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Life table analysis reveals variation in thermal tolerance among three species of the *Lecane* genus (Rotifera: Monogononta)

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Abstract – Variation in thermal tolerance among related species plays an important role in establishing their range and distribution. We conducted life table experiments with three rotifer species of the *Lecane* genus at three temperatures (20, 25 and 30 °C). The rotifers were fed on *Nannochloropsis oculata* at 10^6 cells.mL^{-1} to test the hypothesis that *Lecane papuana* (Murray, 1913) (a warm stenothermal species) would behave like a thermal specialist and perform better at higher temperatures than the cosmopolitan species *Lecane bulla* (Gosse, 1851) and *Lecane cornuta* (Müller, 1786). Consistent with our hypothesis, *L. papuana* grew better at 30 °C than at 20 and 25 °C, while at 30 °C, *L. cornuta* grew poorly and *L. bulla* did not grow at all. All three species have longer lifespans with decreasing temperature. At 20 °C, the net reproductive rates of *L. cornuta* (3.5 h^{-1}) and *L. papuana* (3.58 h^{-1}) were not significantly different, but were significantly greater than that of *L. bulla* (2.75 h^{-1}). At 25 °C, *L. papuana* had a lower net reproductive rate (6.33 h^{-1}) than either *L. bulla* (11.33 h^{-1}) or *L. cornuta* (7.12 h^{-1}). However, at 30 °C, *L. papuana* had a greater net reproductive rate (14.35 h^{-1}) than *L. cornuta* (1.16 h^{-1}).

Key words: Demography / ecotoxicology / endpoints / invertebrates / temperature

Introduction

Life tables provide information on life history strategies based on observations of reproduction and mortality in individuals of a given population (Krebs, 1985). Life table experiments and ecological studies on rotifers have demonstrated that most of the species investigated so far are *r*-strategists and, therefore, have the ability to occupy new niches (Wallace *et al*., 2006). Life table experiments have been performed mainly on planktonic rotifer species, but little information is available for littoral species. In fact, in the *Lecane* genus, perhaps one of the most diverse rotifer genera (Segers, 1995), only six species have been studied to determine their life table characteristics: *Lecane inermis* (Bryce, 1892) (Miller, 1931), *Lecane cornuta* (Pray, 1965) and *Lecane tenuiseta* (Harring, 1914) (Hummon and Bevelhymer, 1980), *Lecane luna* (Müller, 1786) and *Lecane quadridentata* (Ehrenberg, 1830) (Pérez-Legaspi and Rico-Martínez, 1998), and *Lecane furcata* (Murray, 1913) (Hernández-Rodríguez *et al*., 2000).

The diversity of *Lecane* species seems to be related to their versatility and perhaps to the food specialization characteristic of the genus (Segers, 1995). Several species in the *Lecane* genus have been cultured successfully, using different types of media. Hummon and Bevelhymer (1980) developed life table experiments with *L. tenuiseta* fed on baker's yeast. Miller (1931) and Pray (1965) used wheat-grain infusions in their experiments. Pérez-Legaspi and Rico-Martínez (1998), Rico-Martínez and Snell (1997) and Segers and Rico-Martínez (2000) used algae to grow four different *Lecane* species.

Protection of aquatic ecosystems requires new protocols for assessing the impact of potentially toxic compounds that enter freshwater ecosystems (De Zwart, 2002). There are many factors concerning rotifers that favor their use as model test organisms for ecotoxicological studies: (a) they are easy to culture, (b) they achieve exponential growth, (c) their small size, (d) their environmental sensitivity, (e) there is a wide range of species that have been cultured and (f) they have a high level of production of cysts or parthenogenetic eggs that hatch easily (Rico-Martínez *et al*., 2013). Life table parameters have been used in rotifers as the endpoints of ecotoxicological tests (Janssen *et al*., 1993). For example, hatching diapausing embryos (resting eggs or cysts) has been shown to be a sensitive endpoint of petroleum exposure in rotifers (Rico-Martínez *et al*., 2013). However, there is a need to

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find "indigenous species that may be as sensitive or more sensitive" than species recommended by the US Environmental Protection Agency (EPA) due to their better adaptation to local environments (United States Environmental Protection Agency, 2002). This has prompted us to collect species with the potential to be good candidates for developing ecotoxicology/toxicology tests for Mexico. The *Lecane* genus is an excellent candidate for toxicological tests due to its ability to be present in both planktonic and benthic communities. One species of this genus, *L. quadridentata*, has been used extensively for toxicity testing (Rico-Martínez *et al.*, 2000; Pérez-Legaspi and Rico-Martínez, 2001; Santos-Medrano *et al.*, 2007; Torres-Guzmán *et al.*, 2010a), and has been shown to be more sensitive than *Daphnia magna*, as recommended by the EPA, when environmental samples were analyzed (Santos-Medrano *et al.*, 2007).

In our search for more appropriate species, we posited that *Lecane bulla*, *L. cornuta* and *L. papuana* would be good candidates because they grow efficiently in the laboratory under defined conditions, and produce a large number of parthenogenetic eggs that hatch quickly over short periods of time. *L. bulla* and *L. cornuta* are cosmopolitan species, whereas *L. papuana* is considered to be a warm stenothermal species (Segers, 1995). These characteristics enabled us to test the hypothesis that *L. papuana* would achieve a higher growth rate at a high temperature (30 °C) than either *L. bulla* or *L. cornuta*.

The aim of our work was to determine the influence of temperature on three species of the *Lecane* genus: *L. bulla*, *L. cornuta* and *L. papuana*, using life table experiments. These data, once analyzed, were used to: (a) test the hypothesis that *L. papuana* behaves as a high-temperature thermal specialist, and (b) determine the feasibility of using these three species as model organisms to develop sensitive toxicity/ecotoxicology tests.

Materials and methods

The littoral rotifer *L. bulla* was collected at Milpillas de Arriba, Aguascalientes, México (21.880'N, 102.491'W). *L. cornuta* was collected at La Mezquitera, Aguascalientes (21.545'N, 102.192'W). *L. papuana* was collected at El Ocote, Aguascalientes (21.464'N, 102.313'W). All geographic coordinates were determined with a GPS 4000XL Magellan Satellite Navigator. The rotifer species were grown in the laboratory for at least 6 months prior to performing the experiments. EPA medium (U.S. EPA, 1985) was used for all rotifer cultures. The animals were fed the green alga *Nannochloropsis oculata* LB2164 UTEX Culture Collection of Algae grown in Bold's Basal Medium (Nichols, 1973). Algae was harvested by centrifugation and added to rotifer cultures. We studied the effect of three different temperatures (20, 25 and 30 °C) at one food concentration (*N. oculata*, 10^6 cells.mL^{-1}). The life table studies were started with hatchlings from 100 asexual eggs. We observed the eggs every 2 h and assigned a mid-value of 1 h to every individual hatched within the 2-h period until we collected 24 individuals. All animals were acclimated to the corresponding experimental temperature for at least 48 h prior to the start of each experiment, which means that the parthenogenetic eggs used in the experiment were produced at the corresponding temperature and food concentration with the exception of *L. bulla*, which was unable to produce parthenogenetic eggs at 30 °C. Hatching percentages were recorded for up to 72 h. Neonates were then transferred to individual wells in a 24-well polystyrene plate (Corning®) with the appropriate food concentration and incubated at the corresponding temperature under a 16:8 light:dark photoperiod. The total volume in each well was 750 µL. In total 24 individuals were observed at 20, 25 and 30 °C every 24 h, and their neonates were counted and removed from the well. Instead of changing the original individuals to new wells with fresh food (a procedure that may damage the animals), half of the medium was replaced by fresh medium every 24 h. The algae were counted by means of a hemocytometer. The dry weight of 10^6 cells.mL^{-1} of *N. oculata* (2.13 ± 1.90 µg for 1×10^6 cells.mL^{-1}; $n = 10$) was determined by standard methods (APHA, 1995) to ensure comparability of our results with other studies.

The following parameters were analyzed: the 24 h time intervals (x), mean duration of lifespan (D, h), mean generation time (G, h), net reproductive rate (Ro, h^{-1}) and the life expectancy (ex, h). All of these parameters were determined according to Krebs (1985). Reproductive value (Vx), mean generation time (G), net reproductive rate (Ro) and intrinsic growth rate (r) were calculated according to Krebs (1985) and Begon *et al.* (1996), using the following formulae:

$$\text{Survivorship (lx)} = \frac{\text{nx}}{24}$$

$$\text{Mean fecundity (mx)} = \frac{\text{fx}}{\text{nx}}$$

$$\text{Mean duration of lifespan } (D): \quad D = \frac{\sum(\text{age at death})}{\text{Number of individuals in the cohort}}$$

$$\text{Mean generation time } (G) = \sum \frac{(\text{xmxlx})}{\text{Ro}}$$

$$\text{Net reproductive rate (Ro)} = \sum(\text{mxlxx})$$

$$\text{Life expectancy (ex)} = \frac{\text{Tx}}{\text{lx}}$$

$$= \text{proportion surviving for each time interval}$$

$$\text{Tx} = \text{Total number of organisms living at each age interval}$$

$$\text{Reproductive value (Vx)} = \frac{\text{mx}}{x}$$

Table 1. Life table parameters of three species of the rotifer *Lecane* genus.

	Lecane bulla		*Lecane cornuta*			*Lecane papuana*		
Parameters	20 °C	25 °C	20 °C	25 °C	30 °C	20 °C	25 °C	30 °C
D (h)	281 ± 19.08	177 ± 9.67	386 ± 32.59	304 ± 27.88	70 ± 10.89	195 ± 15.91	154 ± 10.80	101 + 6.77
Bootstrap *D*	281.2 ± 18.57	177.15 ± 9.35	385.41 ± 31.60	304.44 ± 26.94	70.14 ± 10.54	195.24 ± 15.42	154 ± 10.52	101.11 + 6.57
*	242.18 to 319.81	157.49 to 196.51	329.70 to 452.29	247.58 to 360.41	47.61 to 92.38	162.91–227.09	132.05 to 175.94	87.38 to 114.61
G (h)	248.36 ± 2.47	160.37 ± 3.07	266.57 ± 2.08	176.28 ± 1.62	113.79 ± 1.65	104.09 ± 4.11	86.68 ± 3.13	80.62 ± 4.40
Bootstrap *G*	249.83 ± 2.36	160.34 ± 2.93	266.36 ± 1.99	174.94 ± 1.58	113.91 ± 4.62	103.57 ± 3.72	86.50 ± 2.89	81.12 ± 3.95
*	142.3 to 354.42	76.35 to 244.38	162.67 to 370.46	109.76 to 242.79	16.39 to 211.19	− 15.02 to 223.20	13.76 to 159.60	2.62 to 158.62
Ro (h^{-1})	2.75 ± 0.02	11.33 ± 0.20	3.50 ± 0.02	7.12 ± 0.08	1.16 ± 0.05	3.58 ± 0.13	6.33 ± 0.24	14.35 ± 0.48
Bootstrap Ro	2.75 ± 0.02	11.26 ± 0.20	3.50 ± 0.02	7.12 ± 0.08	1.17 ± 0.05	3.58 ± 0.12	6.33 ± 0.22	14.41 ± 0.74
*	1.51 to 3.90	5.64 to 7.02	1.98 to 5.01	3.75 to 10.49	0.10 to 2.22	− 0.47 to 7.63	0.69 to 11.97	− 0.063 to 29.38
r (h^{-1})	0.09 ± 0.01	0.25 ± 0.01	− 0.008 ± 0.009	0.11 ± 0.02	− 0.18 ± 0.06	0.15 ± 0.02	0.53 ± 0.02	0.65 ± 0.01
Bootstrap *r*	0.09 ± 0.01	0.25 ± 0.01	− 0.009 ± 0.007	0.12 ± 0.02	− 0.18 ± 0.05	0.15 ± 0.02	0.53 ± 0.01	0.65 ± 0.01
*	0.05 to 0.12	0.22 to 0.28	− 0.03 to 0.01	0.29 to 0.90	− 0.34 to (− 0.03)	0.08 to 0.21	0.48 to 0.58	0.62 to 0.68
Eggs/individual	3.17 ± 0.62	11.67 ± 3.59	3.88 ± 0.72	7.50 ± 1.77	0.79 ± 2.02	3.66 ± 2.58	6.58 ± 3.58	7.16 ± 4.74
Fecundity	11.26 ± 0.15	20.86 ± 0.32	5.17 ± 0.03	10.45 ± 0.09	6.2 ± 0.62	4.08 ± 0.15	7.23 ± 0.26	23.54 ± 1.14

Abbreviations correspond to: mean lifespan (*D*), mean generation time (*G*), intrinsic growth rate (*r*) for this determination $n = 5$, and net reproductive rate (Ro). Values are mean + one standard error. $N = 24$. Bootstrap was set at 10 000 re-samples.
*Variation coefficient for each bootstrap value.

where: x = time (h), nx = number of animals surviving at each age interval, fx = number of neonates produced at each age interval.

$$\text{Intrinsic growth rate } (r) = \ln \frac{[N(\text{t2}) - N(\text{t1})]}{(\text{t2} - \text{t1})}$$

where: ln = natural logarithm, N = number of individuals, t1 = time 1 (d^{-1}), t2 = time 2 (d^{-1}).

All of the statistical analyses were done using Statistica 7.0 software. To estimate the variability of life table statistics, 10 000 bootstrap repetitions were used (XLSTAT 5.03 software). These repetitions represent a good measure of the variability found in the actual replicates ($N = 24$). Analysis of variance (ANOVA) and Scheffe *post hoc* tests were used to compare mean values ($P < 0.05$). A Mann–Whitney *U* test with Bonferroni's correction was applied to the data, because our data were not normally distributed (see online Supplementary data).

Results

Several tests for homoscedasticity showed that, in some cases, our survivorship data did not comply with the assumptions of a normal distribution (Levene's tests for homogeneity of variances, $P < 0.001$). Therefore, a complete analysis comparing results of parametric and non-parametric tests is included in the online Supplementary material. In most cases, Scheffe test results were similar to those from Mann–Whitney *U* tests with Bonferroni correction (see online Supplementary data). There are differences in the life table parameters regarding the influence of temperature on *Lecane*. All three species have longer lifespans at 20 °C than at 25 or 30 °C (Table 1). Of the three species, *L. cornuta* had the longest lifespan (137% of that of *L. bulla*, and 198% of that of *L. papuana* at 20 °C), followed by *L. bulla* and *L. papuana* (ANOVA, $P < 0.05$; Scheffe tests). The influence of temperature on lifespan is also reflected in the life expectancy plots (Fig. 1). At 20 and 25 °C, life expectancy (ex) was greatest for *L. cornuta*, followed by *L. bulla* and *L. papuana*. Life expectancy decreased with increasing temperature and *L. bulla* failed to grow at all at 30 °C. The net reproductive rates of *L. cornuta* and *L. papuana* at 20 °C were not significantly different, but each is significantly higher than that of *L. bulla* (ANOVA, $P < 0.05$; Scheffe tests). At 25 °C, *L. bulla* had the greatest net reproductive rate followed by *L. cornuta* and *L. papuana* (ANOVA, $P < 0.05$; Scheffe tests). The net reproductive and intrinsic growth rates, and eggs per individual for all three species were greater at 25 °C than at 20 °C, suggesting that 25 °C is a more suitable temperature for growth for the three species tested than 20 °C. However, the greatest net reproductive and intrinsic growth rates and eggs per individual were those of *L. papuana* at 30 °C (Table 1). The bootstrap values are quite similar to the actual values obtained for the life table parameters (Table 1). The reproductive value (Vx) in *L. papuana* shows a strong early

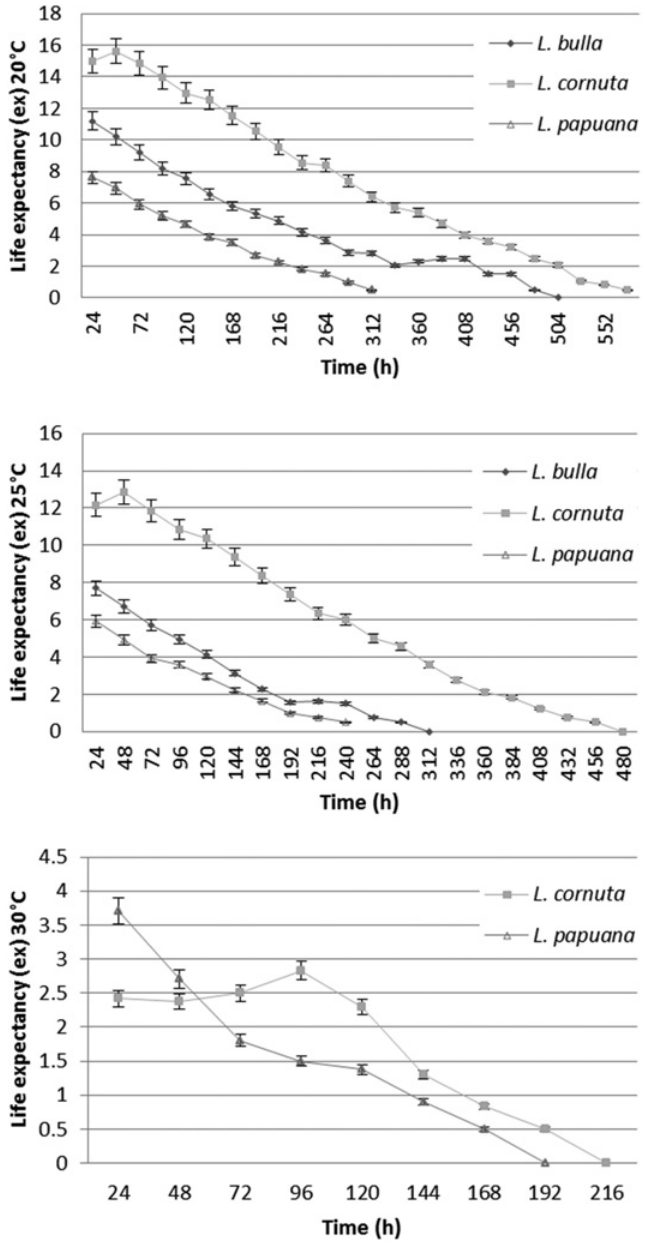

Fig. 1. Life expectancy (ex) of *Lecane bulla*, *Lecane cornuta* and *Lecane papuana* at 20, 25 and 30 °C. Values are represented as mean ± one standard error. $N = 24$.

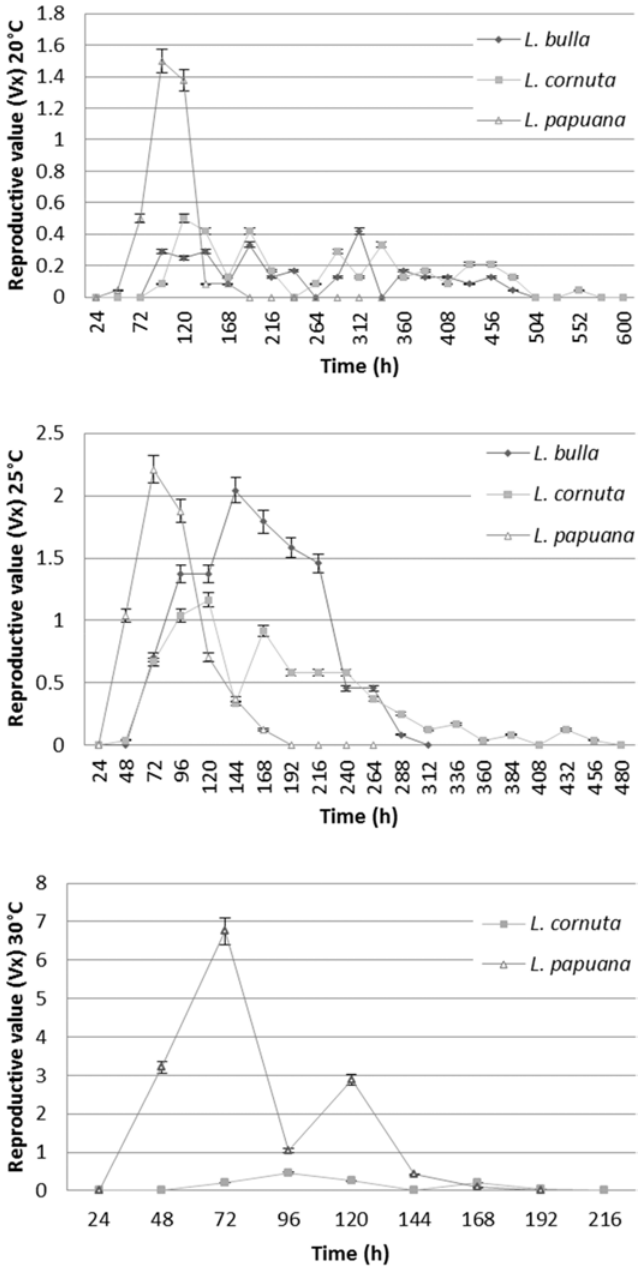

Fig. 2. Reproductive value (Vx) of *Lecane bulla*, *Lecane cornuta* and *Lecane papuana* at 20, 25 and 30 °C. Values are represented by the mean ± one standard error. $N = 24$.

investment in reproduction for this species, as a consequence of its shorter life cycle at 20, 25 and 30 °C (Fig. 2). In *L. bulla* grown at 25 °C, a strong investment in reproduction is evident between 72 and 240 h before decreasing (Fig. 2). On the other hand, *L. cornuta* appears to make a regular investment in reproduction throughout its life (Fig. 2). Survivorship, as expected, is strongly related to life expectancy (ex) and mean lifespan (*D*) (see Table 1). Survivorship is shorter with increasing temperature for all three species, and *L. papuana* has the shortest survivorship in the 20–25 °C interval (Table 1). However, while *L. papuana* excels at 30 °C, the other two species have poor performance at this temperature.

Hatching percentages of parthenogenetic eggs are shown in Table 2. Eggs of *L. papuana* hatched quickly and with higher hatching success at all temperatures. All eggs of *L. cornuta* hatched at 20 and 25 °C after 48 h, but only 60% of eggs hatched after 72 h at 30 °C. *L. bulla* eggs failed to hatch with 100% efficiency after 72 h at 20 and 25 °C and did not hatch at all at 30 °C.

Discussion

These results support the hypothesis that *L. papuana* is a thermal specialist and *L. bulla* and *L. cornuta* behave as

Table 2. Cumulative parthenogenetic egg hatching percentages after 72 h.

Temperature		20 °C			25 °C			30 °C	
Species/time	24 h	48 h	72 h	24 h	48 h	72 h	24 h	48 h	72 h
*Lecane bulla**	57%	89%	95%	78%	91%	91%	–	–	–
Lecane cornuta	78%	100%	100%	92%	100%	100%	56%	60%	60%
Lecane papuana	98%	98%	98%	100%	100%	100%	100%	100%	100%

**L. bulla* was unable to grow at 30 °C; eggs of this species produced at 25 °C are unable to hatch at 30 °C.

thermal generalists. *L. papuana* had the lowest life expectancy and reproductive value at 20 and 25 °C and the best performance for these two parameters at 30 °C. In contrast, *L. cornuta* and *L. bulla* grew well at the lower temperatures, but *L. cornuta* grew poorly and *L. bulla* did not grow at all at 30 °C. These results agree with the thermal specialist hypothesis (Huey and Slatkin, 1976; Huey and Hertz, 1984), which states that an individual performing well at its optimal temperature range might perform poorly at non-optimal temperatures. Our results partially agree with those of Pérez-Legaspi and Rico-Martínez (1998), who found that the optimal temperature for *L. luna* and *L. quadridentata* was 25 °C. Although the Ro values for these two species of *Lecane* at this temperature are 10-fold and 20-fold higher than the Ro values found in our work, our Ro values are ten times higher than those of *L. furcata*. This difference might be due to the fact that: (1) *L. furcata* behaves as a *K*-strategist (Hernández-Rodríguez *et al.*, 2000), and the species in this work behave as *r*-strategists. (2) These studies were performed on different rotifer species with different food qualities. The highest reproductive value (Vx) for *L. luna* and for *L. quadridentata* at the same temperature and food concentration was found at 48 and 60 h, respectively. Hummon and Bevelhymer (1980) also obtained high values of Vx for *L. tenuiseta* at 48 h. However, their experiments were run at 20 °C with a different type of food and a different concentration. In our work, *L. bulla* showed the highest Vx values after 72 h at 25 °C. The *r* values in our work are from 7-fold to four orders of magnitude higher than those reported by Serrania-Soto *et al.* (2011) for the same species (*L. cornuta* and *L. papuana*). This remarkable difference might be explained by either: (a) better acclimation of our strains to culture conditions than those of Serrania-Soto and co-workers, (b) differences in the protocols being used to calculate r values and (c) different algal species used as food.

Development of ecotoxicological tests using different indigenous species of rotifers could provide a valuable tool for assessing the toxicity of materials dissolved in freshwater ecosystems worldwide. A first step in the development of ecotoxicological tests is the study and analysis of life table characteristics of the species that could potentially be used for this purpose. Among rotifers, the *Lecane* genus, with 163 species (Segers, 1995), is the most numerous. In this study, we analyzed the life table parameters of three species of *Lecane* to determine their potential as model organisms for traditional toxicity or ecotoxicology tests. Our results suggest that all of the three species tested have high potential for both traditional toxicology and ecotoxicology tests. In particular, *L. papuana* appears to be an excellent candidate for studies of tropical or subtropical ecotoxicology because it has optimal development at high temperatures (30 °C), which is a characteristic that makes this species very attractive for studies in tropical countries. In terms of ease of obtaining parthenogenetic eggs, the high percentage of hatching after 24–72 h (91–100%, see Table 2) of the three species tested would ensure an abundant supply of neonates for traditional toxicity tests. In addition, the short period over which several life table parameters (*G*, Ro, *r*, Vx, ex, lx) can be obtained, and the differences in reproductive effort or survivorship, among other parameters elucidated in all three species, suggest that these species might be potential candidates as ecotoxicological model organisms.

Use of *Lecane* species for toxicity testing is not new. Finesinger (1926) was the first to propose the use of *L. inermis* to biomonitor the effects of exposure to some chemicals. Pérez-Legaspi and Rico-Martínez (2001) developed acute tests for *Lecane hamata*, *L. luna* and *L. quadridentata* for 11 toxicants (five organics and six metals), arguing that the most representative toxicity tests worldwide are with planktonic species, despite the fact that deposition of contaminants in sediments is an important contribution to toxicity (Rand and Petrocelli, 1985). Since that work, *L. quadridentata* has been used in Mexico to analyze environmental samples in the San Pedro River in Aguascalientes (Rico-Martínez *et al.*, 2000; Santos-Medrano *et al.*, 2007; Torres-Guzmán *et al.*, 2010a). It has also been used in the Southern Huastec region to analyze combined effects of manganese and dichloro diphenyl trichloroethane (Mejía-Saavedra *et al.*, 2005), and in Aguascalientes, it has been used to monitor the effectiveness of drinking water systems (Rico-Martínez *et al.*, 2000) and waste water treatment plants (Torres-Guzmán *et al.*, 2010b; Robles-Vargas *et al.*, 2012). In Poland, Klimek *et al.* (2013) found that *L. inermis* is more sensitive to several trace metals (Al, Cu, Fe, Mn, Sn and Zn) than other species commonly used in toxicity tests.

In our work, we have increased knowledge of the demography of three more species of the specious *Lecane* genus. We found that life table parameters and parthenogenetic egg production and hatching made these three species potentially good candidates for developing toxicity or ecotoxicology tests. We have compared their life table parameters with values found for the same species or others in the literature, finding important differences

among them. Our results confirm that *L. papuana* behaves as a thermal specialist and that the cosmopolitan species *L. bulla* and *L. cornuta* behave as thermal generalists. Our results suggest that more rotifer species and species of other phyla of freshwater invertebrates need to be studied to understand the demographic traits and potential of such animals for environmental assessment.

Supplementary material

The supplementary material for this article can be found at http://dx.doi.org/10.1051/limn/2017009.

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