

Endozoochory by an ilyophagous fish in the Paraná River floodplain: a window for zooplankton dispersal

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Abstract Fish can have an important role in the passive dispersal of freshwater zooplankton. In the Paraná River system the migratory fish *Prochilodus lineatus* (Valenciennes) constitutes about 60% of the fish biomass, the adult individuals have an ilyophagous feeding mode adapted to feed on soft bottom sediments. We hypothesize that *P. lineatus* ingests resting stages of zooplankton along with bottom sediments and that these resting stages are able to hatch after passing through the digestive tract. Forty adult *P. lineatus* individuals were caught in a lake located in the floodplain of Middle Parana River. Content of the last part of intestine was removed and divided into two equal portions and stored (3 months) at 4°C and at room temperature. Later, both portions were incubated for 27 weeks at 25°C. Hatching was controlled at 4-day intervals during the first 9 weeks of the experiment and later less frequently. At the end of the experiment, 8016 individuals were recorded, belonging to 18, mostly littoral species (15 rotifers, 2 cladocerans, and one copepod). Incubation preceded

by a cooling period resulted in hatching of more species and individuals. Our results show that migratory fish may be an important vector for zooplankton dispersal.

Keywords *Prochilodus lineatus* · Zooplankton dispersal · Endozoochory · Resting stages

Introduction

The dispersal of individuals plays an important role in shaping the diversity, structure, and dynamics of aquatic communities. For example, species that occupy temporary habitats may be regulated by traits related to special dynamics such as dispersal (Harrison & Taylor, 1997), and evidence exists that dispersal is significant for species interactions (Bilton et al., 2001; Havel & Shurin, 2004). This is a basic component of the metacommunity concept, defined as a set of local communities linked by the dispersal of potentially multiple interacting species (Wilson, 1992; Leibold et al., 2004).

In floodplain river systems, hydrological connectivity, activated by flood pulse, has considerable influence on the exchange of material between the main river channel and the floodplain (Junk et al., 1989) and is also an important force in the dispersal of zooplankton organisms whose active locomotion is limited. However, zooplankton populations may also be spatially dispersed as resting stages. Indeed, resting

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eggs can remain viable over extended time periods in water body (Hutchinson, 1967; Brendonck & De Meester, 2003).

It has been found that the wall structure of the resting eggs enables them to withstand extreme environmental conditions (Gyllström & Hansson, 2004). The pool of resting stages deposited on the bottom of the lakes constitutes the so-called 'egg banks' (Hairston et al., 1995) that may hatch in the water body or be transported to a new location, so the dormant stages may also constitute an efficient component of dispersal in time (Havel & Shurin, 2004). Experimental studies show that the dispersal of zooplankton resting stages may include hydrochory (Shurin & Havel, 2003), anemochory (Cáceres & Soluk, 2002), antropochory (Duffy et al., 2000), and zoochory (Proctor et al., 1967; Mellors, 1975; Jarnagin et al., 2000).

The process of dispersal by fish (Ichthyochory) has mostly been studied in relation to seed dispersal (Cook, 1988; Correa et al., 2007; Pollux, 2011), and the studies suggest that this dispersal mechanism may play a significant role in the spatial distribution of aquatic and riparian plants. In contrast, ichthyochory, as a dispersal mode for zooplankton, has not been extensively studied. Therefore, the information of this process is more limited (Simberloff & Rejmanek, 2010), and the researches were only performed on planktivorous and carnivorous fish (Mellors, 1975; Jarnagin et al., 2000).

Mellors (1975) observed that *Daphnia ephippia* were able to survive digestion by fishes, their main dispersal agent thus being fish-eating birds and mammals. On the other hand, Jarnagin et al. (2000, 2004) showed that resting eggs of the cladoceran *Bythotrephes* survived passage through fish guts, promoting its dispersal. For rotifers, one of the most important groups of freshwater zooplankton, successful hatching of resting stages after passage through the digestive tract of vertebrate animals has not yet been demonstrated (Segers & De Smet, 2008).

In the floodplain of river systems, fishes may act as good vectors of dispersal of dormant zooplankton stages, mainly those that feed on the organic matter present in the mud (ilyophagous) and those that feed on active zooplankton (zooplanktophagous). Ilyophagous fishes belonging to the genus *Prochilodus* Agassiz (Characiformes, Prochilodontidae) are widely distributed in South America (Leccia, 1972), particularly

in the La Plata River basin, the second largest basin in South America (Del Barco et al., 2007).

In this systems, *Prochilodus lineatus* (Valenciennes) represents the most abundant fish species and constitutes about 60% of the total fish biomass (Bonetto et al., 1969; Espinach Ros & Fuentes, 2000). Its life cycle is considered to be an adaptation to the environmental changes produced by the flood pulse, which is the main structuring force of the Middle Paraná River system (Bayo & Cordiviola de Yuan, 1996; Del Barco et al., 2007). At its early developmental stage, *P. lineatus* is zooplanktophagous (Rossi, 1992) but shifts to an ilyophagous feeding mode as an "adult" and is thus morphologically and functionally adapted to feed on soft bottom sediments (Angelescu & Gneri, 1949). Another important factor of dispersal is the extensive migration of *P. lineatus* along the river, upstream for reproductive purposes and downstream for food seeking during which it enters the lakes of the floodplain (lateral migration) (Bonetto et al., 1981; Tablado & Oldani, 1984; Bonetto & Castello, 1985).

Being a key species and due to its status as trophic web support, ilyophagous *P. lineatus* plays an important role in the bioeconomy of aquatic systems by exploiting an important part of the organic matter deposited in the sediment, thus acting as an extractor of organic detritus and accumulator of these in your stomach (Angelescu & Gneri, 1949; Bowen, 1983). These special features of the behavior and life cycle of *P. lineatus* may allow it to act as a potential vector in the endozoochoric dispersal of zooplankton resting stages found in the bottom sediment. Knowledge of the role of *P. lineatus* as a vector for zooplankton dispersal may help us to understand the integrative and sustaining mechanisms of the diversity of metacommunities in intricate ecological systems such as tropical and subtropical floodplains.

Our aims were (i) to analyze the possible role of *Prochilodus lineatus* as a dispersing vector of zooplankton via its ingestion of zooplankton resting stages present in bottom sediments, (ii) to test two methods of storage of gut contents prior to incubation, and (iii) assessment of the habitat membership (limnetic/littoral) of hatched species. We hypothesized that: (i) *P. lineatus* ingests zooplankton resting stages along with bottom sediments and that (ii) the resting stages may hatch after passing through the digestive tract of the fish; (iii) hatched species are mainly limnetic.

Materials and methods

Field sampling

Specimens of *P. lineatus* were caught using a multi-filament nylon gill net (25 × 2 m) of mesh size 80 mm in October 2011 in Lake Feller (31°10′27.40″S, 60°1′59.60″W) located in the Santa Fe Province (Argentina). This is a semi-lentic water body belonging to the Middle Paraná River floodplain and connected to the main channel (Fig. 1). The Middle Paraná River system, including the main channel and the floodplain, with a surface area of 21,000 km², constitutes an important part of the La Plata River basin (Iriondo, 1993).

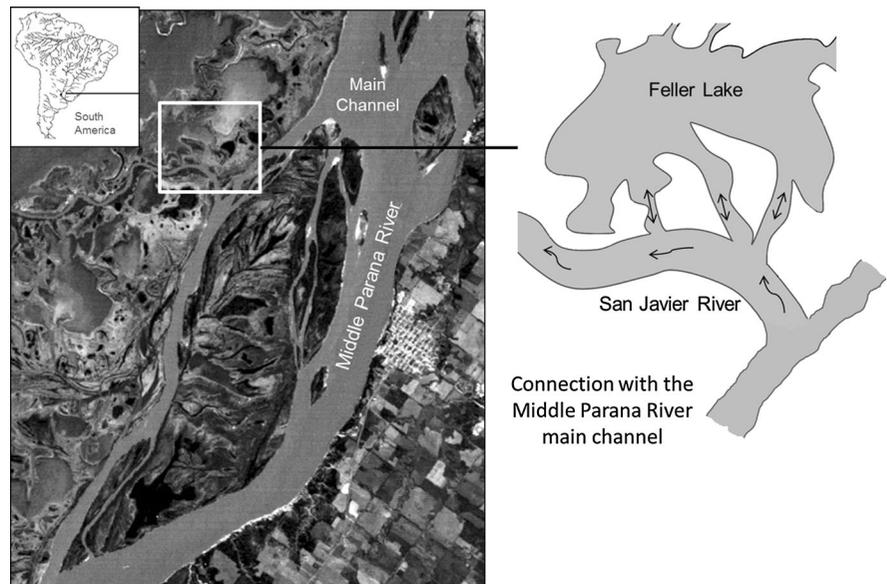
Only adults and young specimens (> 13 cm) were selected for this study since at these levels of ontogenetic development the diet is constrained to organic matter of bottom sediments (Angelescu & Gneri, 1949; Rossi, 1992). The selected individuals had a standard length of 13–47 cm (mean = 28.95 ± 7.16 cm) and weighed 68–3640 g (mean = 910.85 ± 812.90 g).

The complete digestive system was dissected and placed on ice for transportation from the field to the laboratory. Half of the 40 selected specimens had empty intestines, leaving intestine contents from 20 individuals for experimental analysis.

Hatching experiment

We used the ex situ emergency assessment method (Brendonck & De Meester, 2003; Torres & Zoppi de Roa, 2010) to estimate the amount and composition of the pool of zooplankton dormant stages in the gut contents of *P. lineatus* and the dispersal of zooplankton. The emergency assessment method is commonly used to study egg banks in sediments (Garcia Roger et al., 2008). The method generally involves two steps: storage and incubation; but also other factors, such as time, light, and temperature, may be relevant. Several authors have successfully used a methodology including a cold storage period (Vandekerkhove et al., 2005; Palazzo et al., 2008; Allen, 2010; Santangelo et al., 2011). However, it must be emphasized that some studies of zooplankton resting stages using the cold storage methodology did not find a high diversity of cladocerans and copepods in tropical and subtropical environments, as compared with those found in active population in the same habitat (Maia-Barbosa et al., 2003; Palazzo et al., 2008; Battauz et al., 2014). Due to the absence of methodological consensus, in this study we used two different methods of storage for the purpose of comparison. In the laboratory, we extracted the bottom sediment content of the last part of the intestines, which is fecal matter waiting to be expelled.

Fig. 1 Location of Lake Feller in the floodplain of the Middle Parana River, Santa Fe, Argentina



The sediment was placed in plastic circular trays (38.47 cm², each) and covered with a gauze disk in order to prevent contamination by outside particles or organisms after which the sediment was dried at room temperature for 16 days. After drying, the intestine contents were divided into two equal parts which were then subjected to different storage treatments: cold dark (CD) where the gut contents of 10 *P. lineatus* specimens were stored in opaque boxes and kept in a refrigerator (4°C) for 3 months and ambient dark (AD) where the gut contents of 10 *P. lineatus* specimens of were stored in opaque boxes at room temperature for 3 months (\cong 21°C).

The CD and AD treatments were applied to 18.8 and 22.5 g intestinal content, respectively, with ten replicates for each treatment. Each tray contained the intestinal content of one individual and was covered with 2–3 cm of sterile water from Lake Feller (first filtered through a 20- μ m mesh and then boiled). The trays were placed in an incubator at 25°C with a dark:light photoperiod of 8:16 h. The photoperiod used for the experiments is similar to that of the summer time in the region. Afterwards we controlled hatching at 4-day intervals for 9 weeks, the experiment being continued for 18 weeks where recordings were made every 25 days to record any late hatchlings. The supernatant water in the trays was filtered using a 20- μ m mesh and mixed in a single sample fixed in 10% formalin.

The temperature of the hatching experiment was set to 25°C because the temperature in the region is relatively high during summer. During the last 30 years, from December to March, average regional temperature, has ranged between 23.1 and 29°C.

The samples were stained with erythrosine and analyzed under an optical Nikon Eclipse (E100) microscope. Analyses of abundance and richness of hatchlings were carried out in a 1-ml Kolwicz cell. Taxonomic determinations were made using the keys mainly; Koste (1978) and Segers (1995) for Rotifera, Korovchinsky (1992) and Kořínek (2002) for Cladocera and, Battistoni (1995) and Alekseev (2002) for Copepoda.

Data analysis

Similarity of taxonomic composition of hatchlings between the two storage treatments was calculated using the Jaccard similarity index (Magurran, 1988) and Sørensen index (quantitative) (Sørensen, 1948). The

species with the greatest contribution to dissimilarity between treatments were determined using the SIMPER analysis (Clarke & Warwick, 1994), and the non parametric multivariate analysis of variance (NPMA-NOVA) was used to elucidate if those differences found in the SIMPER analysis were statistically significant.

The limnetic and littoral species listed were separated (Shiel et al., 1982; own knowledge of the regional fauna). A Chi square (χ^2) test was used to assess heterogeneity among storage treatments regarding the relative abundance of hatchlings of littoral and limnetic species. Accumulation curve of species hatched in both treatments was calculated.

The index for timing of hatching (ITH) was calculated to assess the incubation time (days) required to break the resting phase of each specific taxon (Vandekerckhove et al., 2004). Statistical analyses were performed using the Past 2.14 statistical package (Hammer et al., 2001).

Results

During the 193 incubation days of both treatments, a total of 18 taxa, 14 Rotifera Monogononta, 1 Rotifera Bdelloidea, 2 Cladocera, and 1 Copepoda were recorded. In the CD storage treatment a total of 17 taxa, 13 Rotifera Monogononta, 1 Rotifera Bdelloidea, 2 Cladocera, and 1 Copepoda were hatched, while in the AD storage treatment a total of 13 taxa, 11 Rotifera Monogononta, 1 Rotifera Bdelloidea, 1 Cladocera, and no Copepoda were hatched (Table 1).

In the CD treatment, the dominant species were, in decreasing order of rank, *Lecane inermis*, *Cephalodella* sp., *Colurella* sp., *Lepadella* sp., and *Lecane nana*, constituting 94% of the individuals hatched out of a total of 6481 hatchlings.

In the AD storage treatment in decreasing order of rank *Cephalodella* sp., *Lepadella* sp., *L. nana*, *L. inermis*, and *Colurella* sp. showed higher abundance, representing 90% of the individuals that hatched out of a total of 1535 hatchlings. In both the treatments the rotifers dominated (> 96% of the total hatch). As depicted in Fig. 2, almost all species were more abundant than in the AD treatment.

There is close similarity in the composition of hatchlings between the two treatments (Jaccard Index: 0.7). However, if we analyze the abundance of species hatched the similarity between treatments is low

Table 1 Zooplankton species hatched in the treatments (+ presence, – absence)

Taxa	Treatments	
	Cold-dark (CD)	Ambient-dark (AD)
<i>Anuraeopsis</i> sp.	+	–
<i>Brachionus angularis</i>	+	+
<i>Cephalodella</i> sp.	+	+
<i>Colurella</i> sp.	+	+
<i>Epiphanes macroura</i>	+	–
<i>Keratella</i> sp.	+	–
<i>Lecane bulla</i>	+	+
<i>Lecane closterocerca</i>	+	+
<i>Lecane inermis</i>	+	+
<i>Lecane lunaris</i>	–	+
<i>Lecane nana</i>	+	+
<i>Lecane cf. nana</i>	+	+
<i>Lecane obtusa</i>	+	+
<i>Lepadella</i> sp.	+	+
<i>Bdelloidea</i>	+	+
<i>Eucyclops neumani</i>	+	–
<i>Coronatella poppei</i>	+	+
<i>Anthalona</i> sp.	+	–

(Sørensen index: 0.4). The SIMPER analysis showed that the dissimilarity was 60% (NPMANOVA: $F = 2.59$, $P = 0.038$), being six species (*Cephalodella* sp., *L. inermis*, *Lepadella* sp., *L. nana*, *Colurella*

sp., *Coronatella poppei*) (Table 2) responsible for 77% of total dissimilarity.

Moreover, both treatments recorded higher hatching of littoral than of limnetic species (Fig. 3) ($\chi^2 = 9.267$, $P = 0.002$). In the AD storage treatment a significant number of species broke their dormancy in the early stages of incubation, approximately before day 28. From this day onwards, there was an increase in species hatching in the CD treatment which behaved similar to the AD treatment, being stable with small variations until the completion of the experiment. However, accumulation of species was higher in the CD treatment. Richness was on average 5.1 ± 2.3 species per sampling in the CD treatment and 4.3 ± 2.0 in the AD treatment (Fig. 4).

The calculation of ITH showed no statistical differences in the zooplankton species between treatments ($t = 1.54$, $P = 0.13$), however some species suggested to be affected by the treatment types, regarding timing of hatching and the abundance (Table 3) (Fig. 5).

Discussion

Zooplankton eggs in bottom sediments and passage through fish guts

The zooplankton resting stages cannot only be ingested by ilyophagous *Prochilodus lineatus* but are able to maintain their hatching viability. Hence, an important

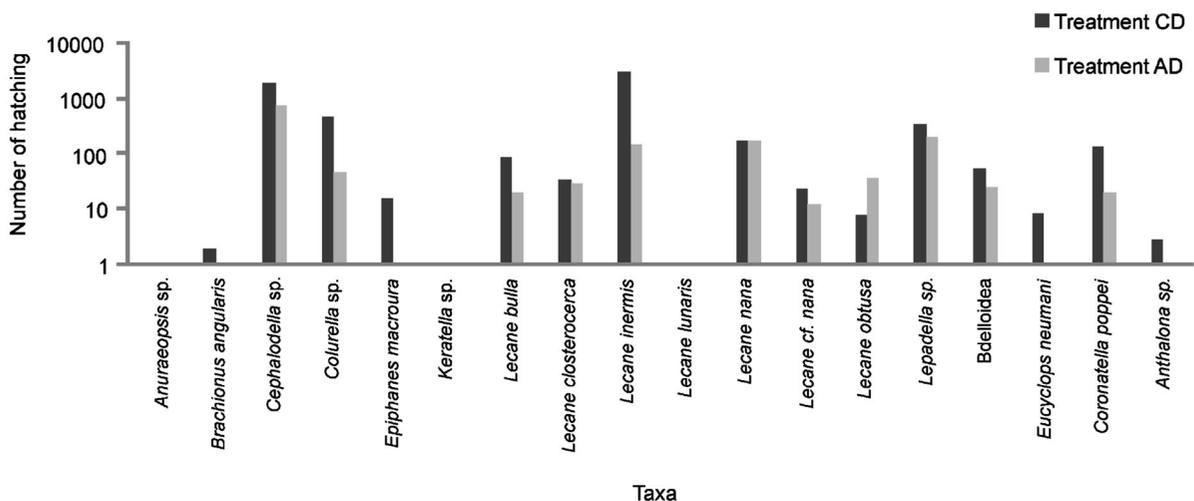
**Fig. 2** Taxonomic composition and abundance (log) of the hatching in cold-dark (CD) and ambient-dark (AD) storage treatments

Table 2 Simper analysis: average abundance of species contributing to dissimilarity (cut-off: 90%)

Taxon	Average dissimilarity	Contribution %	Cumulative %
<i>Cephalodella</i> sp.	29.90	36.72	36.72
<i>Lecane inermis</i>	16.65	20.45	57.17
<i>Lepadella</i> sp.	10.42	12.77	69.94
<i>Lecane nana</i>	7.25	8.90	78.84
<i>Colurella</i> sp.	4.79	5.88	84.72
<i>Coronatella poppei</i>	4.18	5.13	89.85

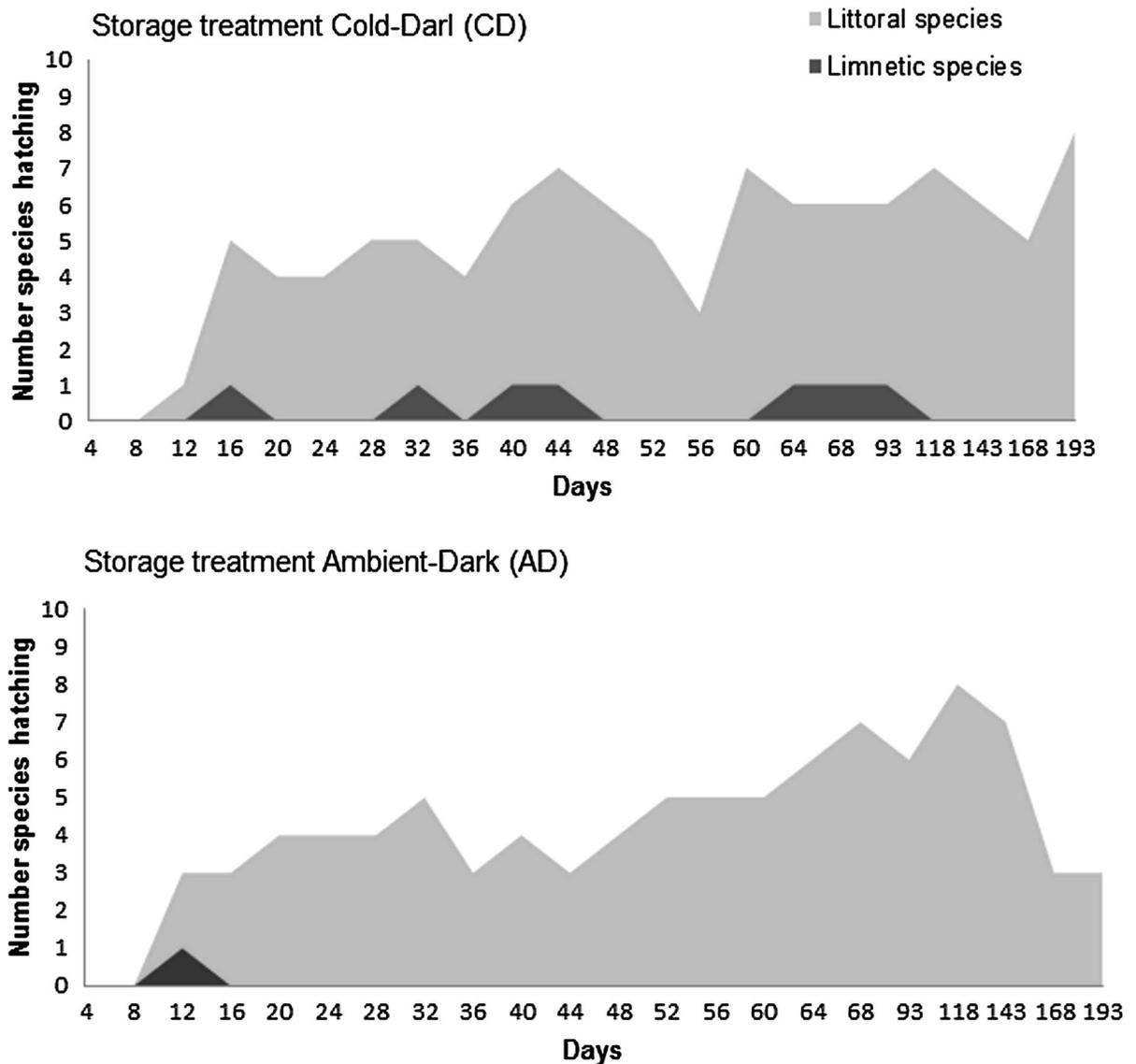


Fig. 3 Number of hatching of the littoral and limnetic species in cold-dark (CD) and ambient-dark (AD) storage treatments during incubation

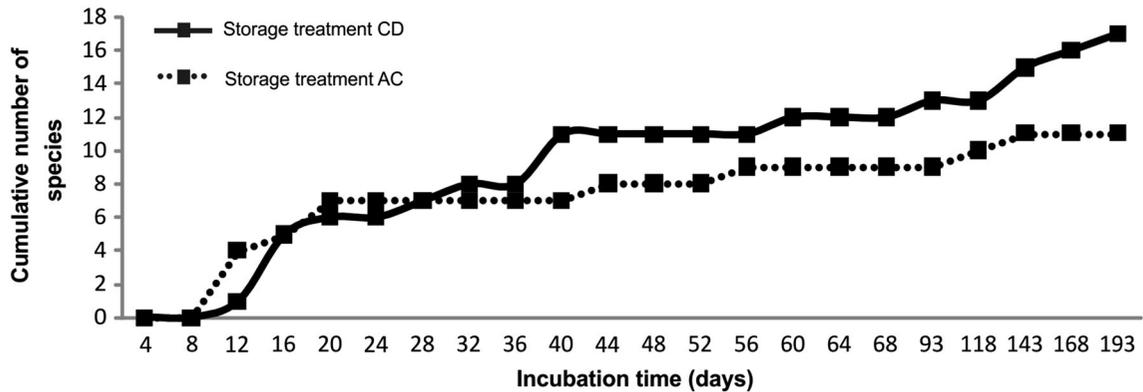


Fig. 4 Cumulative richness of hatched species in cold-dark (CD) and ambient-dark (AD) storage treatments

Table 3 Index for timing of hatching calculated for species hatched in cold-dark (CD) and ambient-dark (AD) storage treatments

Species	Index for timing of hatching (days)	
	Treatment CD	Treatment AD
<i>Anuraeopsis</i> sp.	93	0
<i>Brachionus angularis</i>	16	12
<i>Cephalodella</i> sp.	35	40
<i>Colurella</i> sp.	24	23
<i>Epiphanes macroura</i>	50	0
<i>Keratella</i> sp.	32	0
<i>Lecane bulla</i>	111	118
<i>Lecane closterocerca</i>	71	68
<i>Lecane inermis</i>	23	33
<i>Lecane lunaris</i>	0	143
<i>Lecane nana</i>	60	90
<i>Lecane cf. nana</i>	149	80
<i>Lecane obtusa</i>	184	125
<i>Lepadella</i> sp.	86	75
<i>Bdelloidea</i>	39	22
<i>Eucyclops neumani</i>	162	0
<i>Coronatella poppei</i>	92	102
<i>Anthalona</i> sp.	193	0

number of resting stages present in bottom sediments may survive in the gut passage of *P. lineatus*. This is likely due to the strong structure of the egg walls (Gyllström & Hansson, 2004) as well as the digestive physiology of this fish whose pyloric stomach helps food compaction and removes the water in the sediment (Bonetto et al., 1989) and the cardiac

stomach whose main function being food storage (Bowen, 1983) (Fig. 5).

The number of species hatched from fish gut contents was remarkably high in comparison with the number recorded from the dispersal studies of other vertebrates using similar methodologies of storage and incubation. Jenkins & Underwood (1998) collected duck feces in Washington Park Pond (Milwaukee County, Wisconsin, USA), which was refrigerated for 7 days and incubated at 20°C. No zooplankton species appeared in the incubated feces. However, previous studies involving water flows under controlled laboratory conditions demonstrated different results (Proctor, 1964; Mellors, 1975). Jenkins & Underwood (1998) suggests that such events of hatching are not common and that natural dispersal depends on factors such as ingestion of viable propagules, survival of propagules in the gut, transport from one site to another within the gut passage, and deposition times. Previous studies have evidenced that resting stages are resistant to consumption by planktivorous and carnivorous fish (Jarnagin et al., 2000, 2004). In this sense, Mellors (1975) reported selective ingestion of *Daphnia* ephippia by *Lepomis gibbosus* (Linnaeus) and *Perca flavescens* (Mitchill) in the Fuller Pond (Massachusetts, USA), the *Daphnia* having a hatching success of 1.5% following passage through the guts. On the other hand, in an experiment conducted by Jarnagin et al. (2000) on controlled laboratory feeding experiment involving storage at 4°C and incubation at 10°C, removal of 61 mature resting eggs of the cladoceran *Bythotrephes cederstroemi* from fish fecal pellets of *L. macrochirus*, *Micropterus dolomieu*, and *P. flavescens* (Michigan Lake, USA) resulted in development of 57% and hatching of 41% of the resting eggs.

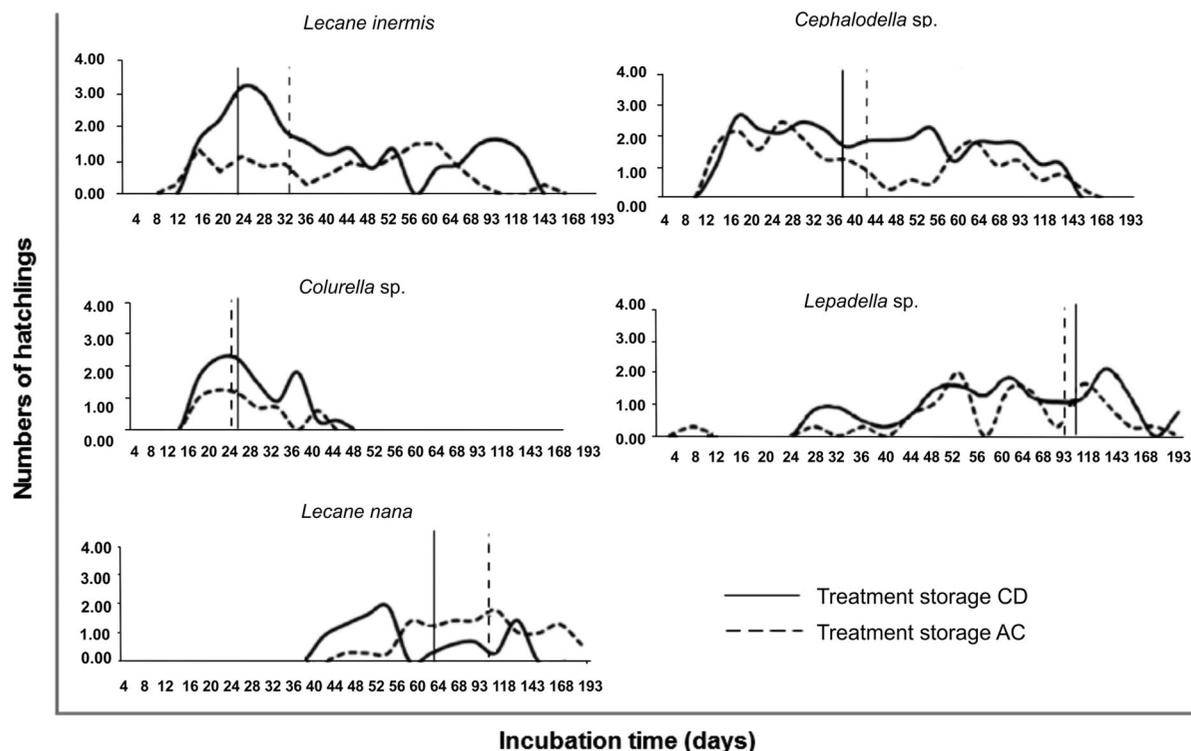


Fig. 5 Analysis of the hatchings and abundance of the most common species per storage treatment. The index for timing of hatching (ITH) proposed by Vandekerckhove et al. (2004) was calculated; the *parallel lines* representing the ITH of the species

of the cold-dark (CD) treatment and the *parallel dashed lines* represent the ITH of the species of the ambient-dark (AD) treatments

Also, in another laboratory experiment Jarnagin et al. (2004) found that out of 113 mature resting eggs of *B. cederstroemi* consumed by *P. flavescens*, *L. macrochirus*, *L. gibbosus*, and *M. dolomieu* 94% survived gut passage. It should be noted, though, that none of the studies on survival of gut passage were assemblage based (including the rotifers, copepods, and cladocerans) but used only a single planktonic species preyed upon by fish.

The results of our study suggest that the survival of zooplankton resting stages after passage through the fish gut could be important for dispersal via *P. lineatus* migration and that, this migratory ilyophagous fish may widely disperse zooplankton resting stages.

Hatching of zooplankton and treatment effects

The results of our laboratory study show that diversity and abundance of zooplankton species are affected by the storage conditions of the gut contents prior to exposure. The highest richness and abundance were

found in the assemblage of zooplankton hatchlings from gut content kept under cold-dark conditions. The high abundance of rotifers hatching during the experiment may be due to in situ reproductive events that take place over a period of 4 days at 25°C (Edmondson, 1965). Similarly, studies undertaken by Chittapun et al. (2005) on rotifers in dried sediments in Thailand, exposed to similar storage conditions for a 2-year period, recorded 15 species after cold-dark treatment and 9 after ambient-dark treatment. The authors argue that the effect of exposure conditions only becomes significant after 6 months; however, we found that an effect can in fact be observed after three months. It should be noted that in both treatments the highest abundance and species richness were recorded for rotifers. Moreover, the hatching of cladocerans and copepods was clearly favored by the exposure of gut contents to cold-dark storage. In the case of copepods, cold storage appeared to be critical for emergence as they were only recorded after exposure to this stimulus.

The emergence of cladocerans was very low, particularly seen in the light of the current knowledge of the cladocerans fauna in the Argentinean Parana River basin, which holds 42 genera and about 100 species of Anomopoda and Ctenopoda (Paggi, 2004). Studies on sediments from the wetlands of floodplain river systems in Brazil and Argentina performed by Maia-Barbosa et al. (2003), Palazzo et al. (2008), and Battauz et al. (2014) also recorded a low hatching rate of cladocerans. The preincubation treatment involving drying and exposure to low temperature was a suggestion as an explanation of this, but such behavior in relation to temperature was not observed in our experimental hatching of intestinal contents, and we observed that cold-dark conditions allow for the hatching of rotifers, copepods, and cladocerans.

The dominance of littoral species in the gut content of *P. lineatus* is seemingly related to its feeding habits. It often feeds in very shallow waters, < 30 cm deep, potentially due to the high nutritional value of shallow water detritus (Bowen, 1983). Another possible interpretation of our results is that littoral species are more likely to survive the passage through the digestive tract or respond more readily to hatching stimuli; this result may be caused by multiple factors as temperature, photoperiod, water pH, oxygen, nutrients, and bacteria not feasible to respond. Regarding the timing of hatching of the different species in the two treatments, suggestions have been forwarded that cool and dark conditions extend the diapause and increase the viability of stored resting eggs, thus preventing degradation of compounds and inhibiting bacterial development that may damage the resting eggs (Chittapun et al., 2005).

Our study provides significantly supports the hypothesis that ilyophagous fish *P. lineatus* may act as a dispersing vector of zooplankton by its ingestion of zooplankton resting stages present in bottom sediments. The movement of the fish in the aquatic network of a floodplain allows for passive dispersion of zooplankton, promoting colonization of new habitats and biological connectivity among communities. The theoretical frame of metacommunities provides an interesting conceptual tool for understanding ecological processes which govern the biological complexes inhabiting the floodplains of large rivers (Leibold et al., 2004). Biological connectivity of communities composed by organisms of passive dispersal strongly depends on the existence of dispersing vectors. In floodplains the main mechanism of dispersal for the zooplankton is hydrochory

transporting of the active and passive individuals in the direction of flow, downstream and transversally. Any upstream dispersal is achieved by zoochory carried out mainly by migrating vertebrates which move in that direction, so endozoochory performed by an abundant and active migrating fish, constitutes an important factor in maintaining biological diversity and connectivity of the floodplain complex. Moreover, it have been shown that there is a close relationship between resilience and biological connectivity as well as the important role of some animals in ecosystem processes and organization as dispersal agents (Frank & Wissel, 1998; Montoya et al., 2008; Botsford et al., 2009).

Our experimental results demonstrate that an important number of zooplankton species, mostly rotifers, was able to hatch successfully after passage through the digestive tract of *P. lineatus*. Moreover, we found that incubation at 25°C, preceded by a cooling period, results in hatching of more species and individuals than storage at room temperature without subsequent cooling. Future experimental works in order to analyze the dispersal probabilities should include the assessment of the proportion of viability of the ingested eggs. This task would be particularly difficult, mainly for rotifers and copepods, because of the likelihood of erroneous inclusion of propagules of other organisms. Picking up of resting stages from sediments could be somewhat easier in the case of cladocerans which are, in general, larger and included in more visible structures (ephippium) which are relatively identifiable at level of families, genera, and even species in limited groups. Anyway, future advances in this type of research are largely conditioned by the development of taxonomical tools specifically designed to identify the resting stages of organisms belonging to the local fauna.

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