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Population dynamics of the tropical cladoceran *Ceriodaphnia rigaudi* Richard, 1894 (Crustacea: Anomopoda). Effect of food type and temperature

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Abstract

The knowledge of population effects of food on tropical, filter-feeding cladocerans is scarce because a reduced number of species has been extensively studied. *Ceriodaphnia rigaudi* Richard 1894, a small-sized cladoceran distributed mainly in tropical and subtropical regions of the world, was studied. The aim of this study was to contribute to the knowledge of the reproductive biology of a poor-known Cladoceran; for this we assessed the effect of feeding and temperature on the reproduction and life cycle of this species. Three microalga species (*Pseudokirchneriella subcapitata*, *Ankistrodesmus falcatus,* and *Chlorella vulgaris*) were supplied as food each at a concentration of 12 mg l^{-1} (dry weight, equivalent to $1.3X10^6$, $0.4X10^6$ and $1.35X10^6$ cell ml^{-1}, respectively, and equivalent to 7.80 µg C ml^{-1}), at two temperatures (20 and 25°C). We evaluated, among other responses, longevity, total progeny, survival, life expectancy at birth and fecundity. Organisms fed with the microalgae *A. falcatus* and *P. subcapitata* presented both higher longevity (30.7± 5.91, 26.6 ± 3.59 days, respectively) and total progeny (45 ± 13.80, 40.7 ± 0.66 neonates $female^{-1}$) values than those organisms fed *C. vulgaris* (13.5± 4.63 days and 17.6 ± 6.19 neonates $female^{-1}$, respectively). On the other hand, temperature affected significantly the population parameters of *C. rigaudi,* recording maximal longevity values (56.1 ± 9.41 days) at 20°C in organisms fed *A. falcatus*; however, age at first reproduction and total progeny were negatively affected by this temperature: sexual maturation of the females was delayed until the age of 16 days and the number of neonates produced was smaller (9.8 ± 3.45 with *C. vulgaris*; 24.7±6.01 with *P. subcapitata,* and 35.5 ± 8.59 neonates $female^{-1}$ with *A. falcatus*). The best reproductive responses for *C. rigaudi* in this study were obtained with *A. falcatus* at 25°C.

Key words

Microalgae, Life table, zooplankton culture, *Pseudokirchneriella subcapitata*, *Ankistrodesmus falcatus*, *Chlorella vulgaris*

Introduction

Cladocerans represent one of the most important zooplankton groups in freshwater ecosystems; they are one of the main primary consumers and influence energy transfer from primary producers to higher trophic levels. Also, they affect the population growth of bacteria, heterotrophic protozoans, microalgae, and even some rotifer species, though tropic relationships and competition (Arnold, 1971; Pace and Vaqué, 1994).

Some cladoceran species have been used extensively in ecotoxicology and experimental hydrobiology, because of their advantages, such as easy handling and culture under laboratory and field conditions. Important is also their short life cycle, which fluctuates, depending on temperature and food supply, between 8 and 12 days for *Moina macrocopa* Goulden, 1968 (Nandini and Sarma, 2000) to more than 60 days for *Daphnia magna* Straus (Martínez-Jerónimo *et al*., 1994). These organisms reproduce asexually under favorable environmental conditions and the embryos produced undergo direct development without larval stages, giving rise to juveniles that are morphologically and genetically identical to the mother (Pennak, 1989).

Despite the wide use of some of some preferred cladocerans, it is important to count upon other options for different environmental conditions, as those distributed in water bodies located in tropical and subtropical latitudes. Currently, most of the studies on the biology and ecology of cladocerans correspond to organisms from temperate regions; consequently, relevant and sufficient information exists for many of these species as compared to lesser known species from tropical environments (Sarma *et al*., 2005; Bunioto and Arcifa, 2007).

Reproductive biology has been studied in some cladoceran species (Nandini and Sarma, 2000, Nandini and Sarma 2002, Nandini and Sarma 2003, Sarma *et al*., 2002; Sarma *et al*., 2005). The use of life tables is one of the best suited tools to generate this information, as this tool allows determining the structural characteristics of a population, as well as its age-specific mortality and fecundity rates. This information is indispensable to understand not only the temporal changes in population characteristics but also to make inferences on the use and management of populations (Krebs, 1985).

Ceriodaphnia rigaudi Richard, 1894, is one of the cladocerans for which scarce autoecological information is available. This planktonic species is distributed mainly in tropical and subtropical regions, in large water bodies, as well as in temporal ponds (Alonso, 1996). An important feature of *C. rigaudi* is its wide tolerance interval to temperature, for it can thrive between 17 and 35^{o}C, besides having a large colonization capacity and being able to give rise to very numerous populations (Alonso, 1996).

Most works on *C. rigaudi* have been restricted to morphological descriptions and other taxonomic aspects (Carruyo *et al.* 2004); therefore, it is important to determine the main population and life history characteristics of this species aimed at providing new information on its reproductive biology. Based on this knowledge, controlled and massive propagation methods might be developed to allow for their possible use as test organisms in aquatic toxicology tests, as well as live-feed source in aquaculture, or as biological material for experimental hydrobiology studies. For this purpose, an important factor to consider is feeding, as it will determine to a large extent the growth and reproduction of the organisms.

The effect of feed on the development of cladocerans has been the objective of many experimental studies, although most have focused on determining the effect of the biochemical composition of feed, particularly to the amount of polyunsaturated fatty acids content, as well as nitrogen and phosphorus contents (Gulati and DeMott, 1997; Sterner and Schulz, 1998). The influence of essential fatty acids on theses organisms' growth has been determined (DeMott and Müller-Navarra 1997; Müller-Navarra *et al*., 2000; Wacker and von Elert, 2001). Recently, other aspects related with filtered microalgae as feed for cladocerans have also been investigated, which could become limiting factors hindering or delaying growth of consumers, such as shape and size of microalgae, as well as the ease of organisms to consume and digest them (Van Donk *et al*., 1997; DeMott and Tessier, 2002; Fileto *et al*., 2004).

Considering that both, food and temperature are two fundamental factors influencing determinately the development of organisms, we evaluated the effect of the diet, consisting of morphologically different microalgae, on *C. rigaudi* organisms reared at two temperatures. We recorded the reproductive and life cycle responses to define adequate conditions for the development and propagation of this cladoceran; in this sense this study is a contribution to the biological knowledge of this cladoceran. This species was selected because it is distributed worldwide and can be easily available in tropical and subtropical latitudes; potentially, it could substitute in ecotoxicological studies to *C. dubia*, a cladoceran difficult to identify taxonomically, because it constitutes a species complex (Elías-Gutiérrez *et al*., 2008), that can hybridize with other *Ceriodaphnia* species (Berner, 1986).

Materials and Methods

We used a *Ceriodaphnia rigaudi* strain from the cladocerans collection of the Experimental Hydrobiology Laboratory, National School of Biological Sciences, IPN, which was isolated from the "Pantanos de Centla" Biosphere Reserve, in the state of Tabasco, Mexico.

The green microalgae *Pseudokirchneriella subcapitata*, *Ankistrodesmus falcatus,* and *Chlorella vulgaris* were chosen as feed; they were obtained from the microalgae collection of the Laboratory of Experimental Hydrobiology, National School of Biological Sciences, IPN. Food was selected based on the difference in shape and size: *P. subcapitata* has a half-moon shape and an average size of 10 µm; *A. falcatus* is fusiform with an average length of 40 µm; and *C. vulgaris* has a spherical shape, with an average diameter of 5.5 µm; all of them are popular food items used for the growth and maintenance of Cladocerans and other filter-feeding plankton species in our laboratory and elsewhere.

Microalgae were cultivated in autoclaved Bold's basal medium (Stein, 1973), and maintained under continuous light and aeration. The algal biomass was separated from the culture medium and kept under refrigeration for a maximal time of one week, to be able to provide only fresh feed for the experiments (Martínez-Jerónimo *et al*., 1994). The concentration supplied of each microalgae was 12.0 mg l^{-1} (dry weight, or 7.80 µg C ml^{-1}), which is equivalent to 1.3 x 10^{6}, 0.4 x 10^{6}, and 1.35 x 10^{6} cell ml^{-1} of *P. subcapitata*, *A. falcatus*, and *C. vulgaris*, respectively, considering their differences in size and shape; food concentration was selected as an adequate value, based in previous feeding experiences with several cladocerans species in our laboratory.

The maximal length and width in adults and neonates (recently hatched juveniles, with an age of less than 24 hr) was assessed in this small-sized cladoceran.

C. rigaudi was maintained under the experimental conditions for more than 3 months to attain its adaptation to the three microalga types and the assayed temperatures (20 and 25^{o}C); temperature values were chose as roughly representative of subtropical and tropical conditions. After this period, a reproductive batch was established for each experimental condition, from which neonates were randomly chosen for the experiments.

We performed two experimental series. In the first, we evaluated the reproductive responses in organisms individually exposed to the aforementioned treatments. In the second experiment, we used cohorts and performed a life table analysis.

For the first series of experiments, we used 50 ml glass flasks with 30-ml test volume of reconstituted hard water, prepared according the U.S. EPA (2002) formulation, with 10 replicates for each treatment. One *C. rigaudi* neonate was placed in each flask. The medium and the food were renewed every other day. All replicates were monitored daily until the death of the last adult female in all treatments. Once reproduction began, the progeny was separated and counted; in addition, we registered the longevity of adult females. With this information, the average clutch size, the total progeny, the age at first reproduction, and the inter-clutch time were calculated.

For the life table study, we used cohorts of 10 *C. rigaudi* neonates for each of the aforementioned treatments. In this case, we used 100-ml flasks with an 80 ml test volume. Ten neonates were placed in each flask and five replicates were made for each treatment. All replicates were monitored daily; we quantified the number of surviving adults from the initial cohort and separated and counted the whole progeny. The culture medium and food were renewed every other day. This experiment was followed until all individuals from the initial cohort had died.

For data analysis, we used the standardized demographic life table methods reported by Krebs (1985) and Pianka (1988), determining the survival (l_x), the life expectancy at birth (E_x), the net reproductive rate (R_o), the generational time (T), and the intrinsic rate of population growth (r).

Results were analyzed with a two-way ANOVA, and the Tukey's test was used for *post hoc* comparisons (Sokal and Rohlf, 1981).

Results and Discussion

Ceriodaphnia rigaudi is a small-sized cladoceran. Adults had an average length of 456 µm (± 13 µm) and an average width of 309 µm (± 25 µm), whereas neonates were 271 µm (± 0.6 µm) long and 160 µm (± 0.5 µm) wide.

The following results are for the reproductive responses and longevity assessed individually in *C. rigaudi*.

The highest values of average longevity were recorded with *A. falcatus* at both temperatures, whereas the smallest values were for organisms fed *C. vulgaris*. (Fig. 1a). Regarding temperature, in general, those organisms reared at 20°C lived longer than those reared at 25°C, with recordings of 43 to 69 days at 20°C, and of 17 to 44 days at 25°C. Two-way ANOVA revealed a significant effect of both temperature and type of food on *C. rigaudi*'s longevity (P<0.001 for both factors). Tukey's test revealed that treatments with *C. vulgaris* at both temperatures presented significantly lower longevity values than treatments with *A. falcatus* (P<0.001) and *P. subcapitata* (P<0.001).

The highest values of total progeny were obtained in organisms fed *A. falcatus,* at both temperatures, whereas those fed *C. vulgaris* produced less neonates (Fig. 1b). Total progeny was higher at 25°C. Two-Way ANOVA revealed that both, temperature and type of food, influenced significantly the total progeny (P=0.004 and P<0.001, respectively). Tukey's test revealed that the organisms fed *C. vulgaris* produced a total progeny that was significantly lower than that obtained with *P. subcapitata* (P<0.001) and *A. falcatus* (P<0.001).

The average number of offspring per clutch is shown in Fig. 1c. At both temperatures, the largest clutch was obtained from those organisms fed *P. subcapitata*, whereas the lowest values were recorded in those fed *A. falcatus*. Two-Way ANOVA demonstrated that temperature had a significant effect (P<0.001) on this reproductive variable, whereas food was not significant (P= 0.5640). Tukey's test revealed that treatments at 25°C yielded clutches that were significantly more numerous than treatments at 20°C (P<0.001).

The smallest number of clutches was obtained with *C. vulgaris*, whereas the highest values were obtained with *A. falcatus* (Fig. 1d). Two-Way ANOVA revealed that temperature (P=0.001) and type of food (P<0.001) affected significantly the reproductive frequency of C. *rigaudi*.

Age to first reproduction ranged from 4 to 7 days at 25°C, whereas those organisms reared at 20°C reached the first reproduction after the 10th day (Fig. 1e). According to Two-Way ANOVA, only temperature affected significantly the age of first reproduction (P<0.001). Tukey's test revealed that organisms reared at 25°C reached sexual maturity significantly faster than those reared at 20°C (P<0.001).

On the other hand, life table analysis revealed that the survivorship curves (Fig. 2) presented different tendencies. For treatments at 20°C fed with *A. falcatus*, survival began to decline gradually starting on day 10 until the death of all organisms on day 63. With *P. subcapitata*, survival started to decline from day 8 on, following this tendency until day 59. With C. *vulgaris*, mortality was recorded from day 8 on, and the maximal longevity of the cohort was 53 days. At 25°C, survival started to decline earlier. With *A. falcatus*, mortality started at day 6 and followed gradually until day 51. With *P. subcapitata*, mortality started on day 4 and continued until day 43, when the last organism died. With *C. vulgaris*, mortality started at day 5 and followed gradually until day 35.

Fecundity (m_x) reached the highest values at 25°C (Fig. 3). With *A. falcatus* at 20°C, a fecundity peak was obtained on day 26, and reproduction ceased on day 32. For females fed *P. subcapitata*, a maximal value of 2.91 neonates female $^{-1}$ was obtained on day

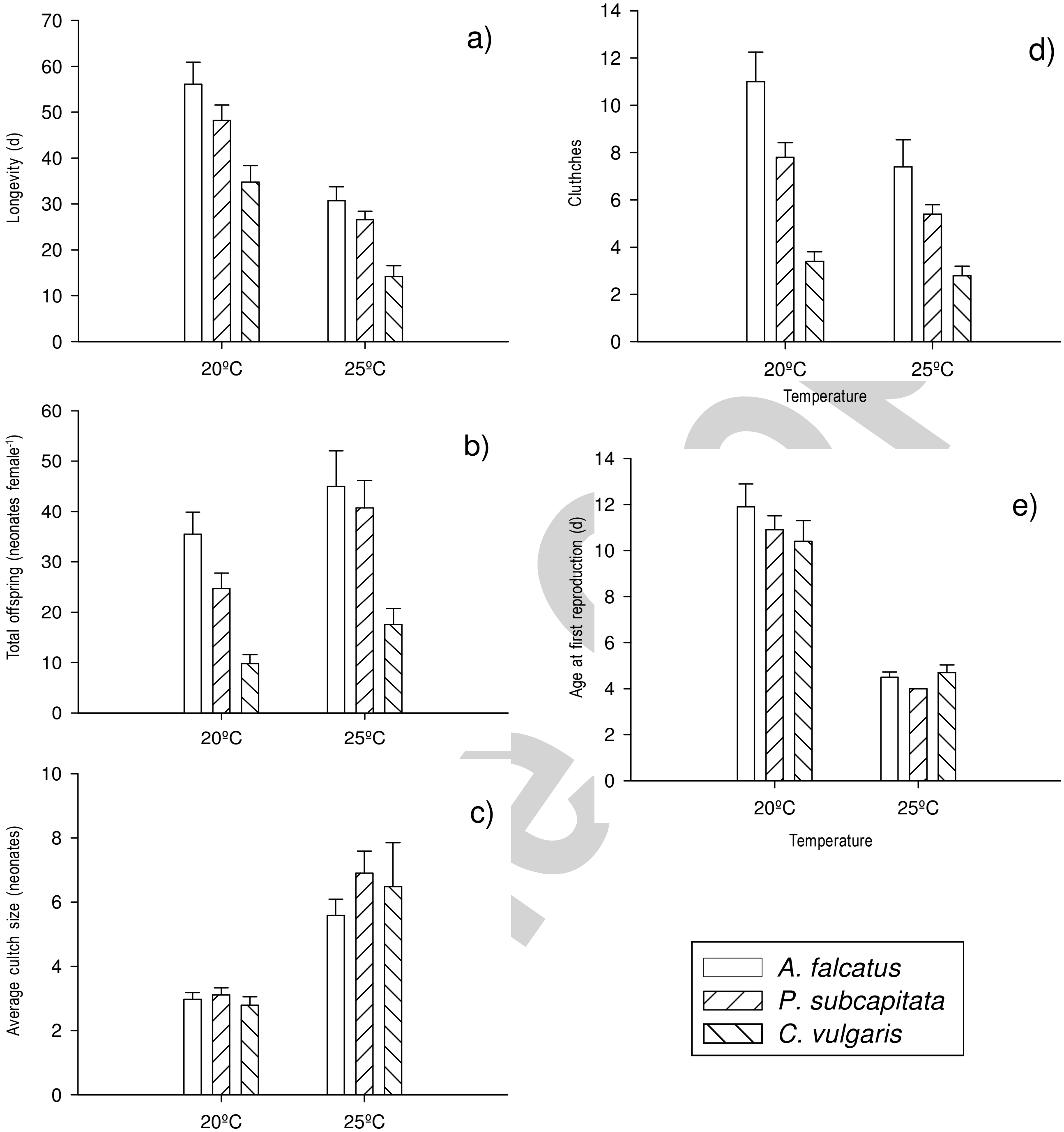

Fig. 1: Longevity and reproductive responses (assessed individually) of *Ceriodaphnia rigaudi* with three types of feed (*Pseudokirchneriella subcapitata, Ankistrodesmus falcatus,* and *Chlorella vulgaris*) and two temperatures (20 and 25°C)

22, decreasing with time until day 56. With *C. vulgaris*, day 23 presented a maximal value of 1.42 neonates female^{-1} until day 40, when reproduction ceased. At 25°C, the highest fecundity values were recorded on days 26 (4.05 neonates female^{-1}), 11 (3.45 neonates female^{-1}) and 9 (3.32 neonates female^{-1}) for *A. falcatus*, *P. subcapitata*, and *C. vulgaris*, respectively, whereas reproduction ceased on day 39 with *A. falcatus*, day 32 with *P. subcapitata,* and day 23 with *C. vulgaris*.

The highest longevity values were recorded at 20°C (Fig. 4a), and those organisms fed *P. subcapitata* long-lived the most (44.74±3.64 days), whereas those fed *C. vulgaris* had a shorter life-span (29.45± 3.38 days). Two-Way ANOVA revealed a significant influence of both, the type of food (P = 0.005) and temperature (P<0.001), on *C. rigaudi*'s longevity, but the interaction between both factors was also significant (P = 0.007), hence, no *post hoc* comparisons could be made.

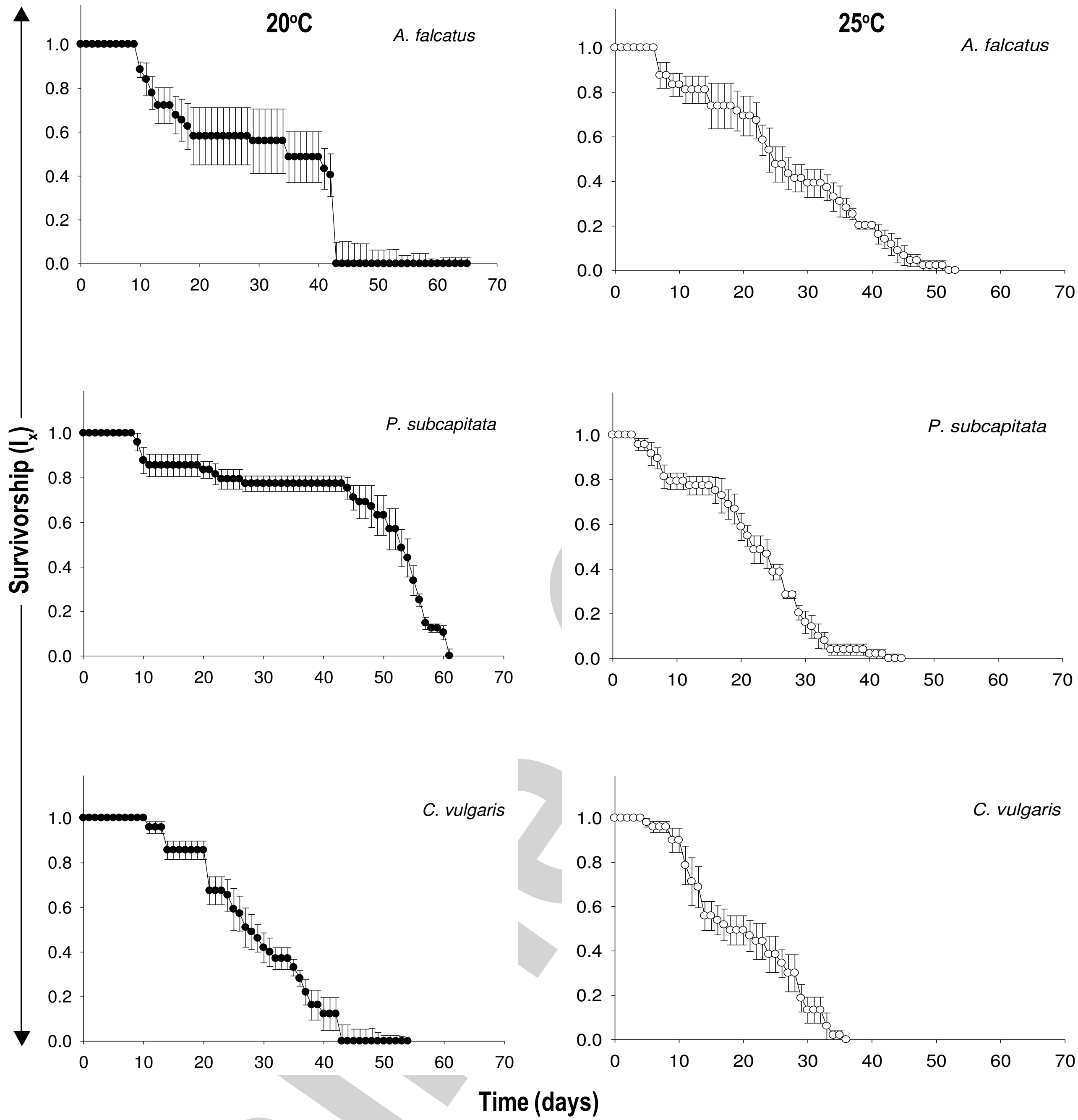

Fig. 2: Survival of *C. rigaudi* fed *Pseudokirchneriella subcapitata*, *Ankistrodesmus falcatus*, and Chlorella *vulgaris*, at two temperatures (20 and 25°C) from a Life Table analysis

At 25°C, the value of net reproductive rate (R_o) was greater in *C. rigaudi* fed *A. falcatus* (42.67± 2.36 neonates female^{-1}), whereas, at 20°C, organisms fed *P. subcapitata* presented the highest R_o (25.54± 4.57 neonates female^{-1}) (Fig. 4b). Two-Way ANOVA indicated that temperature, type of food, and their interaction were significant (P<0.001), hence no *post hoc* comparisons were made.

The generational time (T) at 20°C was larger than that determined at 25°C (Fig. 4c). At 20°C, organisms fed *P. subcapitata* had the highest T value (28.50 ± 1.69 days), whereas at 25°C those fed *A. falcatus* had the lowest T value (17.17 ± 1.15 days). Two-Way ANOVA indicated that the type of food, temperature, and their interaction were significant (*P*<0.001).

The highest intrinsic rate of population increase (*r*) was recorded at 25°C. According to the Two-Way ANOVA, temperature exerted a significant effect on *r* (*P*<0.001), whereas the type of food was not significant (*P*=0.055). Tukey's test revealed that *r* values obtained at 25°C were significantly higher than those obtained at 20°C (*P*<0.001) (Fig. 4d).

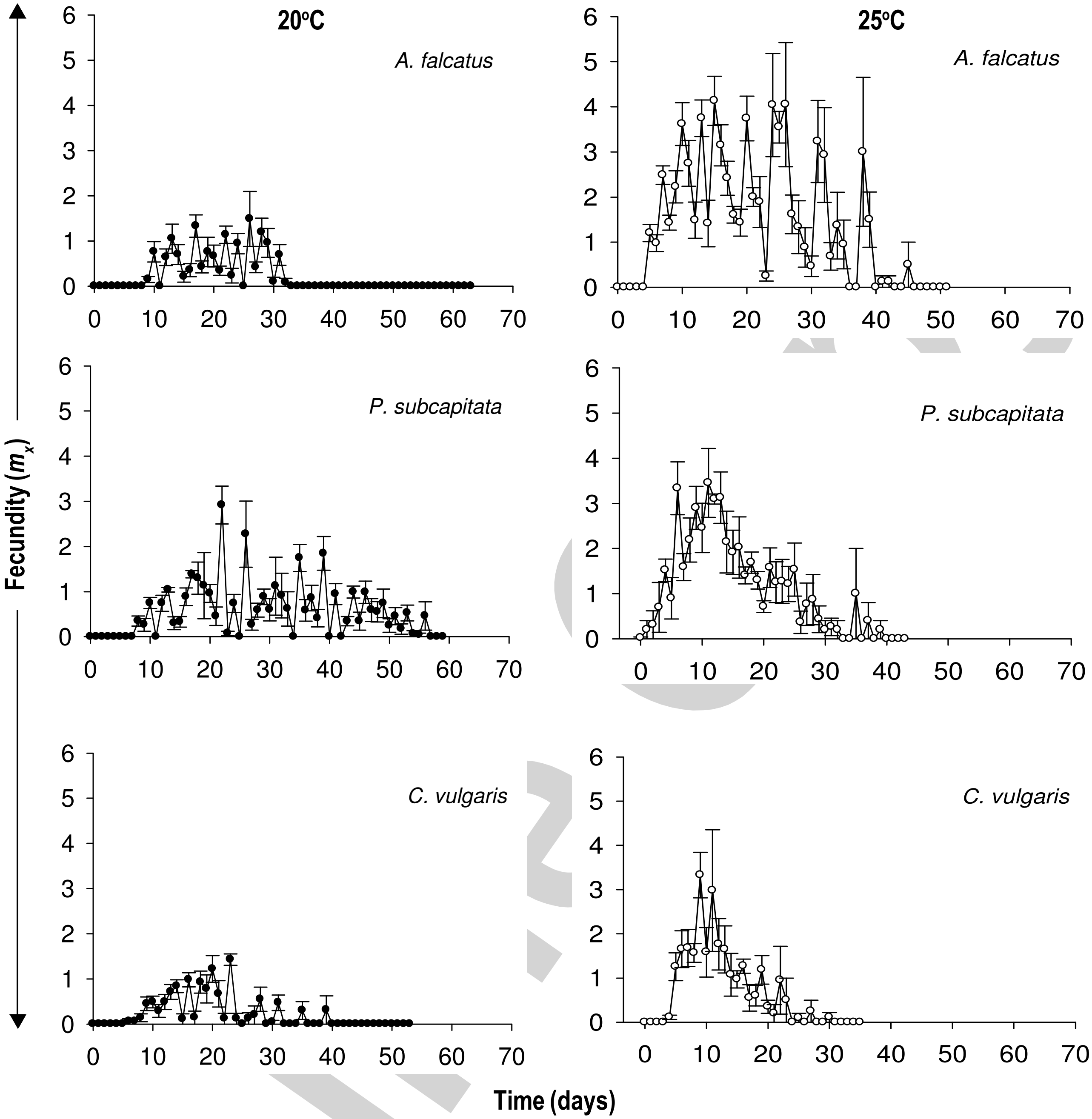

Fig. 3: Fecundity of *C. rigaudi* fed *Pseudokirchneriella subcapitata*, *Ankistrodesmus falcatus*, and *Chlorella vulgaris*, at two temperatures (20 and 25° C) from a Life Table analysis

The reproduction and the life cycle of *Ceriodaphnia rigaudi* were affected by the temperature and the supplied type of food. Organisms that consumed the microalgae *A. falcatus* and *P. subcapitata* had a higher longevity, larger number of clutches, and a greater total progeny than those recorded in *C. vulgaris*-fed organisms. This indicates that *C. rigaudi*, despite being a small-size cladoceran, can ingest food items of different size and shape (in this study, in the range from 5.5 to 40 µm). Although *A. falcatus* was the largest size microalga (40 µm of average length), and its length is barely less than a tenth of the size of *C. rigaudi* adults, it produced, together with *P. subcapitata*, the best reproductive responses and the highest longevity. This result contrasts with that of Fileto *et al*. (2007), who observed that *Ceriodaphnia cornuta* depict a higher reproduction and population growth when fed with particles smaller than 20 µm. It is worthwhile mentioning that *C. rigaudi* is similar in size to *C. cornuta* and smaller than the other two species; therefore, it might be possible that some other factors, such as nutritional quality, digestibility or

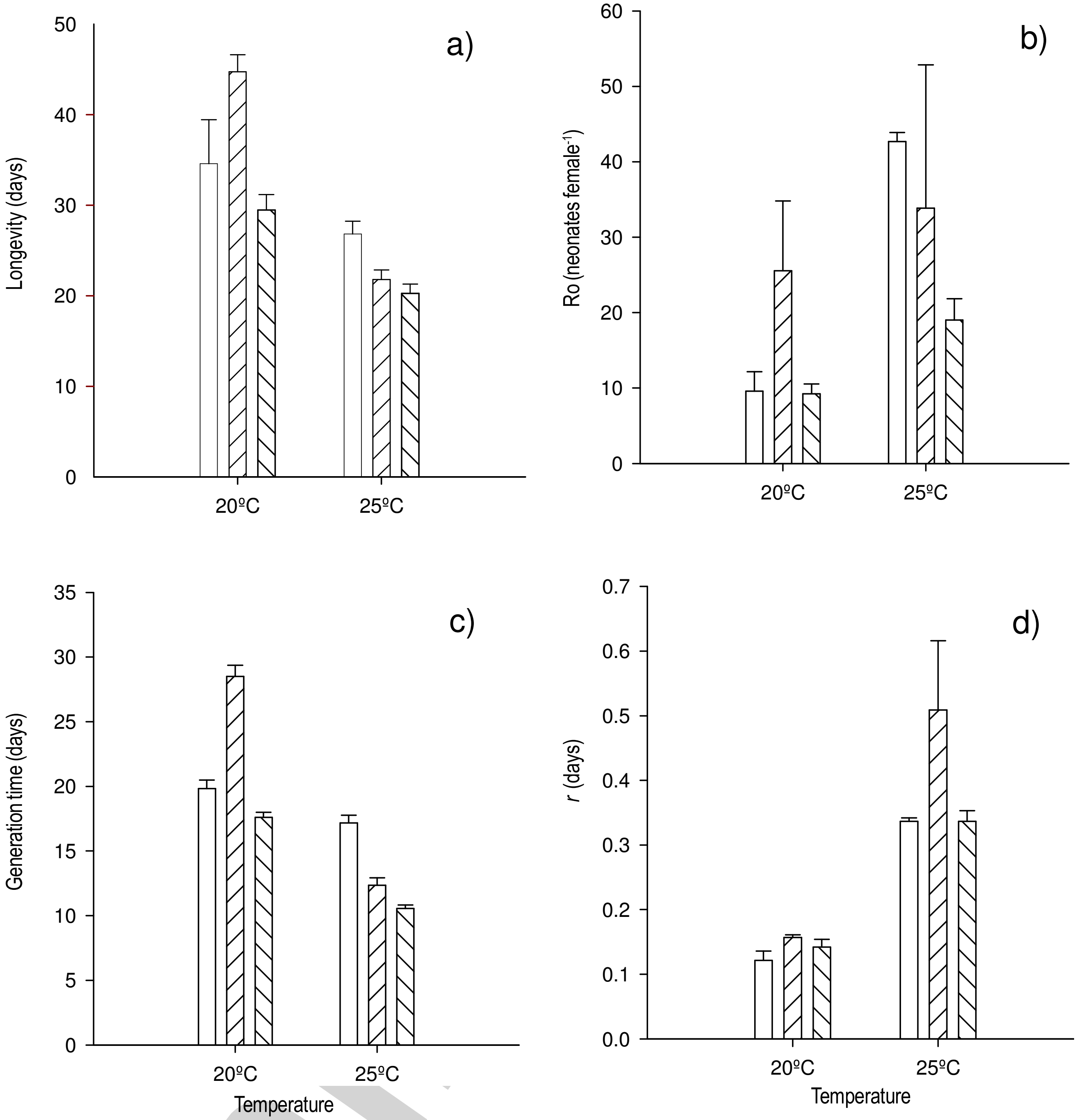

Fig. 4: Life history parameters of C. *rigaudi* with three types of food (*Pseudokirchneriella subcapitata, Ankistrodesmus falcatus* and *Chlorella vulgaris*) at two temperatures (20 and 25°C). Obtained from a Life Table analysis

edibility could influenced our results, but we do not have the elements to explain these differences.

The differences in the effects of the three types of food could be explained in terms of their nutritional content, since the amount of fatty acids, proteins, nitrogen, and phosphorus contained in microalgae affect the growth of cladoceran populations (Wacker and von Elert, 2001*);* nevertheless, the culture medium and growth conditions were exactly the same for the three microalgae in this study.

The reproductive biology of *C. rigaudi* was affected by temperature; organisms lived longer at 20°C, but the total progeny, obtained from numerous clutches with few neonates, was low. At 25 °C, longevity was shorter and although the number of clutches was comparatively low, the number of neonates in each clutch was higher, hence, the total progeny was larger. These results could be related with the physiological effects of temperature, within the tolerance limit of this species, a higher temperature promotes a greater swimming activity and a larger rate of food ingestion, which is also related with higher metabolic rates and a faster maturation of eggs (Watts and Young, 1980; Hardy and Duncan, 1994; Amarasinghe *et al.*, 1997; Loiterton *et al*., 2004). Accordingly, the processes of sexual maturation and reproduction are delayed at lower temperatures as observed in the organisms reared at 20°C, in which the age of first reproduction was higher. Villalobos and Gonzalez (2006) reported for *C. cornuta*, a very similar species, that the greatest fecundity in this species occurs at low temperatures, but they did not explain the cause of this response.

The life table analysis revealed that *C. rigaudi* depicts a relatively constant mortality rate along its life cycle. The highest fecundity in the organisms reared at 25°C was recorded mainly during the first third of the life cycle, with a high Net Reproductive Rate (Ro). Longevity was low as compared to organisms reared at 20°C, resulting in short generational times with a high rate of population increase. In organisms reared at 20°C, fecundity was lower and was recorded during most part of the life cycle, resulting in a low net reproductive rate; average longevity was high resulting in a larger generational time and, hence, in a low rate of population growth. These results confirm the inverse relationship existing between the reproductive parameters and temperature (Bunioto and Arcifa, 2007), since the time of embryonic development and the number of clutches are higher when temperature decreases.

It is difficult to compare the results of the present study with others on *C. rigaudi*, because the published information on this species is scarce. Therefore, the following comparisons correspond to other cladoceran species. *C. rigaudi*'s longevity was 30.7±5.91 days with *A. falcatus*, a value lower than that reported for *Ceriodaphnia dubia* (Cowgill *et al*., 1985) of 125 days at 20°C; however, the differences could be due to the characteristics of each taxon. In small size cladocerans, as for example *Ceriodaphnia* cf. *dubia,* Rose *et al*. (2000) recorded a 17-day longevity using *P. subcapitata* and *A. falcatus* as food at a concentration of 1.5 x 10^5 cell ml^{-1}, whereas Fonseca and Rocha (2004) report a longevity of 29.8 ± 5.89 days for *Ceriodaphnia silvestrii*. In all these small- sized cladocerans, the longevity was lower than that observed for *C. rigaudi* in the present study.

The highest net reproductive rate obtained in this study was 42.67± 2.36 neonates $female^{-1}$, which is higher than that reported by Nandini and Sarma (2002) for *Ceriodaphnia dubia* (36.6 neonates $female^{-1}$), reflecting comparatively a higher reproductive potential for *C. rigaudi*. On the other hand, the maximum average fecundity per clutch for *C. rigaudi* was of 4 neonates $female^{-1}$, which is lower than the value reported by Villalobos and Gonzáles (2006) of 6 neonates $female^{-1}$ for *C. cornuta*, although they did not determine experimentally this value. Considering the size of the neonates in comparison with the size of the adults, the fecundity recorded for *C. rigaudi*, although being reduced, cannot be considered low.

The most adequate propagation conditions here determined for *C. rigaudi*, reflected in a higher reproductive response, were obtained when feeding with *A. falcatus* and cultivating at 25°C. According to the reproductive parameters obtained, such as fecundity, longevity, and survival, it can be inferred that *C. rigaudi* could be produced in massive cultures as feed for aquaculture purposes, especially for small size consumers, such as fish and crustacean larvae and juveniles. On the other side, due to its reproductive characteristics and easy management and maintenance in the laboratory, *C. rigaudi* could be also used as test organism for ecotoxicological assays.

The study of the reproductive biology by methods such as following the reproduction in an individualized manner and the life table analysis allowed us to obtain a complete panorama of the reproductive strategies of *C. rigaudi*, a widely distributed cladoceran in diverse environments, but poorly studied experimentally in regard to its reproductive aspects and life cycle. The gathered information not only serves to have now a procedure for its culture, but also contributes to a better knowledge on the biology of cladocerans.

Ceriodaphnia rigaudi presented different reproductive strategies that varied depending on factors such as type of food and temperature; but, in general, it is a species with a high reproductive capacity and despite being a small-sized cladoceran it can reach high longevity values and is reproductively favored by high temperatures.

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