Life table demography and population growth of the rotifer *Brachionus angularis* in Kenya; influence of temperature and food density

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Abstract

Life table 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^{o}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 ^{o}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 ^{o}C with 2.5×10^7 algal cells ml^{-1} and longest (8.83 ± 0.39 h) at 20 ^{o}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 ^{o}C with 2.5×10^6 cells ml^{-1} on day 8, while the lowest population density (122.0 ± 3.6 ind ml^{-1}) was realised at 20 ^{o}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 ^{o}C with 2.5×10^6 algal cells ml^{-1}.

Keywords: Alga, *Brachionus angularis*, fecundity, generation time, life table parameters, rotifera

Introduction

A life table 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, 2010). Life table 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 critical to understanding rotifer biological behavior 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; Awaiss 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 (Yufera 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 present (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 due to the interaction of food and temperature (Edmondson 1964; Martinez et al. 1998). Temperature affects many parameters which 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 life span 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). Xi 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; Xi and Hu 2008).

Despite numerous studies on rotifer species across the world (e.g. Dumont and De Ridder 1987; Sharma 2000; Hagiwara et al. 1995; Xi 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 (De-Ridder 1987; Murray 2011; Sutherland et al. 2013; Akindele and Adeniyi 2013) without specification of the individual life table demographics under changing environmental stressors. Thus their ecological stability and/or suitability for aquaculture is largely unknown. The aims of the present study were 1) morphologically to identify the Kenyan rotifer strain, and 2) to investigate its reproductive and growth characteristics at various temperatures and food densities using individual life table and small-scale batch culture approaches.

Materials and methods

Rotifers and algal supply

Resting eggs of *B. angularis* were collected from sediments of freshwater ponds at Kisii, Kenya ($00^{o}42'$S; $034^{o}47'$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 µmols $^{-1}$ m^{-2}) and were acclimatised for one month at 25 ± 1 ^{o}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 *C. vulgaris* paste (cell diameter 3-8µm; Super Fresh *Chlorella* V-12®) was regularly supplied by a company in Fukuoka, Japan, and stored at 4^{o}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^{o}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

Life table demography

The life table demography of the rotifers was investigated at 20, 25 and 30 ^{o}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 ^{o}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 ^{o}C under complete darkness in 24 replicates. The rotifers were observed every 6 h under stereo microscope 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 at hatching (e_o), duration of first egg spawning (D_j), net reproductive rates (R_o), generation time (T), and intrinsic rate of natural population increase (r) were estimated using the following formulae (Lotka 1913).

Net reproductive rate (R_o) $= \sum_{0}^{\infty} l_x m_x$

Generation time $(T) = \dfrac{\sum l_x m_x x}{R_o}$

Where x = time interval, lx = 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).

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

Where $s^2_{\bar{r}}$ = variance of the *n* Jackknife pseudo-values, $\bar{r}_1$, $\bar{r}_2$ .....$\bar{r}_n$

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. chlorella* 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 fixation. The experiments were terminated after 14 days. The specific population growth rate (*r*) was calculated during the exponential growth phase using the formula $r = [\ln N_t - \ln N_o] / t$ where, N_o = 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. Two-way ANOVA was used to identify significant effects of temperature and food density on the life table 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 annulated foot and sub-median 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.)

Life table 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 (χ^2 = 4.60, df = 2, p = 0.10) or food density (χ^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 ^{o}C with 2.5×10^{6} algal cells ml^{-1}. Rotifers older than eight days continued to propagate at 25 ^{o}C, but not at 20 or 30 ^{o}C. The age-specific fecundity peaked on day 4 at both 20 and 25 ^{o}C but earlier (day 3) at 30 ^{o}C regardless of food density (Figure 2).

The effects of temperature and food density on the life table demographic parameters are presented in Table 2, while values of the life demographic parameters in relation to different food densities and temperatures are summarised in Table 3. Life expectancy at hatching (e_o) was affected by temperature but not by food density. The longest e_o (12.41 ± 0.28 days) was realised at 25 ^{o}C with 2.5×10^{6} algal cells ml^{-1}, while the shortest e_o (8.91 ± 1.28 days) was obtained at 30 ^{o}C with 2.5×10^{7} algal cells ml^{-1}. There was no significant difference in e_o between 20 and 25 ^{o}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 ^{o}C with 2.5×10^{5} algal cells ml^{-1}, while the shortest D_j was 2.86 ± 0.21 h at 30 ^{o}C with 2.5×10^{7} algal cells ml^{-1}. The highest net reproductive rate (R_o) (8.43 ± 0.24 offspring female^{-1}) was obtained at 25 ^{o}C with 2.5×10^{6} algal cells ml^{-1}, while the lowest R_o (3.01 ± 0.05 offspring female^{-1}) was recorded at 30 ^{o}C with 2.5×10^{5} cells ml^{-1} of the algae (Table 3). The generation time (T) was longer at 20 and 30 ^{o}C than at 25 ^{o}C. The shortest T (2.87 ± 0.03 d) was observed at 25 ^{o}C with 2.5×10^{6} algal cells ml^{-1}, while the longest T (4.96 ± 0.11 d) was realised at 30 ^{o}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 ^{o}C with 2.5×10^{6} algal cells ml$^{-1,}$ while the lowest r (0.22 ± 0.00 d^{-1}) was recorded at 30 ^{o}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, 3B and 3C). The highest population density (255.6 ± 12.6 ind ml^{-1}) was obtained at 25 ^oC with 2.5×10^6 algal cells ml^{-1} (Figure 5D). The specific population growth rate (r) was significantly influenced by temperature ($F = 76.134$, $p < 0.001$), food density ($F = 109.02$, $p < 0.001$) and 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 ^oC with 2.5×10^6 algal cells ml^{-1} and at 20 ^oC with 2.5×10^5 algal cells ml^{-1}, respectively (Figure 4).

Discussion

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

The present study identified a Kenyan rotifer sample as *B. angularis*, and showed the effects of changing temperature and food density on its life table demography and growth characteristics. The morphological observations (e.g. two median occipital spines, with either reduced or lacking sub-median 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). 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; Xi and Hu 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 ^{o}C) could have been due to decreased metabolic rate (Hagiwara et al. 1988), while the shorter life expectancy at 30 ^{o}C could have been due to 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 ^{o}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 though, 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 ^{o}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 ^{o}C might have been delayed by slower ontogenic phases necessary to hasten reproduction (Galkovskaya 1987; Walz 1987), while 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 ^{o}C. Other studies have reported longer pre-reproductive phases at 20 °C for rotifers (Ogata et al. 2011), and shorter duration of embryonic development at warmer temperatures of 25 and 30 ^{o}C (Walz 1987; Hu et al. 2003; Hu and Xi 2008). Baker (1979) reported 8 - 12 h as the duration of first egg spawning for the freshwater rotifers *B. angularis* and *B. calyciflorus* cultured at 20 ^{o}C, which is comparable to the findings of the present study.

The higher net reproductive rate at 25 ^{o}C with 2.5×10^{6} algal cells ml^{-1} could have been due to the continuous reproduction of the older rotifers, unlike under the other culture conditions. The findings resembled those of Xi 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 ^{o}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 et al. (1997) reported that ecological adaptations may cause different reproductive rates among species.

The prolonged generation time at 20 ^{o}C could have been caused by the longer duration of fist egg spawning. There was longer generation time at 30 ^{o}C, perhaps due to the preference of survival over reproduction. According to Chen and Cuijuan (2015), a tradeoff 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 present study are comparable to those of Galkovskaya (1987) and Xi et al. (2010), who reported generation times of 2 to 3 days for *B. calyciflorus* cultured at 27 ^{o}C with 3.0×10^{6} algal cells ml^{-1} of *C. vulgaris*. The higher intrinsic rate of population increase at 25 ^{o}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 thus enhance intrinsic rate of population increase at optimal food conditions (Hu and Xi 2008). Studies by Gilbert (2003) and Xi 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 ^{o}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 ^{o}C (Figure 3C) were probably thermal-regulated and could have been due to 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 ^{o}C, suggesting that the rotifers may have switched to 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 ^{o}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 present 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 (0.39 - 0.49 d^{-1}) (Fig. 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 ^{o}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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TABLES

Table 1: Comparison of lorica length and width in the Kenyan strain of *B. 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)	Present 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

446 **Table 2:** Effect of temperature and food density on the life table demography of the Kenyan
447 strain of *B. angularis*. 2-way ANOVA

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	2685.509	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	1022.1	0.000*
Temperature (B)	2	0.715	0.357	3830.6	0.000*
Interaction (A×B)	4	0.046	0.115	123.73	0.000*
Residuals	18	0.001	0.000		

448 df: degrees of freedom, SS: Sum of squares, MS: Mean square, *F*: F-ratio, *P*: level of
449 significance. * = significant difference at $p < 0.05$

Table 3: Life table demography of the Kenyan strain of *B. angularis* in relation to various food densities and temperatures

Temperature (^oC)	Food density (cells ml^{-1})	Life table demography parameter				
		e_o (d)	D_j (h)	R_o Offspring/female	T (d)	r
20	$2.5x10^5$	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}
	$2.5x10^6$	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}
	$2.5x10^7$	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	$2.5x10^5$	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}
	$2.5x10^6$	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}
	$2.5x10^7$	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	$2.5x10^5$	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}
	$2.5x10^6$	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}
	$2.5x10^7$	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}

Life expectancy at hatching (e_o), duration of first spawning (D_j), net reproductive rate (R_o), 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. 2-way ANOVA; Tukey HSD test, $p < 0.05$, $n = 27$

FIGURES

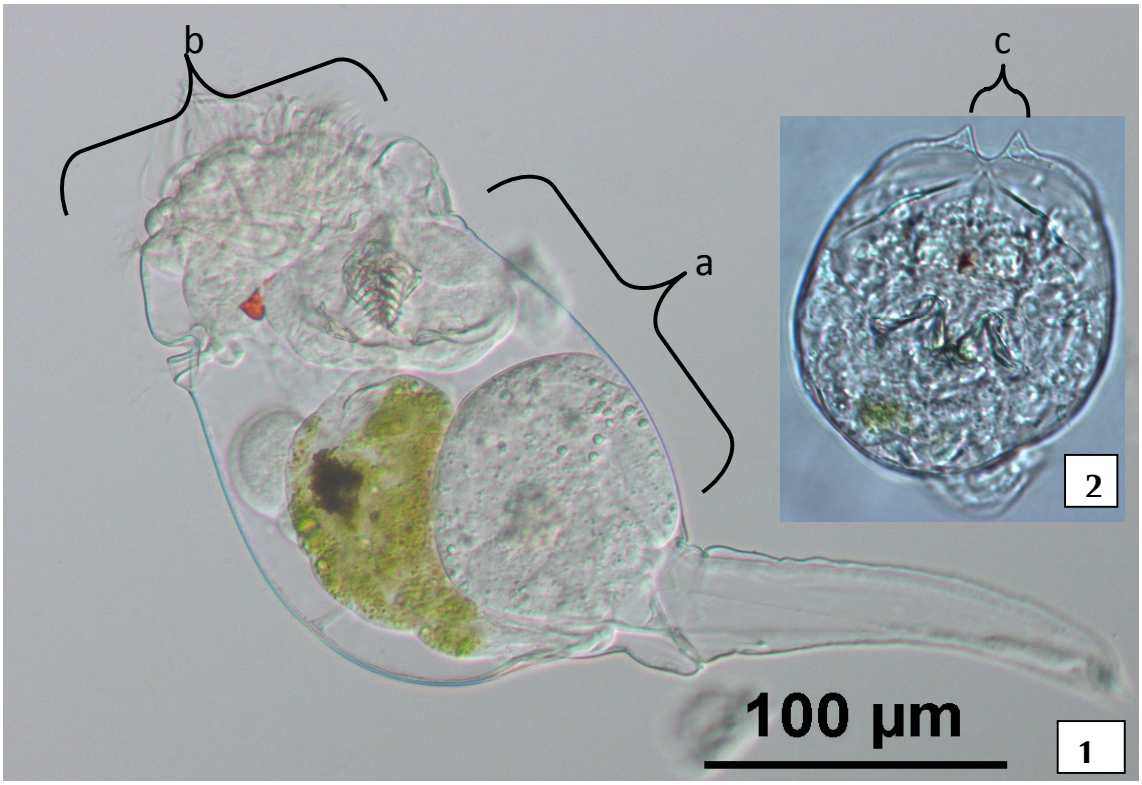

Figure 1: Images (40× magnification) of (1) live and (2) dead adult *Brachionus angularis* isolated from the Kisii ponds a: lorica length, b: lorica width. Median occipital spines (c, inset in image 2) are shown in the coranal area of the dead adult rotifer

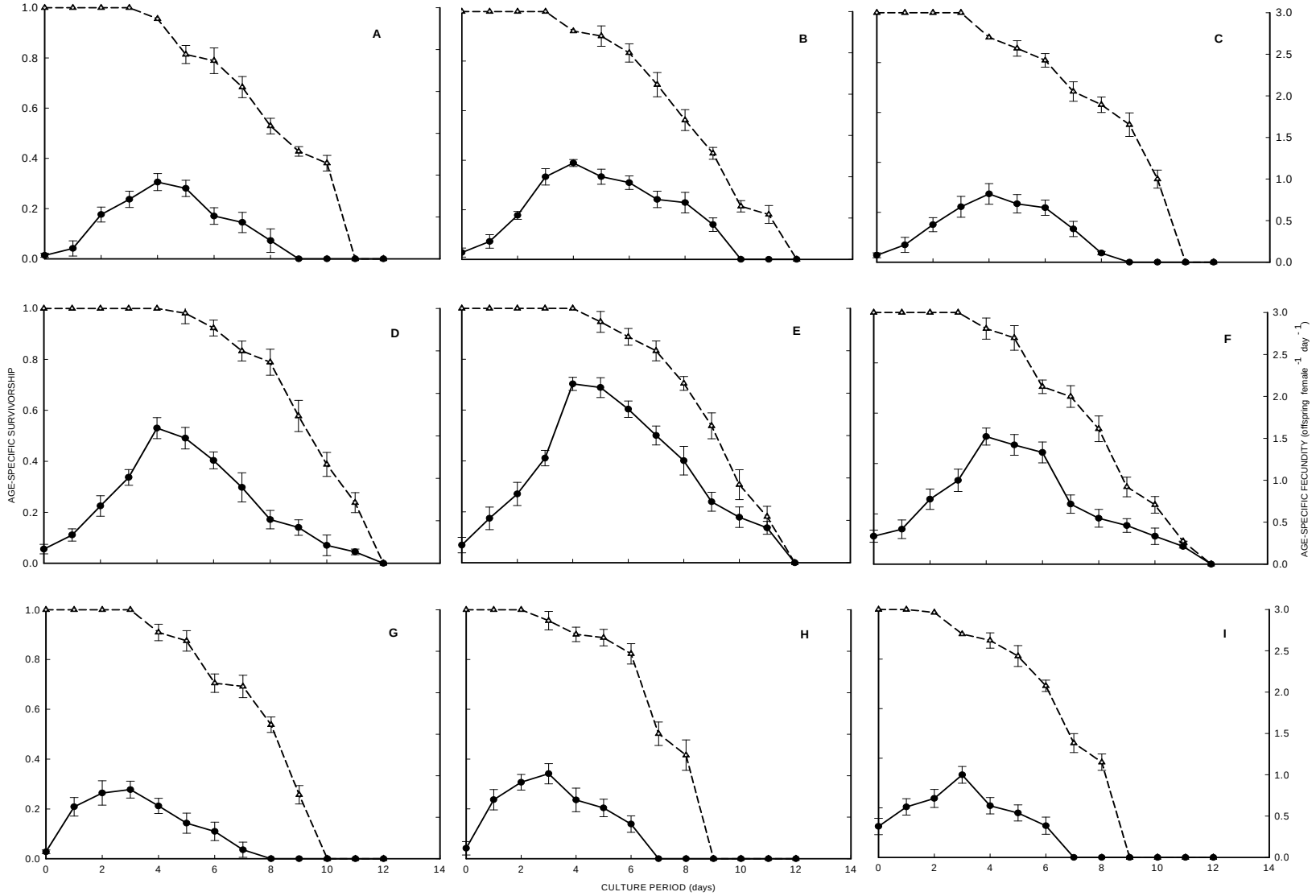

Figure 2: Age-specific survivorships (doted curves) and fecundities (solid curves) of populations of the rotifer *B. angularis* cultured at three different temperatures and algal densities. Values represent mean ± SD based on 24 replicate recordings. A: 20°C; 2.5x10^5, B: 20°C; 2.5x10^6, C: 20°C; 2.5x10^7, D: 25°C; 2.5x10^5, E: 25°C; 2.5x10^6, F: 25°C; 2.5x10^7, G: 30°C; 2.5x10^5, H: 30°C; 2.5x10^6, I: 30°C; 2.5x10^7 cells ml $^{-1}$ of *C. vulgaris.*

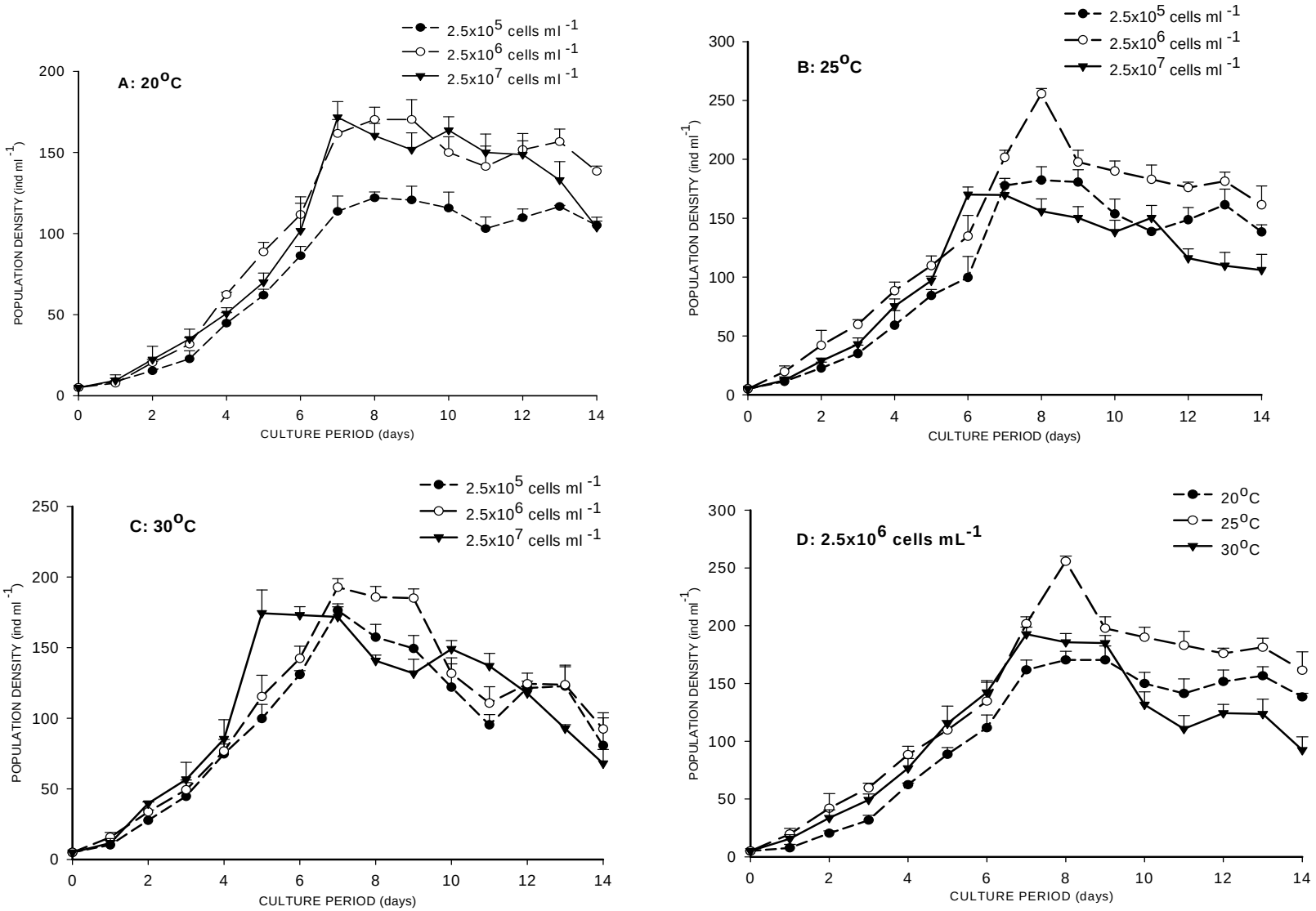

Figure 3: Population density growth curves of the rotifer *B. angularis* in relation to different temperatures and *C. vulgaris* densities. Values are means ± SD based on 3 replicates. Two-way ANOVA, Tukeys HSD test, $p < 0.05$, $n = 378$

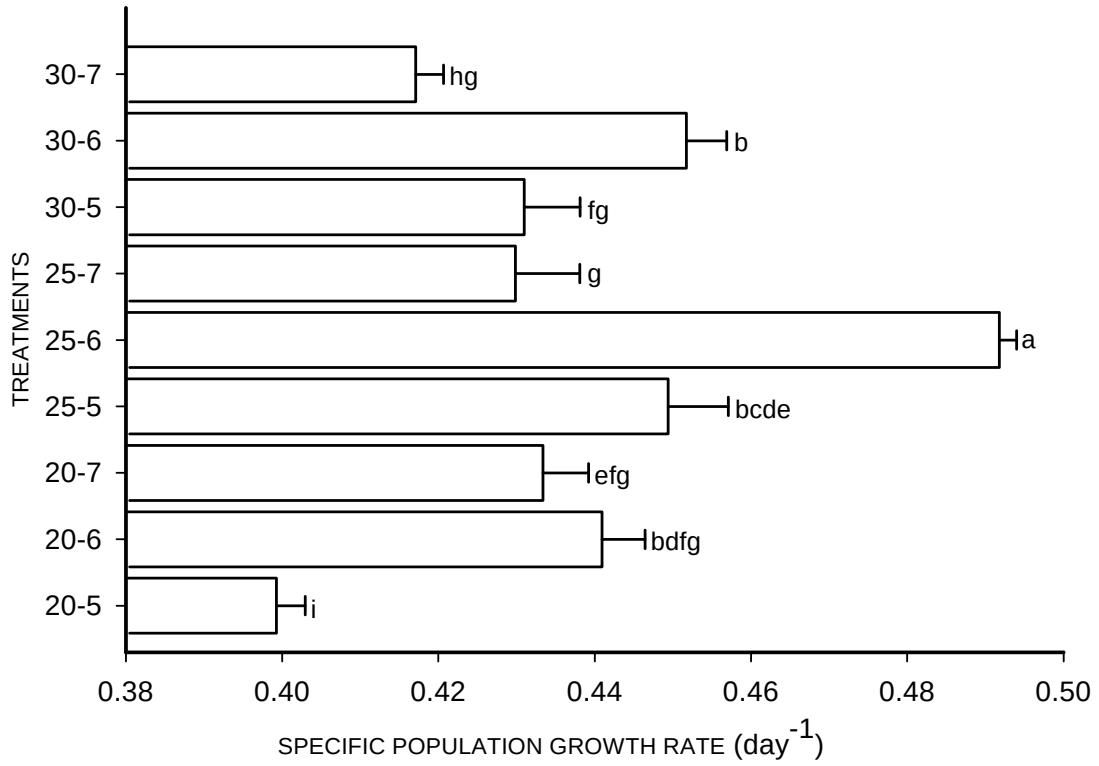

Figure 4: Specific population growth rate day $^{-1}$ for the Kenyan rotifer *Brachionus angularis* in relation to temperature and food densities. Shown are the means ± SD based on three repicate recordings 2-way ANOVA, Tukeys HSD test, $p < 0.05$, $n = 27$. Different letters indicate significant differences a>b>c>d>e>f>g>h>I; Treatments: 20, 25 and 30^{o}C with 5 = 2.5×10^{5}, 6 = 2.5×10^{6} and 7 = 2.5×10^{7} algal cells ml $^{-1}$