Original Article

Egg production and life history of *Alona guttata* Sars, 1862 (Cladocera, Chydoridae): implications for colonization of temporary ponds

Produção de ovos e história de vida de *Alona guttata Sars*, 1862 (Cladocera, Chydoridae): implicações para a colonização de lagoas temporárias

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Abstract

Cladocerans are a diverse group of species that show rapid responses to changes in environmental conditions. This adaptive capacity has important implications for egg production and life cycle, especially in transitory environments such as temporary waterbodies. The present study investigated the life history and egg production of *Alona gutatta* Sars, 1862 (Crustacea, Cladocera), an abundant and frequent species from a high-altitude temporary pond (Lagoa Seca, Minas Gerais, Brazil). Newly hatched neonates were monitored in relation to time of maturation, number of eggs produced per female and time of survival. Neonates required a mean of 8 days to mature. *A. guttata* survived for a mean of 30.9 ± 8.1 days and produced 2 eggs per brood, generating a mean of 10.95 ± 6.41 neonates during the entire life cycle. The rapid development, short time to produce eggs and long life cycle are important adaptations to the adverse environmental conditions of temporary aquatic environments, which can contribute to the rapid colonization of *Alona guttata* in transitory ecosystems.

Keywords: high-altitude pond, hydroperiod, Alonidae, growth rates.

Resumo

Os cladóceros formam um grupo diverso de espécies que apresentam respostas rápidas às mudanças nas condições ambientais. Essa capacidade adaptativa tem implicações importantes para a produção de ovos e para o ciclo de vida, especialmente em ambientes transitórios, como corpos d'água temporários. O presente estudo investigou a história de vida e a produção de ovos da espécie *Alona guttata* Sars, 1862 (Crustacea, Cladocera) coletada em uma lagoa temporária de altitude (Minas Gerais, Brasil). Organismos recém eclodidos foram observados (em condições de laboratório) em relação ao tempo de maturação, número de ovos produzidos por fêmea e tempo de sobrevivência. Os neonatos levaram em média 8 dias para atingir o primeiro estágio de maturação. As fêmeas produziram 2 ovos por ninhada e geraram uma média de $10,95 \pm 6,41$ neonatos durante todo o ciclo de vida. *A. guttata* apresentou uma média de $30,9 \pm 8,1$ dias de sobrevivência. O rápido desenvolvimento, o pouco tempo para a produção de ovos e o ciclo de vida longo são adaptações importantes às condições ambientais adversas de ambientes aquáticos temporários, que podem contribuir para a rápida colonização de *Alona guttata* em ecossistemas transitórios.

Palavras-chave: poça temporária de altitude, hidroperíodo, Alonidae, taxas de crescimento.

1. Introduction

Temporary ponds are highly variable environments, since they remain completely dry for long periods until they fill with the arrival of the rainy season. This filling and drying regime strongly influences the population dynamics of aquatic organisms. Additionally, temporary ponds located in high-altitude areas are subject to daily fluctuations of temperature, luminosity, and radiation. These dominant environmental drivers may select species that have developed special strategies to survive and persist in harsh environmental conditions (Beccato, 2004; Pintar and Resetarits Junior, 2018; Martins et al., 2019).

Most cladocerans may be bacterivorous, herbivorous or detritivorous, feeding upon a wide spectrum of items including organic detritus, bacteria and algae (Rocha et al., 2011; Hayashi-Martins et al., 2017). In addition to their high species diversity, this high functional diversity makes cladocerans a key group shaping food webs and community structure in shallow lakes (Lampert, 1997; Simões et al., 2009). Members of the family Chydoridae are

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Received: April 29, 2020 – Accepted: October 1, 2020

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usually abundant in shallow lakes (Moreira et al., 2016). Their abundance can be associated with the close relationship with the dense presence of aquatic vegetation (Bolduc et al., 2016), since they are specialized in exploiting microenvironments provided by vegetation (Scheffer, 2004; Forró et al., 2008).

In spite of their high ecological importance, few studies have addressed the fundamental aspects of life history and egg production of these zooplankters, especially in tropical high-altitude aquatic environments. Study of the life cycles and reproduction of zooplankton species is essential for understanding the adaptive mechanisms that allow organisms to survive in these changeable habits. In the present study we examined aspects of the life history and egg production of *Alona guttata* Sars, 1862 (Chydoridae), a common and abundant species often found in small highaltitude ponds in Brazil (Santos-Wisniewski et al., 2002; Eskinazi-Sant'Anna and Pace, 2018).

2. Material and Methods

Zooplankton samples were obtained from a seasonal pond located in the State Park of Itacolomi (Minas Gerais state) at 1606 m.a.s.l. (20°25'52"S; 43°29'12"W). The pond is an oligotrophic, slightly acid seasonal aquatic water body, with mean value of pH below 6.5 and mean annual water temperature of 19 °C. (Moreira et al., 2016). Samples were obtained in January 2014 by filtration of 30 L of water in a 68 µm mesh size plankton net. The species A. guttata was identified according to (Elmoor-Loureiro, 1997; Sterza and Fernandes, 2006). In the laboratory, parthenogenetic females were sorted from the samples under stereomicroscope and reared in individual wells of 6-well tissue-culture plates (Corning®), filled with filtered water (Whatman® GFC) from the pond. The females were reared in experimental growth chambers at constant temperature (22 \pm 2 °C) and 16:8 h light/dark cycle

photoperiod. Every two days the water was partially renewed. Organisms were fed with a suspension of the chlorophycean Raphidocelis subcapitata (until reach final concentration of about 104 cells.ml⁻¹). Females with eggs were isolated and maintained in tissue-culture plates until release of the neonates. Then, twenty neonates were isolated in tissue-culture plates and kept in a germination chamber under the same environmental conditions described above. The neonates were observed daily under a stereomicroscope in order to determine the maturation time, number of eggs produced per female, and growth (estimated as body size). To determine body size, twenty adult females and twenty neonates were measured under an optical microscope, using an ocular eyepiece equipped with a micrometer. The growth curve of Alona guttata was estimated through the Von Bertalanffy equation, followed by the Ford-Walford adjustment (Sparre, 1998). Body size from neonates (t_0) and adults parthenogenetic females (t_{30}) were used as reference to estimate the growth curve.

3. Results and Discussion

In the first day of the experiment, two of the twenty neonates died, and a total of eighteen neonates could be grow up to complete development. Production of parthenogenetic eggs was recorded from the second day of culture. The neonates generated by these females required 4.92 \pm 0.26 days to mature. After the 6th day, the neonates had eggs, which were released after 2 days (i.e., newly hatched neonates required a mean of 8 days to mature and begin reproduction). In general, each female produced 2 eggs per brood and generated a mean of 20 \pm 6.92 neonates during its entire life cycle; the females produced a total of 360 individuals during the 37 days of the experiment (Figure 1). Each female produced a mean of 10 \pm 3.46 broods during its life cycle. After egg production halted, females survived for 2.5 \pm 0.98 days,



Figure 1. Reproduction aspects and life cycle parameters of *Alona guttata* for 18 individuals grown under laboratory conditions. (Fed with R. subcapitata, controlled temperature of 22 ± 2 °C and photoperiod of 16 h light/8 h dark.)

Life cycle parameters	Values
Adult length (μm)	390 ± 27
Embryonic Development (days)	2 ± 0.2
Maturation of neonates (post-embryonic) (days)	4.92 ± 0.26
Maximum days of life (days)	37
Maximum number of brood per female	17
Mean longevity (days)	30.9
Minimum days of life (days)	13
Minimum number of brood per female	3
Neonates length (µm)	200 ± 12
Primipara age (days)	5.9 ± 0.37

Table 1. Reproduction aspects and life cycle parameters of *Alona guttata* for 18 individuals grown under laboratory conditions. (Fed with *R. subcapitata*, controlled temperature of 22 ± 2 °C and photoperiod of 16 h light/8 h dark).

for a median of 30.9 \pm 8.1 days of survival (Table 1). Neonates and adults had mean lengths of 0.2 \pm 0.01 and 0.39 \pm 0.03 mm, respectively.

The present results showed that *A. guttata* (Figure 2) produced fewer eggs per female than other cladoceran species such as Ceriodaphnia and Moina, which have a mean of 9 and 4 eggs per brood, respectively (Fonseca and Rocha, 2004). The egg production of A. guttata is similar to other species of Chydoridae, as seen in Table 2. The longevity of A. guttata (30,9 days) is higher to those of other species of Chydoridae (Santos et al., 2006; Santos Silva et al., 2014). Many factors can influence cladocerans longevity, especially water temperature, photoperiod and food quality (Santos et al., 2006; Ferrão-Filho and Azevedo, 2003). Highest temperatures may influence metabolic processes and reproduction (Ahlgren et al., 1990), and the nutritional quality and variety of food sources provided during experiments may determine growth rates, egg production and life cycle duration (Weers and Gulati, 1997). During the experiments, only one algal source food was used. Therefore, the low mortality rate observed (<5% of total individuals), and the relatively long cycle of A. guttata (30.9 days) are indicative that nutritional constrains did not affect the performance of the individuals during the experiment.

A. guttata body size ranged from 190 µm (neonate, lower measured value) to 450 µm (higher value). The neonates had a mean size of 200 μ m (±12 μ m) and adult parthenogenetic females 390 μ m (\pm 37 μ m) (Figure 3 and Table 1). The mean size of A. guttata neonate was slightly lower than that registered to others Chydoridae species (Table 2). Viti et al. (2013) registered mean size of neonates of Coronatella rectangular reaching (204 µm), lower than the observed for Chydorus pubescens neonates (242 µm) (Santos-Wisniewski et al., 2006). Therefore, although neonates of A. guttata had shown a lower mean size in relation to others Chydoridae cladocerans, neonates growth increases substantially during the experiment. The observed mean size for parthenogenetic females of A. guttata are similar to that registered to others Chydoridae cladocerans (Melão and Rocha, 2006; Castilho et al., 2012).



Figure 2. *Alona guttata* Sars, 1862: (A) parthenogenetic female; (B) head pore; (C) post-abdomen details.

Although the egg production of A. guttata can be considered low in relation to others species of Chydoridae (Melão and Rocha, 2006; Castilho et al., 2012), the association of longer life cycle and the constant breeding may represent an efficient life history aspect favoring the maintenance of the population and recolonization of Alona guttata in temporary ponds. In our experiments, parthenogenetic females of A. guttata were able to produce eggs 8 days after hatching, in addition to produce a large number of broods per female. The production of parthenogenetic eggs requires high amounts of energy (Dodson et al., 2010). Food sources to representatives of the Chydoridae family are mainly related to the biofilm attached to macrophytes. Under drastic fluctuation of the environmental conditions, typical of temporary ponds, noticeable reductions of the macrophyte banks can occurs, limiting food supply. The combination of longer life cycle and constant breeding may contribute to surpass periods

Species	EDD	MN	AL	NL	L	LM	F	FM	Reference
Alona guttata	2 ± 0.2	$\textbf{4.92} \pm \textbf{0.2}$	390 ± 3	200 ± 10	37	30 ± 8.1	2.0 eggs/female	20 ± 6.92	Present study
Alona iheringula	1.79 ± 0.2	3.24 ± 0.6	510	288 ± 19	54	46 ± 6	2.0 eggs/female	47.6 ± 6.3	Santos Silva et al. (2014)
Ceriodaphnia silvestrii	-	$\textbf{3.05} \pm \textbf{0.7}$	1040 ± 4	370 ± 30	-	$\begin{array}{c} 29.8\pm5.9\\ 0.37\end{array}$	$9.46 \pm 4.17 \text{ eggs}/$ female	-	Fonseca and Rocha (2004)
Chydorus dentifer	1.9	-	-	-	-	25.4	2.0 eggs/female	22.3	Santos- Wisniewski et al. (2006)
Chydorus pubescens	1.96 ± 0.1	$\textbf{2.37} \pm \textbf{0.43}$	389	241 ± 17.7	31	25.4 ± 4.6	2.0 eggs/female	22.3 ± 5.1	Santos- Wisniewski et al. (2006)
Coronatella rectangula	$\textbf{1.68} \pm \textbf{0.1}$	$\textbf{2.48} \pm \textbf{0.4}$	434 ± 14	204 ± 30	46	$\textbf{28.0} \pm \textbf{9.3}$	2.0 eeggs/female	$\textbf{27.8} \pm \textbf{9}$	Viti et al. (2013)
Daphnia laevis	-	10.20 ± 3	1860 ± 4	62 ± 10	-	$\textbf{28.3} \pm \textbf{0.1}$	$4.45 \pm 1.06 \text{ eggs}/$ female	65	Rocha et al. (2016)
Macrothrix flabelliger	4.9	3.5	1070	310 ± 18	27	12.7 ± 8.5	13.6 ± 4.7 eggs/ female	122.3 ± 0.0	Güntzel et al. (2003)
Oxyurella longicaudis	$\textbf{2.30} \pm \textbf{0.5}$	5.2	883 ± 27.7	503 ± 52.77	58	46.9 ± 9.0	2.0 eggs/female	22.55 ± 3.98	Almeida Castilho et al. (2015)
Scapholeberis armata frevi	1.9 ± 0.37	$\textbf{5.86} \pm \textbf{1}$	827 ± 21	281 ± 21	31	23 ± 4	8 ± 3 eggs/female	47.58 ± 6.27	Castilho et al. (2012)

Table 2. Comparison of embryonic development time and fertility of other species of cladocerans, reported in the literature.

EDD: Embryonic Development (days); MN: Maturation of neonates (post-embryonic in days); AL: Adult length (μm); NL: Neonates length (μm); L: Longevity (days); LM: Longevity Mean (days); F: Eggs number; FM: Mean number of eggs in the whole life cycle.



Figure 3. Growth curve of *Alona guttata* in experimental conditions of controlled light conditions. (Fed with R. subcapitata, controlled temperature of 22 ± 2 °C and photoperiod of 16 h light/8 h dark.)

of extreme variation of environmental conditions, ensuring the constant growth of the population.

The short time that females of *A. guttata* survived after they stopped producing new eggs is similar to records for other species of cladocerans, such as *Chydorus pubescens* and *Oxyurella longicaudis* (Santos-Wisniewski et al., 2006; Almeida Castilho et al., 2015). Our study indicates that *A. guttata* presented a rapid body development, which suggests that this species allocates high amounts of energy to growth, to allow early reproduction in its life cycle. The rapid development and short time that neonates of *A. guttata* require to mature and generate eggs are important adaptations to the harsh environmental

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conditions in temporary ponds, which aid it in colonizing and producing resting eggs in these systems. The results of this study are pertinent to aspects of the population dynamics of *A. guttata*, an important member of food webs of high-altitude temporary ponds.

Acknowledgements

Thanks to the Federal University of Ouro Preto (UFOP) for logistical support during the field work. To the Dean of Research of UFOP for granting a scholarship to Vivian Santos. Many thanks to Dr. Janet Reid for English revision and suggestions to the manuscript. We are very grateful to anonymous reviewers for comments on a previous version of the macnuscript.

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