Acta Limnologica Brasiliensia

Publication of the Brazilian Association of Limnology

Thematic Section "Neotropical Zooplankton Symposium"
Acta Limnologica Brasiliensia, 2024, vol. 36, e104
https://doi.org/10.1590/S2179-975X5724
ISSN 2179-975X on-line version

Hatching of Cladocera (Crustacea: Branchiopoda) resting eggs from permanently hydrated and temporarily dehydrated sediments of an Amazon lake

Eclosão dos ovos de resistência de Cladocera (Crustacea: Branchiopoda) dos sedimentos permanentemente hidratados e temporariamente desidratados de um lago amazônico

Camila de Araújo Couto[1], Raize Castro-Mendes[1], Renan Gomes do Nascimento[1], Alexander Armando Flores Arzabe[1], Luis Geraldes Primeiro[1], Maiby Glorize da Silva Bandeira[1]* and Edinaldo Nelson dos Santos-Silva[1]

[1]Laboratório de Plâncton, Instituto Nacional de Pesquisas da Amazônia – INPA, Av. Bem-Te-VI, 8-406, Petrópolis, CEP 69067-001, Manaus, AM, Brasil
*e-mail: maiby.glorize@gmail.com

Cite as: Couto, C.A. et al. Hatching of Cladocera (Crustacea: Branchiopoda) resting eggs from permanently hydrated and temporarily dehydrated sediments of an Amazon lake. *Acta Limnologica Brasiliensia*, 2024, vol. 36, e104. https://doi.org/10.1590/S2179-975X5724

Abstract: Aim: i) to characterize the composition of the Cladocera species hatched from the resting eggs of permanently hydrated and temporarily dehydrated sediments; ii) to test whether periodic dehydration reduces the hatching of the resting eggs. **Methods:** Cladocera resting eggs were collected from the sediment of Tupé lake, Amazonas, Brazil. Sampling was performed in the dry season, when the sediment was found in two conditions: Permanently Hydrated Sediment (PHS) in the lake main channel and Temporarily Dehydrated Sediment (TDS) on the margin. Hatching was experimented through a temperature of 24 °C (± 2 °C) and a photoperiod of 12h light: 12h dark, for 20 days. **Results:** Eight Cladocera taxa were counted among the two sediments. In PHS five taxa (one exclusive) were identified and seven taxa (three exclusive) occurred in TDS. The comparison of the hatching rate of Cladocera eggs between TDS (0.36 ± 0.48%) and PHS (0.32 ± 0.49%) was not significant (GLM: χ^2_1= 0.012; P > 0.05; Pseudo-R^2_M= 0.0006). **Conclusions:** The hypothesis that periodic dehydration of Cladocera resting eggs reduces egg hatching has been refuted. This leads us to conclude that natural periodic dehydration does not affect the hatching of resistance eggs, therefore, resistance eggs, as already reported in the literature are an important mechanism for the maintenance and success of organisms in environments, even undergoing profound changes caused due to the large variation in water levels that occur in Amazon rivers and associated environments.

Keywords: diapause; dormancy; ephippium; zooplankton.

Resumo: Objetivo: i) caracterizar a composição das espécies de Cladocera eclodidas dos ovos de resistência de sedimentos permanentemente hidratados e temporariamente desidratados; e ii) testar se a desidratação periódica reduz a eclosão dos ovos de resistência. **Métodos:** Os ovos de resistência de Cladocera foram coletados do sedimento do lago Tupé, Amazonas, Brasil. A amostragem foi realizada no período da seca, quando o sedimento é encontrado em duas condições: i) sedimento permanentemente hidratado (SPH) no canal do lago; e ii) sedimento temporariamente desidratado (STD) nas margens. Com isso foi realizado um experimento de eclosão, com temperatura de 24 °C (± 2 °C) e fotoperíodo de 12h claro: 12h escuro, durante 20 dias. **Resultados:** Dos dois tipos de sedimentos foram contabilizados oito táxons de Cladocera. Em PHS foram identificados cinco táxons (um exclusivo) e em TDS ocorreram sete espécies (três exclusivas). A comparação da proporção de eclosão dos ovos de Cladocera entre STD (0,36 ± 0,48%) e SPH (0,32 ± 0,49%) não foi estatisticamente significativa (GLM: χ^2_1= 0,012; P > 0,05; Pseudo-R^2_M= 0,0006). **Conclusões:** A hipótese de que a desidratação periódica dos ovos de resistência de Cladocera reduz a eclosão dos ovos foi refutada. Isto nos leva a concluir que a desidratação periódica natural não afeta a eclosão de ovos de resistência, portanto, os ovos de resistência, como já reportado na literatura são um importante mecanismo de manutenção e sucesso dos organismos nos ambientes, mesmo sofrendo profundas modificações causadas pela grande variação do núvel das águas que ocorrem nos rios amazônicos e ambientes associados.

Palavras-chave: diapausa; dormência; efípio; zooplâncton.

1. Introduction

The Amazon basin has been suffering severe changes in river dynamics, but in the general context, it presents fluctuation in the water level of rivers, causing periodic floods and droughts (Junk et al., 1989; Fleischmann et al., 2022, 2023). The rivers annually flood and drain large areas that correspond to the floodplain system, being favored by the topography of the floodplain (Junk et al., 1989). According to the variation of the water level of the Amazon rivers there is the delimitation of four phases of the river regime: drought (low water), rising, flood (high water), and lowing (Lesack & Melack, 1995; Bittencourt & Amadio, 2007).

In drought, the lakes of the floodplain system have less water volume and may or may not have communication with the main river (Lesack & Melack, 1995). In the flood period, there is a large amount of water from rivers to lake environments and generally observed opposite characteristics to drought, for instance, hydration of the sediments of the margins and the presence of new habitats (Lesack & Melack, 1995). During this variation of the water level, the lakes undergo changes that alter their characteristics (e.g. water volume, formation of new habitats, pH, temperature) modifying the environment to the biota, which responds with adaptations that ensure their permanence and dispersion in space and time (Junk et al., 1989; Lesack & Melack, 1995; James et al., 2008; Waterkeyn et al., 2010).

Zooplankton organisms are part of this biota adapted to the seasonal variations of Amazonian lakes (Brandorff & Hardy, 2009). One of the main representatives of zooplankton is the group of Cladocera (Crustacea: Branchiopoda), which produce resting eggs (dormant eggs) to persist in environments with adverse conditions such as desiccation, low water quality, lack of food, and predation (Pietrzak & Slusarczyk, 2006; Radzikowski et al., 2018). Cladocera resting eggs have the potential to remain viable for several years, although viability decreases over time (Alekseev et al., 2007).

In the sediment of the lake exists cladoceran resting egg banks, which have the function of recolonizing the environment and propitiate the resurgence of a part of the community after some disturbance (Brock et al., 2003; Ning & Nielsen, 2011; Guimarães et al., 2024). However, the resting eggs that are in the sediment of the Amazonian lakes (Aquatic Terrestrial Transition Zone - ATTZ; Junk et al., 1989) may suffer different regimes of hydration and dehydration because of water level variation, while resting eggs from some areas of the lakes (not just the channel) remain hydrated.

The conditions that are necessary for breaking dormancy and induction of hatching of Cladocera resting eggs vary among species, but the main triggers are temperature and photoperiod (Alekseev et al., 2007; Iglesias et al., 2016; Flores-Mendez & Gutierrez, 2024). In addition, studies indicate that hydration time also influences the viability and pattern of hatching of resting eggs (Ricci, 2001; Iglesias et al., 2016; Vargas et al., 2019; Bandeira et al., 2020). However, dehydrated resting eggs may lose viability depending on the desiccation condition, which may be short (hours) or even long-term (months or years) (Schröder, 2005; Branstrator et al., 2013; Radzikowski, 2013).

The species composition from the Cladocera resting egg bank (as well as from other zooplankton groups) is a potentially useful tool for biodiversity studies (Vandekerkhove et al., 2005a; Freiry et al., 2020). Vandekerkhove et al. (2005b) described twice as many species of Cladocera from the sediment egg bank as species found in the active community of the water column. In general, in the same place, the species composition in the active and dormant phases does not match (Crispim & Watanabe, 2001).

The objectives of this work were: i) to characterize the composition of Cladocera species hatched from resting eggs from permanently hydrated and temporarily dehydrated sediments; ii) test whether periodic dehydration affects the hatchability of resting eggs to test whether periodic dehydration reduces the hatching of the resting eggs. We predicted that permanently hydrated resting eggs would have a higher proportion of hatching than those temporarily dehydrated.

2. Material and Methods

2.1. Study area

Cladocera resting eggs were collected from the sediment of Tupé lake, which is located on the left margin of the Negro River, within the Tupé Sustainable Development Reserve, Amazonas, Brazil (Figure 1). This lake is permanently connected to the Negro River by a channel. Water enters during the flood and high-water periods, in contrast, leaves during the low and dry periods (Aprile & Darwich, 2005).

2.2. Sediment sampling in Tupé lake

Sediment samples were taken in the dry period (September and November 2011) in two conditions: Permanently Hydrated Sediments (PHS) present in the lake channel and Temporarily Dehydrated Sediments (TDS) from the margins that remain exposed to sunlight and high temperatures (e.g. 35 °C) constantly throughout the day. For each type of sediment, 16 samples were taken (Figure 1). Each sample was composed of three sub-samples of 50 g of sediment, to increase the representativeness of the environment and provide greater robustness to subsequent experimental observations. The sub-samples were collected five meters away from each other and composed of six superficial centimeters of sediment, where the resting eggs are potentially viable for hatching (Alekseev et al., 2007). These three sub-samples were homogenized in a single sample of 150 g each (sample set of 16 samples/type of sediment; N = 32).

For the PHS sampling, a CORER collector was used, and for TDS a PVC tube, both 60 mm in diameter (Figure 1b). The samples were stored in black plastic bags to block the passage of light and refrigerated in an expanded polystyrene box for transport to the Plankton Laboratory of the National Institute of Amazonian Research (INPA), Manaus, AM, Brazil. In the laboratory, the samples were packaged in a refrigerator (~13 °C) until the hatching experiments (Grice & Marcus, 1981; Schwartz & Hebert, 1987).

2.3. Hatching experiment of resting eggs

The hatching experiment was conducted in January 2012 at the Limnology Laboratory of the Federal University of Rio de Janeiro (UFRJ),

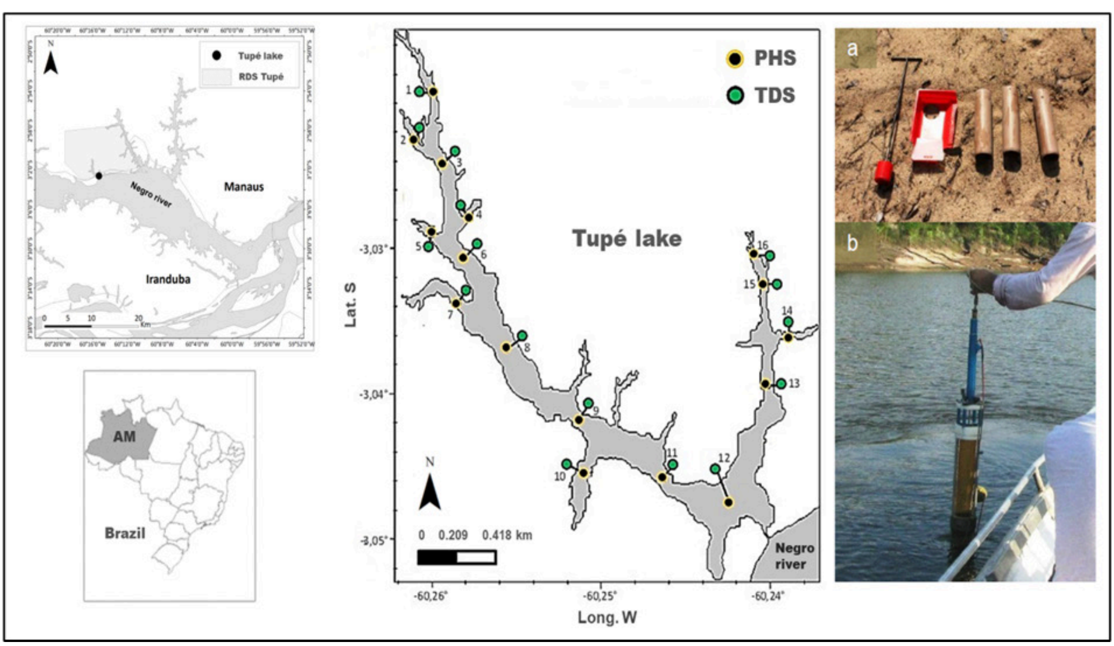

Figure 1. Tupé Lake is located on the left margin of the Negro River, within the Tupé Sustainable Development Reserve (RDS Tupé, in Portuguese), AM, Brazil. In the central map, the provenance of sediment samples in Lake Tupé: black circles indicate Permanently Hydrated Sediments (PHS) and green circles indicate Temporarily Dehydrated Sediments (TDS). In the figures to the right are the sediment collection equipment: (a) PVC tube used in the collections in TDS; (b) Core collector for PHS.

Rio de Janeiro, RJ, Brazil. The sediment was kept in a polystyrene box in a refrigerated room (~22 °C) for two months, until the beginning of the experiments. For the experiment, the resting eggs were separated from the sediment using the method proposed by Onbé (1978), modified by Maia-Barbosa et al. (2003). Each sediment sample was placed in a 250 mL becker containing a sucrose solution prepared in distilled water at a ratio of 1:1. The mixture of sucrose and sediment was centrifuged at 2700 rpm for three minutes. Then, the supernatant material was removed and washed with distilled water for total sugar removal and the resting eggs were removed using a screen of 10 µm.

A total of 233 resting eggs were found. Of these, 99 resting eggs presented the burst or damaged capsule and were not used. Then, 134 resting eggs were used for the hatching experiment, being 45 eggs of PHS and 89 eggs of TDS. The resting eggs were placed in beckers, with 250 mL of artificial culture medium prepared in the laboratory and adjusted with pH 7.0, following the methodology of Tollrian (1993). The beckers remained in a culture room, with a temperature of 24 °C (± 2 °C) and photoperiod of 12 h light: 12 h dark, for 20 days (Santangelo et al., 2011). The entire volume of water in each becker was filtered every two days through a net of 20 µm mesh. This is to prevent hatched organisms from dying before they are accounted for and also to prevent parthenogenetic reproduction. The material retained in the net was deposited in a Petri dish, being observed with a stereomicroscope.

The hatched individuals were removed and fixed in buffered formalin for counting and identification. They were removed and separated becker posts when still very young (without feeding) and observed in the following two days to give a more accurate identification. Eggs not yet hatched were placed back into the becker for observation in the following days. All the material used was thoroughly washed to avoid contamination of the experiment. The artificial medium of each becker was renewed after 10 days of experiment, to prevent the proliferation of bacteria and fungi. The taxonomic determination of the individuals was based on the guides of Smirnov (1992, 1996), Elmoor-Loureiro (1997), Orlova-Bienkowskaja (2001) and Kotov & Štifter (2006).

2.4. Data analysis

To characterize the composition of Cladocera species hatched from the PHS and TDS resting eggs, the percentage of hatching per taxon was calculated, because a low number of hatchings occurred. The percentage was calculated according to the Formula 1:

$$(\%) = n.100/\ (N) \tag{1}$$

where: n = number of hatched individuals of each taxon; N = total number of hatched individuals.

To test if the PHS resting eggs presented a higher hatching percentage than those in TDS, the hatching rate was calculated for each environment. For this, the number of hatches in 20 days was divided by the number of eggs arranged in each aquarium. Due to the reduced number of hatches in the experiment, the Generalized Linear Model (GLM) was adopted in consideration of the non-normal disposition of the obtained data (Dobson, 2002). To test the statistical hypothesis of proportional equality between sediment types (PHS and TDS), the data were submitted to the likelihood ratio test with an approximation of the Quasibinomial distribution fit for proportions (Dobson, 1990). Afterward, hatching proportion data were transformed by arcosene$\sqrt{y}$ to calculate the values of mean, standard deviation, and plot boxplots of the two types of sediments (Abramowitz & Stegun, 1972).

3. Results

In the hatching experiment of the resting eggs of the two types of sediments (PHS and TDS) of Tupé lake, eight taxa of Cladocera were counted, in addition to a group that could not be identified (Figure 2). Of the 45 PHS eggs hatched 14 eggs and five taxa of Cladocera (one exclusive) were identified, being *Holopedium amazonicum* (28.6%) and *Diaphanosoma* sp. (21.4%) presented the highest percentage of hatching. Of the 89 TDS eggs hatched 24 eggs of seven corresponding species (three exclusive), and *Ilyocryptus spinifer* (29.2%) and *Ceriodaphnia cornuta* (12%) had the highest percentage of hatching.

When comparing the hatching rate of Cladocera eggs between TDS (0.36 ± 0.48%) and PHS (0.32 ± 0.49%), there was no statistically significant difference (GLM: $\chi^2_1 = 0.012$; $P > 0.05$; Pseudo-$R^2_M = 0.0006$) (Figure 3).

4. Discussion

In the hatching experiment of Cladocera resting eggs, a discrete taxa number was observed compared to the active community described by Ghidini & Santos-Silva (2018) for Tupé lake (78 species). This result may be related to the method of separating

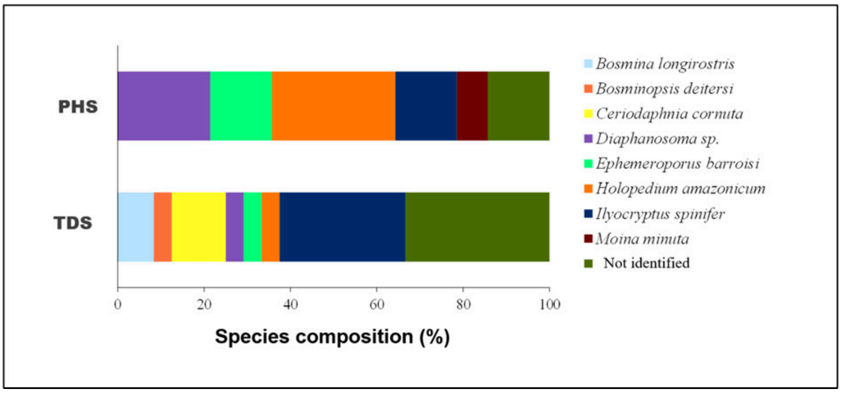

Figure 2. Percentage of Cladocera hatching of Permanently Hydrated Sediments (PHS) and Temporarily Dehydrated Sediments (TDS) of Tupé lake, AM, Brazil.

the resting eggs from the sediment, which may have increased the inviability of the eggs. This is because the number of eggs found in the sediment was high (233 eggs), however, this number reduced after centrifugation (134 eggs), and of these, only 38 eggs hatched in the experiment. Carvalho & Wolf (1989) mentioned that eggs fail to hatch in laboratory experiments after becoming unfeasible by inappropriate conditions to which they are subjected. Probably, in future studies, the adjustment of the centrifugation process for the reduction of revolutions per minute increases the efficiency of the method, that is, minimizes damage and increases the probability of hatching. Still, depending on the question of the study, it would be interesting to test methodologies such as Sars (1901), redescribed by Van Damme & Dumont (2010), which does not need to separate the eggs from the sediment and can increase hatching success.

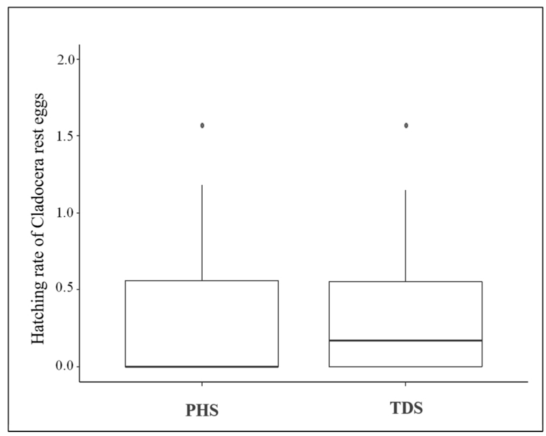

Figure 3. Boxplot of hatching rate of Cladocera resting eggs of Permanently Hydrated Sediments (PHS) and Temporarily Dehydrated Sediments (TDS), without significant difference.

Another factor that may have influenced the reduction of hatching was the experimental conditions in the laboratory. In this work, the resting eggs were incubated at 24 °C, however, this temperature has not yet been recorded in Tupé lake, and this may have affected the hatching of resting eggs since temperature is one of the important factors for egg hatching. The permanently hydrated sediments of the Amazon lakes remain at high temperatures (≈ 25 °C to 33 °C) as usual in an equatorial region. A low number of taxa hatched in experiments was observed in other studies. The study by Maia-Barbosa et al. (2003) hatched a few specimens of *Daphnia laevis* and *Daphnia* sp. Araújo (2012) hatched 16 species but with a low number of individuals. This may be related to the sensitivity of organisms during maintenance experiments. Vandekerkhove et al. (2005b) in several lakes from Europe observed that individuals of Chydoridae and Moinidae have a high mean mortality in hatching experiments. As these families present many representatives in the Amazon lakes, this may have contributed to the reduced number of hatched taxa. However, it is important to note that the reduced number of hatches does not mean a smaller number of resting eggs produced by the identified species. This is because species do not need a large number of eggs to recolonize the environment when conditions are favorable for active forms, where, in each favorable occasion in the environment, only a portion of eggs hatch (García-Roger et al., 2006). Hairston et al. (1999) studied *Daphnia exilis* from a lake in New York City, USA, and revealed that colonization occurred from the hatching of a single egg since in Cladocera there is also reproduction by parthenogenesis.

In the present study, only eight hatched taxa were identified, although a considerable number of individuals did not reach morphological maturity for identification. In PHS, *Holopedium amazonicum* and *Diaphanosoma* sp. had higher rates of hatching. These two taxa have a planktonic habit and are widely found in Tupé Lake (Ghidini & Santos-Silva, 2018). The species *H. amazonicum* is commonly found in lake environments since it has a habit of living in the limnetic region (Korovchinsky, 1992). However, females with resting eggs have not yet been recorded in Lake Tupé. These eggs were found only in the sediment. *Holopedium* eggs have already been found in large quantities and viable for hatching in the sediment of lake channels up to 20 m deep (Lampert & Krause, 1976; Smyly, 1977). This may be related to the higher fecundity of *Holopedium* gametogenic females carrying many eggs (3-10, max. 22 eggs), at the same time (Korovchinsky & Boikova, 1996). Individuals of *Diaphanosoma* could not be identified at the species level, because the neonates presented significant mortality until 48h after hatching, not holding morphological conditions for taxonomic identification. Maia-Barbosa et al. (2003) point out that the success of hatching eggs from Cladocera is still in progress and, in their experiments, they obtained newborn individuals that survived less than 24 hours, making it difficult to identify the species.

The TDS presented a higher percentage of hatching of *Ilyocryptus spinifer* and *Ceriodaphnia cornuta*. The species *I. spinifer* is benthic, commonly found in the habitats of the margins of Tupé lake, mainly living associated with the macrophyte *Utricularia foliosa* (Ghidini, 2011; Couto et al., 2009). The high abundance of this population of Cladocera in the environment, possibly compensates for the low production of resting eggs, since *I. spinifer* produces two eggs at a time (Kotov & Dumont, 2000). *Ceriodaphnia cornuta* is planktonic, widely found in Lake Tupé, and different from *I. spinifer*, because it produces 6 to 20 eggs (Villalobos & González, 2006). From this evidence, we consider the justification for the second largest contribution of hatching in the experiment.

When statistically comparing the hatching rate of Cladocera eggs between PHS and TDS, there was no significant difference. Therefore, the hypothesis that periodic dehydration of Cladocera resting eggs reduces egg hatching has been refuted. Still, the inverse of what was predicted occurred, since TDS had the highest proportion of hatching. Due to the species composition of TDS, a larger number of taxa was found hatching exclusively from this sediment. However, most taxa hatched from both types of sediment. This points out that benthic species will not necessarily have their eggs deposited only on the shore, and planktonic organisms will have their eggs deposited only in the deepest regions of the lake. Some resting eggs sink and others float, and this can occur even with the eggs of individuals of the same taxonomic genus, causing a spatial heterogeneity of the eggs in the lake (Brede et al., 2007). Some species produce resting eggs with substances that allow adherence in plants and some have hooks and/or spines that can influence their distribution inside or between aquatic environments (Gyllström & Hansson, 2004).

With this study, it was possible to suggest that the taxa of Cladocera adjust their life cycle to the variation in the water level of the lake. Possibly, these organisms produce resting eggs when the water level is falling. These eggs undergo a period of dehydration in the drought and when the water level rises, the hydration of the sediment and eggs occurs, with the hatching and recolonization of the habitats of ATTZ. In addition, this study is the first record of these resting eggs in the sediment of a lake in the Western Amazon. Still, it is recommended, more comprehensive studies in the Tupé Lake and other Amazonian aquatic environments.

5. Conclusions

The species composition found is still low in relation to the active community in the lake, with the likelihood of increasing with future studies. The hypothesis that periodic dehydration of Cladocera resting eggs reduces egg hatching has been refuted. This leads us to conclude that natural periodic dehydration does not affect the hatching of resistance eggs, therefore, resistance eggs, as already reported elsewhere, are an important mechanism for the maintenance and success of organisms in the environments, even undergoing profound changes caused due to the large natural variation in water levels that occur in Amazon rivers and associated environments.

Acknowledgements

To Prof. Dr. Reinaldo Bozelli, Prof. Dr. Jayme Santangelo, and Dr. Luciana Araújo for all the patience, support, and teachings in Rio de Janeiro to carry out the hatching experiments. To the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPQ) and Programa Nacional de Cooperação Acadêmica – Novas Fronteiras (PROCAD-NF) for scholarships to Camila de Araújo Couto.

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Received: 13 June 2024
Accepted: 14 October 2024

Associate Editors: Cláudia Bonecker, Gilmar Perbiche-Neves, Maria Stela Maioli Castilho Noll.