



## Factors stimulating the hatching of resting eggs and their contribution to the composition of cladoceran assemblages in tropical temporary lagoons

Fatores que estimulam a eclosão de ovos de resistência e a sua contribuição para a composição das assembleias de cladóceros em lagoas temporárias tropicais

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**Abstract: Aim:** We aimed to verify the contribution of cladocerans' resting eggs to the active communities of temporary lagoons and, through an experiment, identify which conditions induce high hatching rates. **Methods:** Cladocera assemblages were sampled in four temporary lagoons in the Turvo River floodplain (20° 22'S and 49° 16'W), in the northwest region of São Paulo State, Brazil. Sediment samples were taken during the dry season from a depth of 5 cm, using a 4.5 cm diameter corer. Plankton samples were taken from the water column before and after the dry season. For the hatching test, two treatments were performed 1. Natural condition – without light and temperature control; 2. Controlled condition – with controlled photoperiod and temperature. Temperature, pH, conductivity, dissolved oxygen and hatching of resting eggs were monitored for two weeks. The influence of the parameters on hatching in both treatments was evaluated using Hierarchical Partition Analysis. **Results:** Hatching of resting eggs was higher in the Controlled condition than in the Natural one. Thirty percent of species observed in the active community after flooding hatched in the laboratory test. Conductivity, pH, and dissolved oxygen were positively correlated to the hatching of some species, e.g., *Ephemeropterus hybridus*, *Leydigia ornata*, *Notoalona sculpta* and *Ilyocryptus spinifer*. The first species to hatch were those living associated with macrophytes and at low depths. **Conclusions:** Our results show that stable temperature and photoperiod with similar light and dark hours stimulate greater hatching of Cladocera resting eggs. Variables such as pH, conductivity and dissolved oxygen were also correlated with the hatching of some species. We observed that the first contributions to activating the community after drought came from hatching of species usually associated with macrophytes and low depth conditions.

**Keywords:** dormant community; sediment; ephippium; flood plain; experiment.

**Resumo: Objetivo:** Este estudo tem como objetivo verificar a contribuição dos ovos de resistência



de cladóceros para as comunidades ativas de lagoas temporárias e testar experimentalmente as condições específicas para a eclosão destes ovos de resistência. **Métodos:** Amostras de cladóceros foram obtidas em quatro lagoas temporárias na planície de inunda  o do rio Turvo (20° 22'S e 49° 16'W), na regi  o noroeste do Estado de S  o Paulo, Brasil. Amostras de 5 cm de sedimento foram coletadas durante a esta  o seca, usando um corer de 4,5 cm de di  metro. Amostras de pl  ncton foram coletadas antes e depois da esta  o seca. Para o teste de incubac  o, foram realizados dois tratamentos a saber, 1. Condi  es naturais - sem controle de luz e temperatura; 2. Condi  es controladas - com fotoper  odo e temperatura controlados. A condi  o da   gua e a eclos  o dos ovos de resist  ncia foram monitoradas por duas semanas. A influ  ncia dos par  metros na eclos  o em ambos os tratamentos foi avaliada por meio da An  lise de Partic  o Hier  rquica. **Resultados:** A eclos  o dos ovos de resist  ncia foi maior no tratamento Condi  es controladas do que Condi  es naturais. Trinta por cento das esp  cies observadas na comunidade ativa ap  s o alagamento eclodiram no teste de laborat  rio. Condutividade, pH e oxig  nio dissolvido foram positivamente correlacionados com a eclos  o de algumas esp  cies como *Ephemeropterus hybridus*, *Leydiglops ornata*, *Notoalona sculpata* e *Ilyocryptus spinifer*. As primeiras esp  cies a eclodirem foram aquelas associadas a macr  fitas e em ambientes com baixas profundidades. **Conclus  es:** Nossos resultados mostram que condi  es constantes de temperatura e fotoper  odo estimulam maior taxa de eclos  o dos ovos de resist  ncia de Cladocera. Vari  veis como pH, condutividade e oxig  nio dissolvido tamb  m foram correlacionados com a eclos  o de algumas esp  cies estudadas. Observamos que as primeiras contribui  es para a comunidade ativa ap  s a seca vieram da eclos  o de esp  cies geralmente associadas a macr  fitas e condi  es de baixa profundidade.

**Palavras-chave:** comunidade dormente; sedimento; ef  pio; plan  cie de inunda  o; experimento.

## 1. Introduction

In floodplains, temporary lagoon conditions become extreme for aquatic organisms when water disappears and ponds dry out during the dry season. When this event begins, organisms such as cladocerans, from the zooplankton communities, begin to reproduce sexually, producing resting eggs that go into the sediment, forming banks of eggs in a state of dormancy. When water returns to the lagoon, these eggs hatch and populations recolonize the environment, allowing the species to survive during adverse periods (De Stasio Junior, 1990). These egg banks have an important role in ecological and evolutionary processes, also representing a stock of genetic variability of organisms (Hairston Junior & C  ceres, 1996; Walsh et al., 2014).

Panarelli et al. (2021) detected differences in richness and abundance between temporary and permanent wetlands, pointing out the importance of studies in these kinds of environment. Comparing temporary and permanent wetlands, the former seem to present more favorable conditions for the occurrence of sexual cycles in cladocerans and, consequently, the production of resting eggs (Santangelo et al., 2015). Environmental changes in physical and chemical variables can promote hatching from the egg bank (Santangelo, 2009), which trigger the reestablishment of cladoceran populations adapted to the new environmental conditions. In this way, in each period of flooding of the lagoons, in the rainy season, the contribution of individuals from hatching resting eggs is decisive

for the colonization of the active community. Even so, the active cladoceran assemblage does not always reflect the dormant community, as suggested by Santangelo et al. (2015).

Reasons for these differences in composition between active and dormant communities in floodplains may be related to the dispersal mechanisms that can occur. The composition of the active zooplankton community in these lagoons is affected by eggs hatching from the egg bank in the sediment, but it also relies on dispersion taking place through the water that connects the aquatic environments during the flood period (Dias et al., 2016). In addition, dispersion of the resting eggs themselves occurs due to wind (Lopes et al., 2016) and animals such as birds (Morais-J  nior et al., 2019).

Once established in new environments through dispersal, resistance eggs may or may not hatch for local colonization. Many studies have investigated which factors stimulate the hatching of resting eggs, because detecting stimuli for hatching can help understand the link between active and diapause stage (Vanderkerkhove et al., 2005a). This also sheds light on the factors providing zooplankton community structure in aquatic environments, especially in temporary lakes, where there is faster colonization after flooding.

Ice-out, temperature, photoperiod and predators have already been reported as stimuli to the hatching of resting eggs in a temperate environment (Vanderkerkhove et al., 2005b; Lass et al., 2005; La et al., 2009). In these types of temperate

environments, higher hatching rates were obtained at low temperatures (10 and 15 °C) and long, well-marked photoperiods (Vanderkerkhove et al., 2005a).

In tropical environments, the factors that promote the breaking of dormancy of resting eggs in cladocerans are still unknown (Iglesias et al., 2016; Vendramin et al., 2023). Physical and chemical factors such as temperature, conductivity, pH, dissolved oxygen and photoperiod have already been investigated as an influence on hatching of some species. Rojas et al. (2001) determined optimum hatching conditions at pH 5-9, temperature 25 °C, photoperiod eight or more hours of light per day for *Moina micrura*; Paes et al. (2016) found that temperature was the most important factor for the hatching of *Daphnia* resting eggs, but it was dependent on the environment. In addition to these, other studies have observed that slightly variable or even constant temperature seems to be important for breaking diapause (Panarelli et al., 2008; Araújo et al., 2013).

More recently, some studies have investigated the influence on zooplankton resting eggs of changes in the water conditions due to antropogenic actions. Studies on the influence of pesticides have shown that these chemicals present in the water damage the hatching of zooplankton resting eggs (Portinho et al., 2018, 2021). Also regarding the effect of pollutants, Coelho et al. (2021) found a greater abundance of dormant stages of zooplankton in the most polluted environment, and iron-enriched mine tailings present in the sediment negatively impacted zooplankton resting eggs (Souza-Santos et al., 2021). DOC (water brownification) was observed to affect the hatching patterns in zooplankton by blocking light (Vargas et al., 2022).

In tropical areas, even though there has been an increase in publications over the last two decades, many questions still remain on how the hatching of resting eggs contributes to the active zooplankton community, and defining general standards still seems to be a complex task. Therefore, it is crucial to investigate the conditions under which dormancy is induced or broken, and what the trends in hatching rates are. It is now well established that experimental data are fundamental to obtain responses to unsolved questions; however, there is a lack of data, especially for tropical environments (Iglesias et al., 2016).

Thus, we aimed to verify the contribution of cladocerans' resting eggs to the active communities of temporary lagoons, in an attempt to answer the

following questions: Do cladocera species which are hatched in the laboratory correspond to the active populations observed in lagoons before and after drought? Does temperature stability favor the hatching of resting eggs? Could temperature, pH, conductivity, and dissolved oxygen be associated with breaking dormancy under experimental conditions?

## 2. Material and Methods

### 2.1. Study area

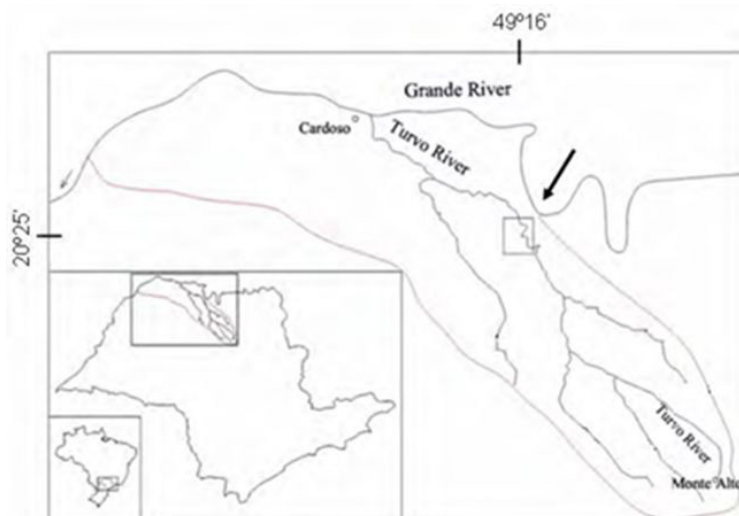
Sample collections of the cladocerans and sediment were carried out in lagoons (Meia Lua, Mazer, Pistia and Eichhornia) located along the Turvo River floodplain (20° 22'S and 49° 16'W), in the northwest region of São Paulo State, in Brazil (Figure 1). The selected lagoons are temporary ones, connected to the river during extreme flood periods; they can dry out completely in the dry season, and present a large abundance of free-floating macrophytes, such as *Eichhornia* sp. and *Salvinia* sp. during hydroperiods. Terrestrial vegetation in the region consists of fragments of semideciduous seasonal forest, deciduous forest, and a transitional vegetation between savanna (Cerrado) and tropical rain forest (Atlantic Forest), mostly replaced by pastures and other crops (Ranga et al., 2012).

The climate in the region is classified as tropical hot and humid (Alvares et al., 2013); the winter is dry – average of 120 mm monthly (May to October) – and summer is rainy – average of 438 mm monthly (November to April).

### 2.2. Hatching of resting eggs test

Superficial sediments to a 5 cm depth were collected, by using a 4.5 cm diameter core, at five sites randomly distributed in the central region of two lagoons – Meia Lua and Pistia. The sediment samples were homogenized and stored in flasks. The hatching tests were performed in the laboratory based on Crispim & Watanabe (2001); 500 mL glass flasks were used containing 40 g sediment hydrated with 400 mL river water, in order to simulate the same water conditions found in the environment. The treatments are described below:

- 1) Natural conditions (NC): 12 flasks – 6 with sediment from Pistia Lagoon and 6 with sediment from Meia Lua Lake – under uncontrolled conditions (laboratory room temperature and light);
- 2) Controlled conditions (CC): 12 flasks– 6 with sediment from Pistia Lagoon and 6



**Figure 1.** Map of the State of São Paulo highlighting the Water Resources Management Unit (UGRHI 15 Turvo-Grande), where the Turvo River floodplain is located. The arrow indicates the location of the lagoons where the study was carried out.

with sediment from Meia Lua Lake – inside a germination chamber, incubated at 23 °C and with a photoperiod of 12h light/12h dark.

The cladoceran hatching was monitored every 48 hours for two weeks, and the following water parameters were measured: temperature, pH, conductivity and dissolved oxygen using a Horiba model U-10 multiparameter probe. After two weeks, the monitoring was performed weekly, until the 60<sup>th</sup> day.

To check the hatching, all the water from all the flasks was removed and fixed with 4% formalin for further analysis under a stereomicroscope. After that, water from the same place in the environment was replaced in the flasks, always maintaining the same volume. The hatched cladocerans that were found in the fixed sample were collected with a Pasteur pipette, placed on a slide and identified under a microscope up to the species level. The identification was performed using identification keys (Elmoor-Loureiro, 1997; Sousa & Elmoor-Loureiro, 2019). After identification, all individuals of each species were counted in each flask where they were found.

### 2.3. Sampling of cladoceran assemblages

Active cladoceran assemblages were sampled from the water column of four lagoons, and from two of these the sediment was obtained for the hatching test, before (May 2014) and after (February 2015) the dry season. Due to the low depth, 21 L of water were collected with a bucket and filtered through a plankton net (50 µm mesh).

The samples were preserved in 4% formalin. Organisms were identified up to the species level. Three 2 mL subsamples were quantified, or the entire sample when abundance was low, in counting chambers under the stereomicroscope, and the presence of ephippia was checked. Characteristics of the lagoons can be seen in Table 1.

Lagoon depth and water transparency were evaluated using a Secchi disk; temperature, pH and conductivity data were measured with a Horiba model U-10 multiparameter probe; dissolved oxygen concentration was determined by Winkler method (Golterman et al., 1978); chlorophyll-a and suspended materials were determined according to Golterman et al., (1978) and Teixeira & Kutner (1962), respectively.

### 2.4. Data analysis

To detect differences between the hatching observed in both treatments, we compared the number of hatching events between Controlled and Natural conditions through a Paired T-test. We also compared the mean of the variables each day – temperature, pH, conductivity and dissolved oxygen – through a T-test.

The influence of physical and chemical parameters on the hatching of resting eggs in the two tested treatments was evaluated with Hierarchical Partition Analysis (Chevan & Sutherland, 1991). In this analysis, two parameters (“I” and “J”) are calculated for each predictor variable, in which “I” is the

**Table 1.** Lagoon characteristics.

Lagoons	Macrophytes	Dynamics	Connection with the river	Depth (m)	Sediment granulometry (%)
Meia Lua	Present	Temporary - completely dry in the dry season	Only at the rainy season	0.27	Clay: 63.98 Silt: 6.7 Sand: 21.57 Organic matter: 7.75
Mazer	Present	Temporary - completely dry in the dry season	Only at the rainy season	0.62	Clay: 63.2 Silt: 6.32 Sand: 0.23 Organic matter: 30.55
Pistia	Present	Temporary - completely dry in the dry season	Only at the rainy season	0.43	Clay: 66.36 Silt: 6.68 Sand: 3.46 Organic matter: 23.5
Eichhornia	Present	Temporary - completely dry in the dry season	Only at the rainy season	0.37	Clay: 64.58 Silt: 10.72 Sand: 1.21 Organic matter: 23.5

independent contribution of each predictor and “J” is the interaction between predictors (Mac Nally, 2002). Predictors analyzed were temperature, conductivity, pH and dissolved oxygen, but temperature was excluded from analyses of Controlled Condition since the variable was constant in this treatment. We ran 1,000 randomizations, and the significance of each variable is given by 95% confidence interval, i.e., Z values > 1.65 (Mac Nally, 2002). The Spearman correlation was used in the nonparametric data in order to verify the positive or negative correlation between the parameters and hatching of resting eggs. These analyses were performed in R statistical software version 2.15.2 (R Development CoreTeam, 2014), by using the packages “hier.part” (Walsh & MacNally, 2012), “gtolls” (Warnes et al., 2013), “vegan” (Oksanen et al., 2013) and “car” (Fox & Weisberg, 2011).

In order to compare the species composition between lagoons, before and after drought, and for the hatching test, a PERMANOVA was performed. For species richness between lagoons, before and after drought, and hatching test, One-Way ANOVA was used. The differences were assessed through the Tukey post hoc test. Finally, in order to verify the differences in physical and chemical variables in the lagoons between the periods, before and after the drought, a Student’s T-test was used.

For all analyses we tested the normality of data distribution and, when necessary, data were converted into  $\log(x + 1)$  to homogenize the variance.

### 3. Results

#### 3.1. Hatching of resting eggs

The comparison between the number of resting eggs that hatched indicated no significant differences between treatments ( $t = 2.1997$ ,  $df = 131$ ,  $p = 0.029$ ). In total, 431 eggs hatched in CC and 118 hatched in NC. During the 60-day period, hatching numbers in CC remained mostly higher than those in NC, with their peak near the end of the test, on the 50<sup>th</sup> day, when 158 hatchlings were recorded (Figure 2). On the same day, the hatching peak occurred in NC, with 32 eggs hatching. No organisms with ephippia were observed throughout the test.

In the Natural Condition (NC), six cladoceran species were identified, and in the Controlled Condition (CC), just four species (Table 2). Almost all species were common to both treatments, but *Ovalona glabra* (Sars, 1901) and *Oxyurella longicaudis* (Birge, 1910) were observed only in NC. *Ephemeroporus hybridus* (Daday, 1905) and *Leydigiopsis ornata* Daday, 1905 were the most abundant species in CC, with 191 and 179 individuals, respectively. In NC, *Ovalona glabra* and *Ilyocryptus spinifer* Herrick, 1882 had the highest number of eggs hatching, 48 and 64, respectively (Table 2).

The water conductivity ranged from 10.16 to 13.16  $\mu\text{S}\cdot\text{cm}^{-1}$  in NC, and from 9.16 to 12.33  $\mu\text{S}\cdot\text{cm}^{-1}$  in CC (Figure 3). The pH was acid in both treatments, ranging from 4.28 to 5.38 in NC, and from 4.90 to 5.36 in CC. Temperature varied from 21.97 to 28.31 °C in NC and was constant at 23 °C in CC.

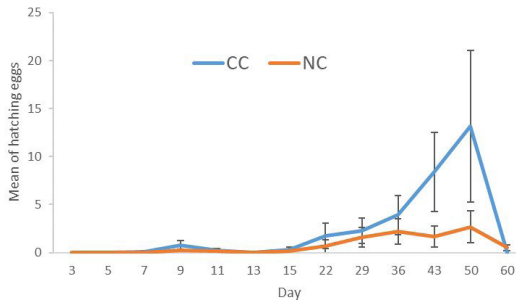


The average dissolved oxygen concentrations were 5.17 and 5.29 mg.L<sup>-1</sup> in NC and CC respectively, at the beginning of the test. On the 36<sup>th</sup> day, the oxygen

concentration decreased in both treatments, reaching 3.28 mg.L<sup>-1</sup> in NC and 2.08 mg.L<sup>-1</sup> in CC. There were no statistical differences between variables from each treatment (Figure 3).

**Table 2.** Number of individuals from each species which hatched during hatching test in Natural and Controlled Conditions.

Species	Natural Condition	Controlle Condition
<b>Chydoridae</b>		
<i>Ovalona glabra</i> (Sars, 1901)	48	0
<i>Ephemeropterus hybridus</i> (Daday, 1905)	1	191
<i>Leydigiopsis ornata</i> Daday, 1905	1	179
<i>Notoalona sculpta</i> (Sars, 1901)	3	5
<i>Oxyurella longicaudis</i> (Birge, 1910)	1	0
<b>Ilyocryptidae</b>		
<i>Ilyocryptus spinifer</i> Herrick, 1882	64	56
<b>Total</b>	<b>118</b>	<b>431</b>



**Figure 2.** Mean and standard error of the number of resting eggs of cladocerans hatched per day in the Controlled Condition (CC) and Natural Condition (NC) during hatching test.

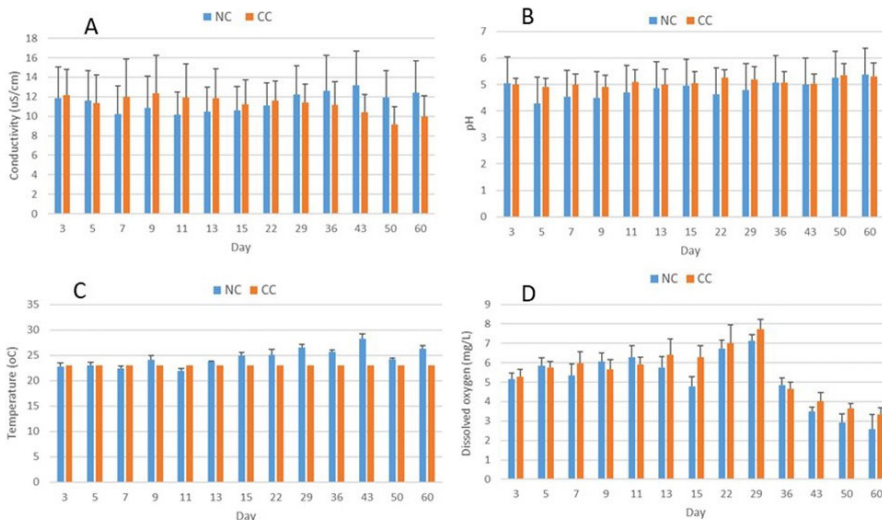
From the hierarchical partition analysis, the results indicate that, in the Natural Condition, conductivity and dissolved oxygen explained 34.62% and 50.02% of the hatching of resting eggs, respectively, and together 84.64% of the hatches.

In CC, conductivity was positively correlated with the hatching of *I. spinifer*; *E. hybridus* hatchings were positively correlated with pH and negatively with dissolved oxygen; *L. ornata* hatchings were positively correlated with pH and negatively with conductivity and oxygen (Table 3). In NC, *O. glabra* hatchings were negatively correlated with pH and dissolved oxygen (Table 3). All presented data are statistically significant ( $p < 0.05$ ).

### 3.2. Cladocera assemblages in lagoons before and after drought

Significant differences were observed in the transparency ( $t = -4.74$ ,  $p = 0.003$ ) and temperature ( $t = -4.88$ ,  $p = 0.002$ ) between the periods, before and after the dry season (Tables 4 and 5); transparency was higher before the dry period and temperature was higher after the dry period. Other physical and chemical parameters, such as conductivity, dissolved oxygen, pH and suspended matter did not differ significantly between the two periods (Tables 4 and 5).

Species richness was significantly different between samples before drought, after drought and



**Figure 3.** Averages and standard deviation for (A) conductivity; (B) pH; (C) temperatures; (D) dissolved oxygen, during the hatching test. NC: Natural Condition; CC: Controlled Condition.

**Table 3.** Z-score values and Spearman correlation ( $r_s$ ) between physical and chemical variables and the species that hatched from the resting eggs in the Controlled Condition and Natural Condition. Data obtained through Hierarchical Partition Analysis with significance level of  $p < 0.05$ . Only the significant results are presented.

Variables	Controlled Condition				Natural Condition			
	<i>I. spinifer</i>		<i>E. hybridus</i>		<i>L. ornata</i>		<i>O. glabra</i>	
	Z- score	$r_s$	Z- score	$r_s$	Z- score	$r_s$	Z- score	$r_s$
Conductivity ( $\mu\text{S.cm}^{-1}$ )	2.69	0.19			2.94	-0.17	2.42	-0.15
pH			3.21	0.18	1.92	0.14		
Dissolved oxygen ( $\text{mg.L}^{-1}$ )			2.21	-0.18	2.45	-0.15	1.69	-0.13

**Table 4.** Average, standard deviations (SD), and T-test of the physical and chemical variables from the lagoons before and after the drought. Data of each lagoon can be seen in Table 5.

	Before		After		t	p
	Average	SD	Average	SD		
Depth (m)	0.42	0.15	0.75	0.27	-2.156	0.074
Transparency (m)	0.22	0.14	0.15	0.07	-4.747	<b>0.003</b>
Temperature ( $^{\circ}\text{C}$ )	21.13	2.08	27.13	1.30	-4.888	<b>0.002</b>
Conductivity ( $\mu\text{S.cm}^{-1}$ )	180.50	6.45	174.00	48.55	0.265	0.799
Dissolved oxygen ( $\text{mg.L}^{-1}$ )	4.29	1.64	4.73	2.78	-0.270	0.795
pH	6.66	0.41	6.64	0.19	0.098	0.924
Chlorophyll_a ( $\mu\text{g.L}^{-1}$ )	71.49	80.26	54.72	22.29	0.402	0.701
Suspended Material ( $\text{mg.L}^{-1}$ )	92.65	111.38	94.63	69.54	1.546	0.173

**Table 5.** Physical and chemical variables from the lagoons before and after the drought.

Lagoons	Period	Depth (m)	Transp. (m)	Temp. ( $^{\circ}\text{C}$ )	Conduct. ( $\mu\text{S/cm}$ )	DO (mg/L)	pH
Meia Lua	Before drouth	0.27	0.13	19.9	179.0	5.04	6.63
	After drouth	0.44	0.10	27.5	238.0	5.53	6.45
Mazer	Before drouth	0.62	0.13	21.0	185.0	4.15	7.25
	After drouth	0.62	0.10	26.0	185.0	2.77	6.82
Pistia	Before drouth	0.43	0.43	19.5	172.0	2.07	6.44
	After drouth	1.0	0.25	28.8	132.0	8.31	6.78
Eichhornia	Before drouth	0.37	0.18	24.1	186.0	5.90	6.32
	After drouth	0.94	0.14	26.2	141.0	2.30	6.50

Abbreviations: Transp: transparency; Temp.: temperature; Condu.: conductivity; DO: dissolved oxygen.

during the hatching test ( $F = 19.58$ ,  $p = 0.001$ ). A post hoc test resulted in differences in richness between samples before drought and the hatching test ( $p = 0.003$ ), and between samples before and after drought ( $p = 0.003$ ). Twenty-three cladoceran species were recorded in the samples of all lagoons before drought, 16 species after drought, and six species during the hatching test (Table 6). Among the hatched species, *Notoalona sculpta* (Sars, 1901) was found only before drought; the other five species were registered in both periods. These five species represent at least 30% of the species that colonized the lagoons after flooding and had been in the dormant community. In both periods, Chydoridae has the

largest number of species, whereas Daphniidae, Moinidae, Ilyocryptidae, and Macrothricidae (Table 6) were also present. In the hatching test, only Chydoridae and Ilyocryptidae organisms were recorded. All lagoons presented similar species numbers before and after drought (Table 4).

Species compositions were statistically different between samples from lagoons before drought, after drought and during the hatching test (PERMANOVA test,  $F: 2.981$ ,  $p = 0.002$ ). The main differences were observed between samples from lagoons before and after drought ( $p = 0.02$ ); no differences were observed between the hatching test and lagoon samples.

**Table 6.** Occurrence of Cladocera species before and after lagoon drought, and during hatching test.

Species/Lagoon	Before					After					Hatching test	
	Meia Lua	Mazer	Pistia	Eichhornia	FO (%)	Meia Lua	Mazer	Pistia	Eichhornia	FO (%)		
<b>Chydoridae</b>												
<i>Magnospina dentifera</i> (Sars, 1901)	x		x		50					0		
<i>Ovalona glabra</i> (Sars, 1901)	x	x			50			x		50		x
<i>Anthalona verrucosa</i> (Sars, 1901)	x				25							
<i>Chydorus eurynotus</i> Sars, 1901	x	x	x	x	100		x			25		
<i>Chydorus nitidulus</i> (Sars, 1901)	x	x	x	x	100		x			50		
<i>Chydorus pubescens</i> Sars, 1901	x		x		50					0		
<i>Dadaya macrops</i> (Daday, 1898)	x		x		50							
<i>Ephemeroporus hybridus</i> (Daday, 1905)	x	x	x	x	100		x		x	75		x
<i>Euryalona brasiliensis</i> Brehm & Thomsen, 1936	x		x		50			x		25		
<i>Karuilona muelleri</i> (Richard, 1897)	x	x			50		x		x	75		
<i>Leydiglops brevirostris</i> Brehm, 1938					0					25		
<i>Leydiglops ornata</i> Daday, 1905	x	x	x	x	100		x		x	50		x
<i>Notalona sculptata</i> (Sars, 1901)	x	x	x	x	100					0		x
<i>Oxyurella longicaudis</i> (Birge, 1910)	x	x	x	x	100		x			25		x
<b>Daphniidae</b>												
<i>Ceriodaphnia cornuta</i> Sars, 1886			x	x	50					0		
<i>Ceriodaphnia reticulata</i> (Jurine, 1820)	x		x	x	75		x			25		
<i>Ceriodaphnia richardi</i> Sars, 1901	x	x	x	x	100		x			25		
<i>Simocephalus lheringi</i> Richard, 1897			x		25					0		
<b>Moinidae</b>												
<i>Moina minuta</i> Hansen, 1899					0			x	x	50		
<i>Moina reticulata</i> (Daday, 1905)	x				25			x		25		
<i>Moinodaphnia macleayi</i> (King, 1853)	x				25					0		
<b>Macrothricidae</b>												
<i>Macrothrix elegans</i> Brady, 1886	x	x	x	x	100		x	x	x	100		
<i>Macrothrix squamosa</i> Sars, 1901		x		x	50					0		
<i>Grimaldina brazzai</i> Sars, 1901	x	x	x	x	100					25		
<b>Ilyocryptidae</b>												
<i>Ilyocryptus spinifer</i> Herrick, 1882	x	x		x	75			x	x	50		x
Species number	20	13	16	13		7	8	6	7			6

Abbreviation: FO: frequency of occurrence.



#### 4. Discussion

Our results demonstrate that a constant temperature favors hatching of a greater number of Cladocera resting eggs. Variations in water physical and chemical parameters, such as conductivity, pH, and dissolved oxygen, stimulate the hatching of resting eggs of some Cladocera species, depending on temperature and photoperiod control. The results from this study also indicate that at least 30% of the species that recolonized the lagoon after flooding were present in the dormant community.

The highest number of resting egg hatches that we observed under constant conditions of temperature and photoperiod agrees with the data of others who also found similar results (Palazzo et al., 2008a; Panarelli et al., 2008; Araújo et al., 2013), reinforcing the importance of these two variables for the mechanisms of hatching. In fact, temperature and photoperiod have been considered some of the most important factors to trigger the hatching of zooplankton's resting eggs in temperate regions (Schwartz & Hebert, 1987; Vandekerkhove et al., 2005a).

Temperature is one of the main factors which may induce diapause in Cladocera (Crispim & Watanabe 2001; Maia-Barbosa et al., 2003). Paes et al. (2016) found that high temperatures and absence of light had negative effects on the hatching of *Daphnia laevis* and *D. ambigua* in two tropical aquatic environments. On the other hand, higher hatching rates under stable temperature and light conditions, such as those found in our study, may be associated with higher stability of the aquatic environment, thus representing favorable conditions for dormancy breakage and establishment of the active population.

In addition to temperature and photoperiod, some variables, such as pH, dissolved oxygen, and conductivity, are possible triggers for some Cladocera species to hatch in the laboratory. During the test, the pH in the treatment chamber remained around 5, showing a positive correlation with hatching in *Ephemeroporus hybridus* and *Ledygiopsis ornata*. Rojas et al. (2001) reported that pH had an influence on *Moina micrura* hatching, hence demonstrating a pH optimum range (5 to 9) for hatching to occur. Conductivity and dissolved oxygen were negatively correlated to the hatching of *E. hybridus*, *L. ornata*, and *O. glabra*. Studies have shown that low concentrations of oxygen influence the metabolic activities in Branchiopoda in general and, consequently, their development (Brendonck, 1996), which can be related with the

hatching events as observed in our study. On the other hand, low conductivity has been associated with other variables in lagoons in relation to resting egg production (e.g., Palazzo et al., 2008b). All these results reinforce the hypothesis that the conditions for hatching are specific for each species and kind of environment.

The low species richness observed during the hatching test in our study may seem incompatible with the long-term richness accumulated in the egg bank on the sediment of the lagoons, as suggested by Vandekerkhove et al. (2005b) and Coronel et al. (2009). Other studies have already verified a greater richness in the water column, in tropical regions, when compared to the number of species hatched in the laboratory (Palazzo et al., 2008a; Panarelli et al., 2008; Santangelo et al., 2015; Gerhard et al., 2017). A reduced number of hatchings can be related to the absence of the specific conditions which may be required to induce dormancy breakage (Cáceres & Tessier, 2004). Freiry et al. (2021) also reported that the diversity of the active community that could come from the egg bank was not found in subtropical ponds. They suggest the existence of a complex relationship between local and climatic predictors and the community structure of the zooplankton resting-egg bank, which can result in the diversity observed.

Besides that, the diversity of species present in the egg bank may decrease, because resting eggs may have a limit to tolerating environmental adversities when disturbances are frequent and too intense (Waterkeyn et al., 2011; Brendonck et al., 2017). One example of intense and stressful conditions is the high temperature of sediment during drought, which can prevent resting eggs from hatching (Nielsen et al., 2015), as happens in floodplain dynamics. In addition, only some of all these viable eggs in the sediment can hatch under test conditions (Havel et al., 2000). Moreover, egg bank composition depends on the active community, from which not all species will produce eggs, and diapause stimuli are not the same for each species (Santangelo et al., 2015). *Notoalona sculpta* was one of the species found before drought and during experimental conditions, whereas it was not registered after drought, which shows that even though it does not occur in the active community of the lagoons, it can be dormant in the sediment.

The flood pulse favors the entrance of species into the lagoons; a way of dispersion is that of resting eggs associated with the roots of floating macrophytes (Battauz et al., 2017). Wind (Lopes et al., 2016) and

animal transport (Morais-Júnior et al., 2019) are other ways in which resting eggs disperse. Thus, after a flood, the active Cladocera assemblage arrives in the lagoon through the hatching from the local egg bank added to the different already mentioned dispersion methods. So, the low richness obtained during the experiments suggests the hatching from metapopulations is more important than from the egg bank. Even so, it is important to consider egg banks as a strategy by which to maintain the diversity of the aquatic environment (Melo et al., 2022).

In general, Cladocera species from Daphniidae, Bosminidae, Sididae and Moinidae are present in flood plain lagoons, as observed in the samples taken before drought in the present and other studies (e.g. Stephan et al., 2017), but Chydoridae, Macrothricidae, and Ilyocryptidae species were the most representative in the samples taken after the drought period and in the experimental test. This fact can signal that the first species that initiate the recolonization of the environment are those strongly associated with shallow lakes and macrophytes, such as species from the families of Chydoridae, Macrothricidae, and Ilyocryptidae (Sacherová & Hebert, 2003; Fryer, 1968). It is likely that, when the lagoons are at the beginning of flooding, these species present characteristics more adapted to colonization and, after being completely flooded, presenting more limnic characteristics, the other species that are more adapted to this condition start to hatch. This approach is based on other studies that suggest that different environmental cues can stimulate zooplankton egg hatching (Iglesias et al., 2016; Jones & Gilbert, 2016; Santangelo, 2009; Santangelo et al., 2014; Walsh et al., 2014) and in the asynchrony in the timing of hatching (Vendramin et al., 2023)

In spite of the small number of species hatched in our study when compared to the species richness in the water column, the experimental results are significant because the hatched families in the test were the same families which are predominant during the active phase in the water column of lagoons. We believe it would be very useful if further studies taking other controlled physical and chemical variables into account were conducted, in order to verify more accurate richness in the sediment in comparison with the active community.

In conclusion, our study showed that at least 30% of the species that recolonized a floodplain lagoon after flooding can come from the dormant community and are species usually associated

with macrophytes and low depths. Species that hatched in the laboratory were found in the active community, reinforcing the potential of the egg bank for recolonization of the aquatic environment. Stable temperature and a photoperiod with similar light and dark hours stimulate greater hatching of Cladocera resting eggs. The hatching events of only a few species were associated with the variables, suggesting the specificity of these conditions to stimulate the hatching of resting eggs.

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