



Invertebrate Richness and Hatching Decrease with Sediment Depth in Neotropical Intermittent Ponds

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Abstract

Some groups of invertebrates from intermittent wetlands produce dormant stages in response to environmental fluctuations. Dormancy is a strategy to survive such fluctuations and to persist in extreme aquatic habitats, such as temporary habitats. We investigated the hatching responses of invertebrate dormant stages across different depths of sediment in intermittent ponds. Our hypotheses were: (1) the richness and abundance of invertebrate hatchlings decrease as the depth of the sediment column increases, and (2) the composition of invertebrate hatchlings varies over the wetland sediment depth. Four intermittent ponds were sampled in southern Brazil. One sediment column of 30 cm depth was collected in each pond and stratified into 1 cm thick slices for analysis of the dormant stages. A total of 1,931 hatchlings distributed among 31 taxa were collected from the sediment columns over the experiment. The total richness and abundance of hatchlings (after bdelloid taxa exclusion) were negatively related with the sediment depth. The composition of aquatic invertebrates varied among the different strata over the sediment depth. As intermittent wetlands are ecosystems extremely susceptible to climate variations, the results help to understand the resilience of aquatic resistant communities from different sediment strata after drought events.

Keywords Dormant stages · Invertebrate hatchlings · Sediment column · Temporary wetlands · Viability

Introduction

Some groups of invertebrates from intermittent wetlands produce dormant stages in response to environmental fluctuations (Brendonck and De Meester 2003; Parra et al. 2021), such as resistant eggs and cysts (Williams 2006). Dormancy is a strategy to survive such fluctuations and to persist in extreme aquatic habitats (Santangelo 2009; Strachan et al. 2015; García-Roger et al. 2017). Several taxa of invertebrate use dormancy as a survival strategy, and wetland sediments may contain thousands of dormant stages of different

species per square meter, particularly rotifers, cladocerans and copepods (Hairston 1996; Panarelli et al. 2008; Day et al. 2010; Brendonck et al. 2017).

The production and hatching of invertebrate dormant stages in intermittent wetlands are influenced by several environmental variables. Frequency and length of hydroperiod are important variables to hatching patterns and production of invertebrate dormant stages (Nielsen et al. 2000; Vargas et al. 2019; da Silva Bandeira et al. 2020). Temperature and photoperiod are also key factors for invertebrate hatching patterns (Gyllström and Hansson 2004; Wang and Chou 2015). Water chemistry factors (e.g., salinity, conductivity and dissolved oxygen) are also important abiotic hatching cues (Brendonck 1996; Vanschoenwinkel et al. 2010).

The bank of dormant stages of aquatic invertebrates is a historical ecological archive, formed by the overlap of several generations, which allows correlating the dynamics of communities to environmental changes (Brendonck and De Meester 2003; Rogalski 2015; Rogalski et al. 2017; García-Roger and Ortells 2018). For instance, the hatching of

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dormant stages of rotifers, cladocerans and copepods after decades of dormancy has been reported in sediments from the estuary of the Pettaquamscutt River in Rhode Island, USA (Marcus et al. 1994). There are examples of even older hatchlings, such as copepods around 300 years old (Hairston et al. 1995), cladoceran genetic material dated to 600 years old (Frisch et al. 2014) and a bdelloid rotifer of 24,000 years dormant in the permafrost of the Alazeya River in Siberia, Russia (Shmakova et al. 2021). This feature can be used as an important ecological and evolutionary tool for studies of dormant aquatic invertebrate communities (Brendonck and De Meester 2003; Angeler 2007).

Studies indicate that the upper layer of the sediment (between 4 and 10 cm) has the highest concentrations of viable dormant stages (Herzig 1985; Cáceres 1998; Cáceres and Hairston 1998; Hairston et al. 2000; Santangelo 2009). Therefore, the unhatched dormant stages accumulate at greater depths over time (Ellner and Hairston 1994; Brendonck and De Meester 2003), and the hatching rate tends to decrease with depth (Hairston et al. 1999; Kerfoot et al. 1999). Nonetheless, studies correlating the viability of dormant stages and the depth of the sediment were carried out mainly in intermittent wetlands in temperate regions of Europe and North America (Herzig 1985; Hairston et al. 1995; Kerfoot et al. 1999; Gyllström and Hansson 2004). This relationship was poorly studied in Neotropical region (Iglesias et al. 2016). The studies that report the presence of dormant stages in southern and southeastern Brazil wetlands (Maia-Barbosa et al. 2003; Stenert et al. 2010, 2016, 2017; Santangelo et al. 2014; Ávila et al. 2015; Freiry et al. 2016, 2020a, b; Vargas et al. 2019; Brazil et al. 2022) only analyzed the top layers of the sediment (3–5 cm).

Here, we investigated the hatching responses of invertebrate dormant stages across different depths of sediment in intermittent ponds. The objectives were to: (1) evaluate the richness, abundance and composition of hatched invertebrates along a vertical gradient of the sediment column, and (2) compare the hatching of the main taxonomic groups along the sediment column. Our first hypothesis is that the richness and abundance of invertebrate hatchlings decrease as the depth of the sediment column increases since the largest fraction of viable and more responsive dormant stages occurs in the top layers of the sediment (Hairston et al. 2000; Brendonck and De Meester 2003; Yousey et al. 2018). Our second hypothesis is that the composition of invertebrate hatchlings varies over the wetland sediment depth considering that several invertebrate taxa use dormancy as a survival strategy (Brendonck et al. 2017) and that not all dormant stages have the same ability to survive for long in the egg bank (Hairston 1996).

Materials and methods

Study Area

This study was conducted in the Coastal Plain of Southern Brazil, a region extending across approximately 640 km with a high concentration of wetlands (Maltchik et al. 2003) (Fig. 1). The climate is moist subtropical with a mean annual temperature of 17.5 °C, and the annual mean rainfall ranges from 1,200 to 1,500 mm (Rambo 2000). The flat topography of the landscape and the low altitudes (lower than 20 m) makes climate conditions very similar throughout the study region.

Sampling Design

Four intermittent depressional ponds were sampled in April 2019 (Fig. 1). The isolated ponds analyzed were intermittent, with similar sizes (1 ha) and water depth (0.5 m on average) distant at least 15 km from each other. On each pond, one sediment column of 30 cm depth was collected using a *Russian peat borer* (Modelo 2460-F20) (5-cm diameter). To collect the sediment, the tube corer was pushed vertically, avoiding disturbance in the deeper part of the sediments. The sediment sampling was carried out when the ponds had water. Each sediment column was transferred to a PVC corer adapted to receive the sediment column, without alteration. The samples were kept in darkness by wrapping in aluminum foil and refrigerated (4 °C) until experiments start (Cousyn and De Meester 1998; García-Roger and Ortells 2018). Data collection complied with the current Brazilian environmental laws (SISBIO 36365-2).

Laboratory Procedures

Each sediment column was stratified into 1 cm thick slices for analysis of the dormant stages. Since the upper centimeters of the sediment contains the active egg bank, the slice thickness varied with depth, with smallest intervals (1 cm) in the top layers (up to 6 cm) and 4 cm for deeper sediment layers (Hairston et al. 1995, 2000; Kerfoot et al. 1999; Brendonck and De Meester 2003). In total, eleven slices per sediment column (pond) were incubated in our experiment all in the same period (0–1 cm, 1–2 cm, 2–3 cm, 3–4 cm, 4–5 cm, 5–6 cm, 10–11 cm, 15–16 cm, 20–21 cm, 25–26 cm e 30–31 cm), totalizing 44 samples (11 samples x 4 selected ponds). All slices were dehydrated in a dark oven for 96 h at 40 °C.

In the incubation experiment, each sediment slice was submersed under a depth of 2 cm of distilled water into plastic trays without aerators, and water temperature (23 ± 2 °C) and photoperiod (12 h light/12 hours dark) were kept

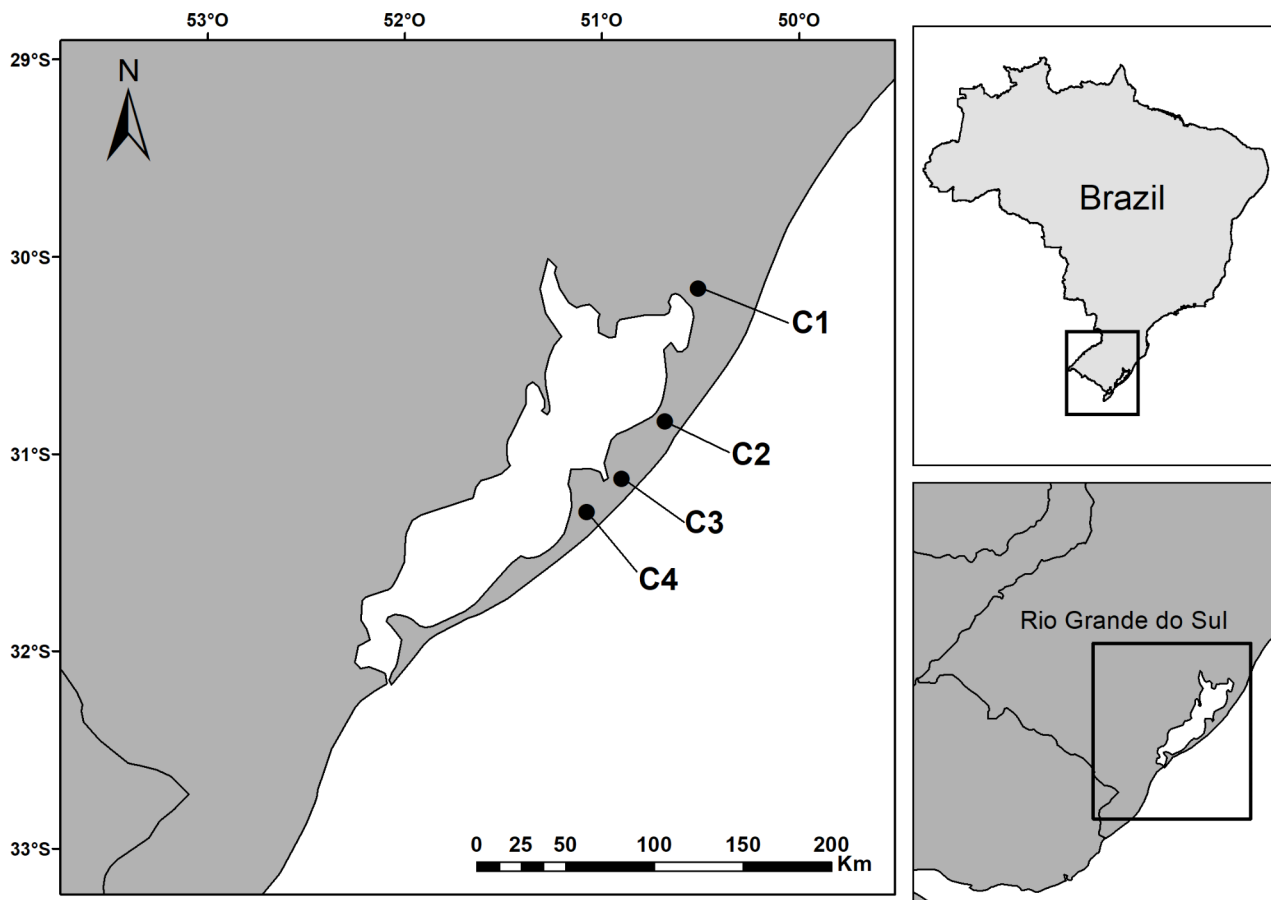


Fig. 1 Location of the study region and of the four ponds (C1 – C4) studied in the southern Brazilian Coastal Plain

constant (Ávila et al. 2015; Stenert et al. 2010). The experiment was maintained in the laboratory for 4 weeks (June 7th to July 5th, 2019), and hatchlings were collected three times per week, corresponding to 12 sampling days, by filtering all the water content from each plastic tray through a 50- μ m mesh size net. The collected hatchlings were transferred to 1.5-mL polypropylene microtubes with 80% alcohol or 4% formaldehyde (Rotifera) (Freiry et al. 2016). The distilled water was changed after each sampling day. The duration of the experiment (4 weeks) was based on previous work from our research group (Freiry et al. 2020b; Vendramin et al. 2020) and others (Brock et al. 2003). Hatchlings were quantified under stereomicroscope (Zeiss Stemi 2000) and identified to species level whenever possible using specialized literature (Koste 1978; Elmoor-Loureiro 1997; Gazulha 2012) and aid of specialists.

Data Analyses

The richness and abundance of aquatic invertebrates were the taxa number (number of species or genus – whenever possible – added to the number of taxa identified at lower

taxonomic resolutions – phylum, class, or family level) and number of hatchlings, respectively. The relationship of invertebrate richness and abundance with different sediment depths was tested with generalized linear models (GLMs). As both response variables were discrete, GLMs were fitted with Poisson (richness) and negative binomial (abundance) distributions (because of major overdispersion of residuals) and log link function. The predictor variable (sediment depth) was included in the models as a numerical variable. The models were tested for richness and abundance of the total community.

Each sediment column was divided into three different strata: superficial (from 1 to 5 cm, represented by five slices – 1, 2, 3, 4 and 5 cm), intermediate (from 6 to 20 cm, represented by three slices – 6, 11 and 16 cm) and deep (from 21 to 31 cm, represented by three slices – 21, 26 and 31 cm) to analyze the spatial variation in the composition of hatchlings. The spatial variation in the composition of aquatic invertebrates among the different depth strata was assessed using nonmetric multidimensional scaling ordination diagram (NMDS) and a nonparametric multivariate analysis of variance (PERMANOVA) with 9,999 permutations.

The NMDS and PERMANOVA analyses were based on an incidence matrix (Jaccard index). A similarity percentage analysis (SIMPER; Clarke 1993; 999 permutations) was used to identify the taxa that mostly contributed to differences among depth strata. We used the PERMDISP approach (*betadisper* function) (Anderson 2006) to test for differences in the multivariate dispersion among the sediment depth strata. All statistical analyses were conducted with the functions from packages *vegan*, *car*, *MASS*, *lme4* and *ggplot2* in the R software v. 4.0.3 (R Development Core Team 2020). The Panplot2 portable software (Sieger and Grobe 2013) and CorelDRAW were used to visualize the total hatching percentage of the main invertebrate taxa in relation to sediment depth.

Results

A total of 1,931 hatchlings distributed among 31 taxa were collected from the sediment columns over the experiment. Phylum Rotifera comprised most of the hatchlings (82%), followed by the Phylum Gastrotricha (8%) and Phylum Annelida (Family Aeolosomatidae – 6%). The Subphylum Crustacea (2.5%) was represented by the Class Ostracoda (1.8%), Subclass Copepoda (only 1 nauplius – 0.05%) and Order Anomopoda (Cladocera, 13 individuals – 0.7%). Phylum Nematoda (1.2%), Phylum Tardigrada (0.4%) and Phylum Platyhelminthes (class Turbellaria – microturbellarians – 0.3%) corresponded to the rest of the hatched individuals. The most abundant taxa were the bdelloid rotifers *Philodina* sp. (52%) and *Adineta* sp. (12%), and the monogonont rotifers *Lecane leontina* Turner, 1892 (9%) and *Ptygura pilula* (7%) (Table 1). Although the highest percentage of hatchlings of these taxa occurred in the surface layers of sediment, some individuals hatched at depths greater than 20 cm (Table 1; Fig. 2).

The total richness of taxa was negatively influenced by the sediment depth, since the hatchlings showed greater richness in the top layers compared to the deeper ones ($Z = -5.533$; $p < 0.001$; Fig. 3). The total hatching abundance was not influenced by depth ($Z = -1.197$; $p = 0.231$) (Fig. 4). Considering that the dominance of the Bdelloidea rotifers could influence variation in abundance, we excluded these taxa and reanalyzed the data. After bdelloid taxa exclusion, the abundance was also negatively influenced by the sediment depth ($Z = -5.460$; $p < 0.001$) (Fig. 5).

The composition of aquatic invertebrates varied among the different strata over the sediment depth (PERMANOVA, $F_{2,41} = 3.022$; $p < 0.001$) and this variation was displayed by two axes of the NMDS diagram (stress = 0.125) (Fig. 6). The PERMANOVA results were not affected by multivariate dispersion within the sediment depth strata ($F_{2,41} = 0.846$;

$p = 0.446$). The similarity percentage (SIMPER) analysis revealed that nine taxa significantly contributed to the dissimilarity in the composition of the different strata, and the taxa with the highest contribution were *Adineta* sp., *Ptygura pilula*, Ostracoda, Gastrotricha and Aeolosomatidae (Online Resource 1).

Discussion

Our hypothesis that the total richness and abundance (after exclusion of bdelloid rotifers) of invertebrate hatchlings decrease with sediment depth was supported in this study. Similarly, a range of studies on other wetland systems report greater abundance of hatchlings in the top layer of the sediment for several taxa, including Ostracoda, Cladocera and Copepoda, but mostly for rotifers (Carvalho and Wolf 1989; De Stasio 1990; Hairston et al. 1995; Ning and Nielsen 2011). Our results are in line with the idea that the surface layers of the sediment have the highest concentrations of viable dormant stages, responding better to hatching stimuli (Cáceres 1998; Cáceres and Hairston 1998; Hairston et al. 2000; Santangelo 2009). Another plausible explanation for hatching pattern observed may be related to the temporal degradation of the dormant eggs at deeper sediment depths that leads to higher mortality due to senescence, disease, and parasitism (Hairston et al. 1995, 2000; Kerfoot et al. 1999; Brendonck and De Meester 2003). Although it was not possible to date the sediment in our study, the positive relationship between the depth at which the invertebrate dormant stages are found in the sediment and their age is well known in undisturbed aquatic systems (Brendonck and De Meester 2003; Kerfoot and Weider 2004).

Studies that report the presence of dormant stages in southern Brazil wetlands only analyzed the top layers of the sediment (Palazzo et al. 2008; Ávila et al. 2015; Freiry et al. 2016; Stenert et al. 2016, 2017). This study evaluated the hatching of dormant stages of aquatic invertebrates across different depths of sediment (from top to deeper layers) in intermittent ponds, showing that most hatchlings were from the Phylum Rotifera, Phylum Gastrotricha and Phylum Annelida. Some studies that evaluated only the top layers of the sediment in intermittent ponds of the same region (Freiry et al. 2020a, b; Vendramin et al. 2020, 2022) showed that the crustaceans from the Order Anomopoda (cladoceran species) were the most representative in the hatched invertebrate community. In our study, the hatchlings of the cladoceran species were also mainly related to the top layers of the sediment (5–6 cm).

The bdelloid rotifers represented by *Adineta* sp. and *Philodina* sp. comprised 64% of the total abundance found in this study. The high dominance of these two genera may

Table 1 Total abundance of invertebrate hatchlings along the sediment depths of the studied ponds

Taxonomic classification		Depth strata (cm)																		
Phylum	Class	Subclass	Order	Family	Species	0-1	1-2	2-3	3-4	4-5	5-6	10-11	15-16	20-21	25-26	20-31				
Annelida	Polychaeta	Brachiopoda	Phyllopoða	Anomopoda	Acolosomatidae		2	2	40	38	1	1	16	1	1	1	9			
					Clydoridae	<i>Chydorus eurynotus</i> Sars, 1901	0	0	0	1	1	1	1	0	0	0	1	0	0	
Rotifera	Eurotatoria	Bdelloidea	Ploima	Ilyocryptidae	<i>Leydigia</i> sp.	0	0	1	0	0	3	0	0	0	0	0	0			
					<i>Ilyocryptus sordidus</i> Liévin, 1848	0	0	0	0	1	0	0	0	0	0	0	0	0		
				Macrothricidae	<i>Ilyocryptus spinifer</i> Herrick, 1882	1	1	0	0	0	0	0	0	0	0	0	0	0	0	
					<i>Macrothrix</i> sp.	0	0	2	0	0	0	0	0	0	0	0	0	0	0	
Gastrotricha	Turbellaria	Eurotatoria	Ploima			11	3	5	3	6	7	0	0	0	0	0	0			
						1	0	0	0	0	0	0	0	0	0	0	0	0		
Rotifera	Eurotatoria	Bdelloidea	Ploima	Adinetidae	<i>Adineta</i> sp.	42	16	29	25	11	29	5	3	0	0	0	0			
				Philodinidae	<i>Philodina</i> sp.	3	0	0	0	2	0	1	0	0	0	0	0	0	0	
				Notommatidae	<i>Cephalodella</i> sp.	0	0	0	18	132	7	32	31	5	0	0	0	0	0	
					<i>Cephalodella gibba</i> Ehrenberg, 1830	26	7	54	32	110	194	173	9	99	244	47	0	0	0	
					<i>Monommata dentata</i> Wulfert, 1940	2	1	6	1	2	2	0	0	0	0	0	0	0	0	0
					<i>Notommata</i> sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
					<i>Dipleuchlanis propatula</i> Gosse, 1886	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
					<i>Epiphanes brachionus</i> Ehrenberg, 1837	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0
					<i>Lecane</i> sp.	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
					<i>Lecane bulla</i> Gosse, 1851	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0
Nematoda	Eurotatoria	Bdelloidea	Ploima	Lepadellidae	<i>Lecane leontina</i> Turner, 1892	164	1	2	0	1	0	0	0	0	0	0	0			
				Brachionidae	<i>Lepadella</i> sp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
				Trichocercidae	<i>Platylas quadricornis</i> Ehrenberg, 1832	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
					<i>Trichocerca</i> sp.	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
					<i>Trichocerca elongata</i> Gosse, 1886	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
					<i>Trichocerca flagellata</i> Hauer, 1937	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
					<i>Pygura pilula</i> Cubitt, 1872	16	6	7	14	60	24	0	0	0	0	0	0	0	0	0
					<i>Floscularia</i> sp.	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0
					<i>Testudinella patina</i> Hermann, 1783	0	0	0	0	2	3	0	0	0	0	0	0	0	0	0
						3	0	13	5	0	0	0	0	1	1	0	0	0	0	0
Tardigrada	Eurotatoria	Bdelloidea	Ploima			4	2	0	0	1	0	0	0	0	0	0	0			
						0	0	0	0	0	0	0	0	0	0	0	0	0		

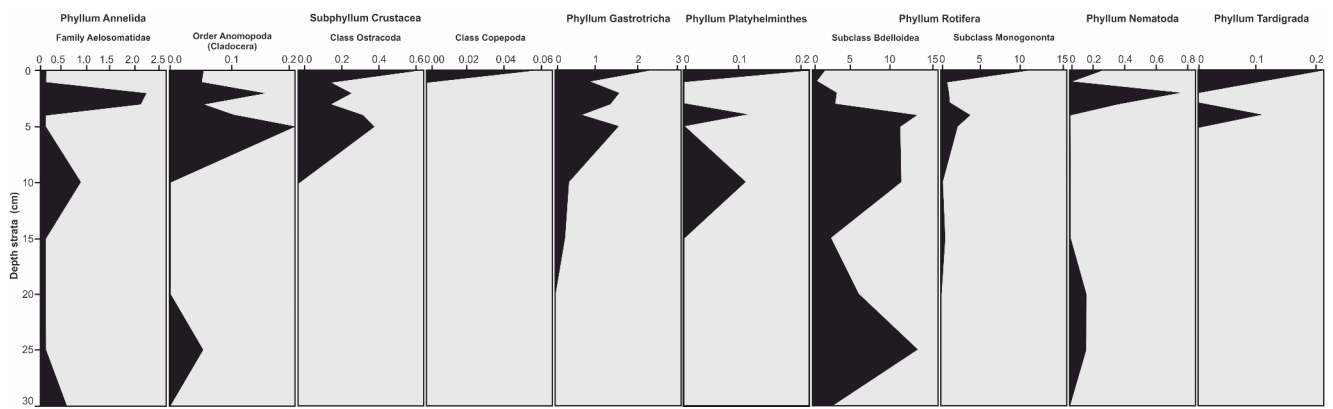


Fig. 2 Percentage of hatchlings of aquatic invertebrates along the sediment depths over the experiment

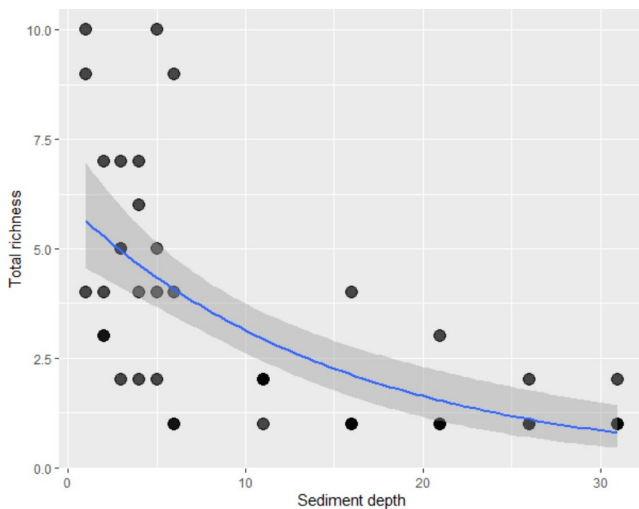


Fig. 3 Total richness of aquatic invertebrates along the sediment depths of the studied ponds

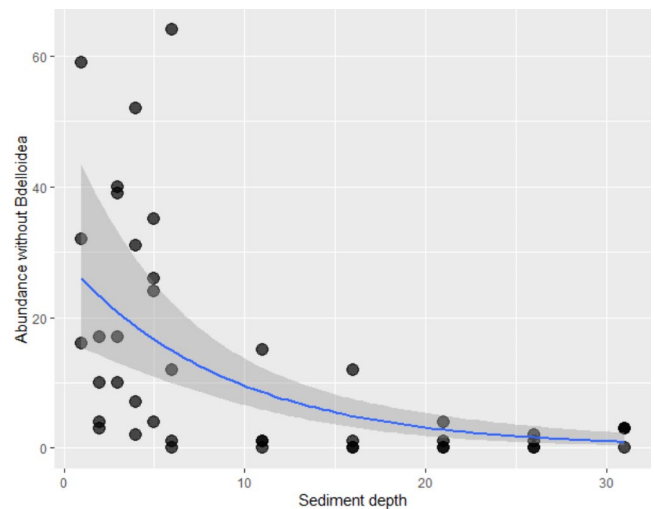


Fig. 5 Abundance of aquatic invertebrates after bdelloid taxa exclusion (see main text for details) along the sediment depths of the studied ponds

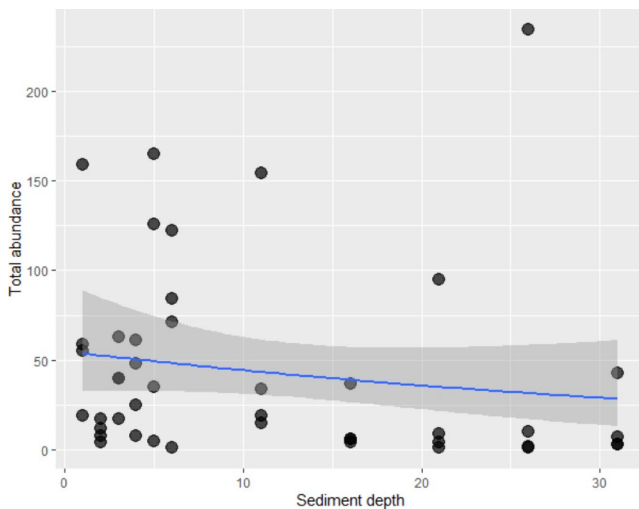


Fig. 4 Total abundance of aquatic invertebrates along the sediment depths of the studied ponds

be related to two factors: quick response from its dormant stages to environmental cues and asexual reproduction within 24 h. Rotifers of the Subclass Bdelloidea are known for their parthenogenesis and their dormant stage (anhydrobiosis), which allow them to withstand severe periods of desiccation (Ricci 2001). The physiological mechanisms that allow bdelloid rotifers to survive dehydrated during dormancy involve the protection of molecules such as sugars, proteins, and antioxidants (Rebecchi 2013), and the ability to recover their DNA when rehydrated (Hespeels et al. 2014). When water returns to the system, dormancy is broken, and within 24 h the individuals can reproduce by parthenogenesis (Ricci 2001). In this sense, although the sampling intervals of 2–3 days were used to minimize the chance of parthenogenetic reproduction (Brock et al. 2005; Nielsen et al. 2013), we cannot assume that all individuals of Bdelloidea found in this study are hatchlings from dormant stages.

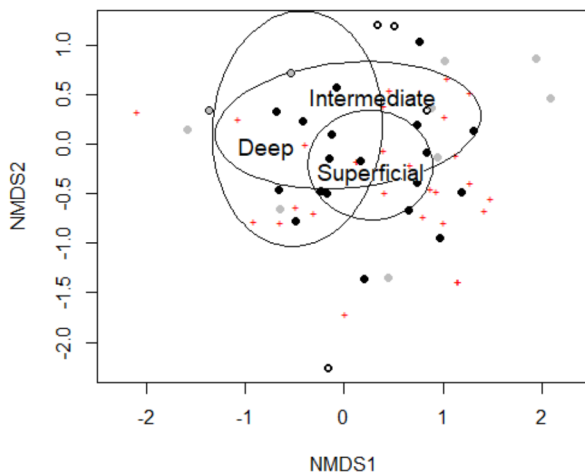


Fig. 6 Nonmetric multidimensional scaling ordination for aquatic invertebrate hatchlings from superficial, intermediate and deep strata along the sediment of the studied ponds. The red crosses (+) are the invertebrate taxa; the filled black dots (●) corresponded to the superficial stratum; the filled gray dots (●) corresponded to the intermediate stratum; and the unfilled black dots (○) corresponded to the deep stratum

In our experiment, taxa such as Aeolosomatidae, Nematoda and Gastrotricha hatched at depths greater than 20 cm. These taxa have specific dormancy characteristics, sheltering in the sediment until they finish the metabolic processes related to the dormant stages (Poinar Jr 2010; Strayer et al. 2010; Alekseev and Pinel-Alloul 2019; Fontaneto 2019). Aeolosomatidae can form desiccation-resistant cysts (hardened membrane of mucus secreted by the worm) that allow them to survive adverse environmental conditions (Glasby et al. 2021). Gastrotrichs produce resting eggs that are thick-shelled and very resistant to freezing and drying (Strayer et al. 2010). These organisms generally occur in the upper 5 cm of the sediment, but depending on environmental conditions, they may occur at greater depths (Ricci and Balsamo 2000). Nematodes can coil, losing most of their internal water and halting their metabolic activity, remaining in this dormant condition until water becomes available again (Rebecchi et al. 2007). There is evidence that the survival of adult dormant nematodes can be extremely long, reaching over 30 years (McSorley 2003).

Our result showed the presence of dormant stages capable of hatching in sediments up to 30 cm deep in intermittent wetlands. In ecological terms, this information is important, even if the stimuli necessary for hatching are reduced in deeper sediments. Dormant stages of deeper sediments can reach the surface through the stirring of the sediment by animals. Fish, insects, worms and wetland molluscs can

commonly disturb sediments (Brendonck and De Meester 2003). Intermittent ponds are often visited by different species that, when interacting with the environment, can disturb the sediment and expose the dormant stages to the surface, such as watering cattle, birds and other large mammals (Brendonck and De Meester 2003). The reduction of dormant stages along the sediment depth of wetlands also is important in terms of conservation and restoration. The existence of dormant stages in the deepest parts of the sediment can be fundamental for the resilience of aquatic invertebrates when the dormant forms of the surface sediment are compromised with environmental impact.

A greater richness and abundance of invertebrate hatchlings were observed in the top layers of sediment (up to 10 cm). Our results demonstrate that the hatching rate of invertebrates decreases with depth in sediments from temporary wetlands. These results help to understand the dormancy breaking strategies of aquatic invertebrates that produce dormant stages in temporary wetlands, and they are important to understand the recovery capacity of dormant community from different sediment strata after drought events. As intermittent wetlands are extremely susceptible to climate variations, the results help to show the resilience of drought resistant communities in the face of unstable hydrological dynamics of these ecosystems.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s13157-023-01675-6>.

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Author Contributions Pedro Henrique de Oliveira Hoffmann, Cristina Stenert and Leonardo Maltchik contributed to the study conception, design and writing – first draft, review and editing. Field and laboratory work were performed by Allana Gonçalves Piu, Lidiane Martins, Vinicius Weber and Daiane Vendramin. Data analysis were performed by Cristina Stenert, Pedro Henrique de Oliveira Hoffmann and Andressa Adolfo. Funding acquisition, project administration and supervision were performed by Cristina Stenert and Leonardo Maltchik. All authors read and approved the final manuscript.

Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Code Availability Not applicable.

Declarations

Statements and Declarations Funding.

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Conflict of interest/Competing Interests The authors declare no conflict of interest regarding this publication. The authors have no relevant financial or non-financial interests to disclose.

Ethics Approval We declare that data collection complied with the current Brazilian environmental laws (SISBIO 36365-2).

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