamental fishes such, as gold fish (*Carassius auratus*), whose mouth gap is very small (Lim et al. 2003). Further studies on the population growth of this rotifer strain are recommended using other food types.

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