

RESEARCH PAPER

Passive zooplankton community in dry littoral sediment: Reservoir of diversity and potential source of dispersal in a subtropical floodplain lake of the Middle Paraná River (Santa Fe, Argentina)

Yamila S. Battauz¹, Susana B. José de Paggi^{1,2} and Juan C. Paggi¹

¹ Instituto Nacional de Limnología (CONICET-UNL), Ciudad Universitaria, 3000, Santa Fe, Argentina

² Facultad de Bioquímica y Ciencias Biológicas (UNL), Ciudad Universitaria, 3000, Santa Fe, Argentina

During the low water or contraction phase, the Parana floodplain lakes show a marginal area with the littoral sediments exposed to the air. They were studied as “resting stage bank” and potential zooplankton diversity storage as well as a source of propagules for exozoochoric dispersal by terrestrial and semiaquatic vectors, mainly birds. The aims of the study were to analyze (i) specific composition of the zooplankton hatchling assemblage, (ii) time and hatching pattern of each species, (iii) similarities and differences between hatchlings and active assemblages, (iv) assessment of the habitat membership (limnetic/littoral) of hatched species. Sediment samples were taken from three sites of a representative floodplain lake of Paraná River and hatching experiments were conducted under laboratory conditions at 25°C for 90 days. Twenty-seven species of rotifers and four of cladocerans hatched in the laboratory. Hatchlings (7097 specimens) were recorded (92.4% rotifers, 7.6% cladocerans). The number of hatched species increased significantly from day 4 to day 30, showing oscillating trends and then began to decrease until day 90. Thirty percent of hatched species were unrecorded for the lake, and 12% species were new records for Argentina. Seventy-seven percent of the hatched species were littoral in habit.

Received: November 4, 2013

Revised: November 22, 2013

Accepted: December 6, 2013

Keywords:

Active population / Cladocerans / Resting stage bank / Rotifers

1 Introduction

Zooplankton populations of continental waters produce diapausing stages as an adaptative mechanism that allows them to survive in adverse conditions of aquatic environments [1, 2]. The accumulation of these resting stages in the sediment of lakes produces the so-called “egg banks” which can remain viable for many years [3–6].

The structure and hatching dynamics of resting eggs in the sediment would be determined by life history of the

species, hatching phenology, habitat, and microhabitat characteristics [2]. Moreover, timing and amount of egg production can be related to loss by senescence rate, predation, disease, and dispersal [7].

These dormant propagules not only allow the permanence in time of different species of rotifers, copepods, and cladocerans in the same aquatic body, but they also represent an efficient dispersal mechanism. The wall structure of diapausing eggs enables them to withstand extreme physical conditions [8], to persist in lake sediments over several years [9] or to be transported by different dispersal vectors, water, wind, anthropogenic activities, and animals [10–13]. Probably one of the most important dispersal mechanisms is exozoochory, which is carried out mainly by birds transporting resting stages attached to the feathers, legs, and feet [14].

River floodplains are very dynamic systems in which the degree of hydrological connectivity between their structural

Handling Editor: Norbert Walz

Correspondence: Lic. Yamila S. Battauz, Instituto Nacional de Limnología (CONICET-UNL), Ciudad Universitaria, 3000 Santa Fe, Argentina

E-mail: yamilabattauz@gmail.com

Fax: 54 342 4511645

components depends upon the seasonal changes in the level of water [15]. Zooplankton communities of the lotic and lentic components of these complex hydrological systems are connected by dispersal to form metacomunities. As ecological systems, river floodplains have a characteristic functional feature, which is the flood pulse or expansion–contraction cycle [16]. According to the Flood Pulse Concept [17], dispersal of organisms would occur during the high-water period with the expansion of the river network, when the main channel is well connected with the floodplain. During the low-water phase (contraction phase) as the water recedes, the areas of the floodplain called the aquatic/terrestrial transition zone (ATTZ) become unsubmerged so that soil and sediment remain partially dried or muddy, important repositories of resting eggs produced during the aquatic phase [18]. The marginal areas of the lakes are frequented by a number of terrestrial vertebrates, mainly birds, which walk and collect their food from the ground. Birds belonging to the “walkers” ecological guild [19] are frequent and abundant in the floodplains of South American rivers. In the Parana River during low waters, they constitute about 38% of total birds [20]. Therefore, egg banks in the wet and dry sediments of the shores frequented by birds represent a reservoir of zooplankton species that can potentially serve for the colonization of new habitats via transport in feet or feathers.

The analysis of the composition of egg banks from zooplankton has proved to be an important tool for biodiversity studies [21] because it is a complement for water column composition studies, due to in most cases, the comparison of active and inactive phase composition reveals that the species do not overlap completely [22].

The shallow lakes on floodplain of the Paraná River are a great reservoir of zooplankton diversity [23]. However, their richness has been evaluated only through the analysis of water column populations. In this study, we try to assess, from hatchlings, the egg bank richness of dry littoral sediments for the first time in these freshwater

habitats, as zooplankton diversity storage and potential source of propagules available for dispersion by external vectors, especially waterfowl. The aims of the study were to analyze (i) specific composition of the zooplankton hatchling assemblage, (ii) time and hatching pattern of each species, (iii) similarities and differences between hatchlings and active assemblages, (iv) assessment of the habitat membership (limnetic/littoral) of hatched species.

2 Methods

2.1 Study site

The freshwater habitat studied is located in the Ecological Reserve of the University Campus, Santa Fe, Argentina (31°37'S, 60°41'W), characterized by a rich fauna of birds, of which 164 species have been recorded [24]. It is a permanent floodplain lake (Paraná River basin) of 12 hectares and a maximum depth of 1.70 m. In periods of flooding, it first receives groundwater inputs, and later the indirect inputs from the Paraná River through nearby water bodies. Duration of flooding in the Paraná River system is highly fluctuating, in our study the high water period began in November 2009 and lasted until June 2010. The range of river hydrometric level was about 5 m. During the low water period, a littoral fringe (area of 970 m²) without vegetation located at the southern part of the lake remains with the bottom sediments exposed to the air (Fig. 1).

The littoral area of the lake supports a moderate to poor cover of aquatic plants, composed primarily by the emergent *Panicum elephantipes* Nees and *Cyperus alternifolius* Linn., and small mats of the free-floating plant *Eichhornia crassipes* (Mart.) Solms. The main physico-chemical characteristics of the water are the following: Secchi disk 0.12–0.70 m, pH 6.89–9.75, conductivity 245–1584 μ S/cm; this lake is considered eutrophic because of its nutrients contents and phytoplankton

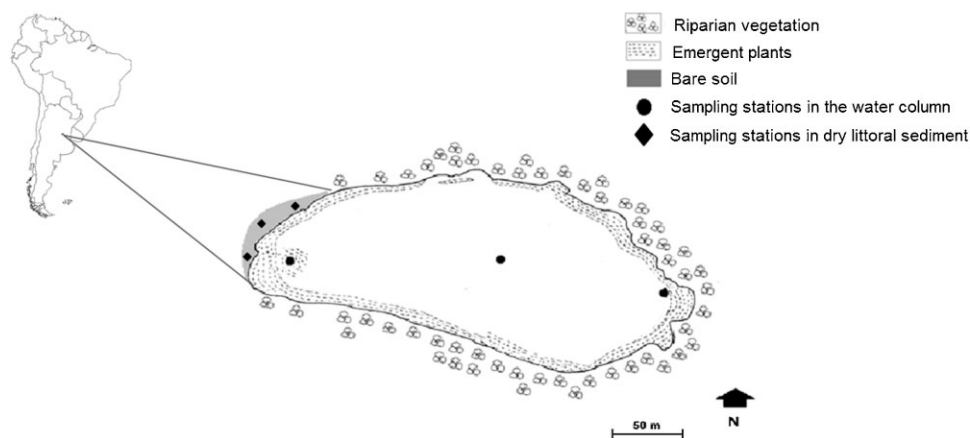


Figure 1. Location of studied lake in the floodplain of the Middle Parana River, Santa Fe, Argentina.

abundance [[25] and Frau et al. unpublished]. Previous studies recorded dominance of rotifers in the zooplankton assemblage of the lake and the presence of abundant small fish species (<70 mm), mainly Characidae [25].

2.2 Sediment sampling and incubation experiment design

To assess the hatching of the zooplankton resting stages, we used the emergence assessment method *ex situ*, that provide an estimation of the number of animals contributing to population recruitment from the egg bank in the sediment [1, 22].

Sediment samples were collected during the summer 2011 from the exposed surface sediment (<10 cm deep) at 3 equidistant points on the shore of the lake along a transect (50 m long approximately) parallel to the shoreline. The collections were then composited and thoroughly mixed and dried at 21°C for 48 h. Afterwards, they were stored in the dark at 4°C for 7 months [21]. After storage in the refrigerator, the sediments were exposed to room temperature for 3 h. A total of 15 subsamples (20 g each) were incubated in plastic trays, (165 cm² of surface, each tray), covered by 2–3 cm of sterile water (filtered from the lake, with a 20 µm mesh and brought to boil). Trays were placed in an incubator at 25°C with a dark:light photoperiod of 8:16 h. We controlled for hatchlings at 3 days-intervals for 90 days. The supernatant water of the all trays was filtered using a 20 µm mesh and mixed in a single sample fixed in 10% formalin.

The storage temperature was determined considering that the winters in the region have very low temperatures (the minimum monthly the last 30 years varied between 3.7 and 10.3°C, data from CIM, Universidad Nacional del Litoral, the timing experience was of 90 days, Chitapum et al. [26] observed that no additional species were found to hatch after 3 months, besides the warm period in the region lasts more than 3 months. The emergence experiment temperature was selected because during the warm season temperatures in the region are very high (monthly averages of the last 30 years from December to March, varied between 23.1 and 29°C).

The samples were stained with erythrosine and observed under an optical Nikon Eclipse (E100) microscope. Analyses of abundance and richness of hatchlings were carried out on a 1 mL Kolkwitz chamber. Taxonomic determinations were made using keys of different authors [27–32].

2.3 Water column sampling

The zooplankton was sampled fortnightly between December 2009 and November 2010 at three sites (two littoral and one limnetic) of the lake. In order to collect an

integrated zooplankton sample through the water column of the lake, two or three samples were taken at different depths, with a Schindler-Patalas trap of 30 L capacity, equipped with a 50 µm mesh, and pooled in a composite sample per station. Analyses of abundance, richness and taxonomic determinations were carried out with the same methodology as in dry littoral sediments.

2.4 Data analysis

Taking into account the dominant patterns of hatching, and to make their descriptions easier, the experimental time was divided into four periods, early (E: days 1–21), middle early (ME: days 22–46), middle late (ML: days 47–67) and late (L: days 68–90). The index for timing of hatching (ITH), was calculated according the formula given by Vandekerckhove et al. [33], adapted to our case. Beta diversity was estimated [34] and the similarity between taxonomic composition of the hatching and active community assemblage was calculated using the Jaccard index [34]. Discrimination between limnetic and littoral species was done according to Shiel et al. [35] and our own experience on the regional fauna. The data analyses were performed with software PAST [36].

3 Results

3.1 Composition and abundance

A total of 31 taxa, 26 Rotifera Monogononta, 1 Rotifera Bdelloidea (indetermined) and 4 Cladocerans hatched. Rotifers were represented by *Lecane* (8 spp.), *Cephalodella* (4 spp.), *Brachionus* (3 spp.), *Euchlanis* (3 spp.), *Keratella* (2 spp.), *Lepadella* (2 spp.), *Filinia* (1 sp.), *Epiphanes* (1 sp.), *Colurella* (1 sp.), and *Trichocerca* (1 sp.), Cladocerans by, *Alona* (2 spp.), *Anthalona* (1 sp.), *Karualona* (1 sp.). Copepods were not observed, 77% of the hatched species were littoral, and the rest limnetic.

A total of 7097 hatchlings were recorded. The average number of hatchlings by sampling was 273 (CV = 0.88), the minimum was recorded on day 4 then it rose rapidly to reach the maximum values during the middle of the experimental period (1025 hatchlings at day 39). After this increase, toward the end of the experiment, there was a progressive decrease in the number of hatchlings, (mean = 73, CV = 0.38). From the total of hatchlings, 6555 (92.4%) corresponded to rotifers and 542 (7.6%) to cladocerans. The most abundant species were *Lecane clostercerca* (Schmarda), *Lecane nana* (Murray) and *Lepadella patella* (Müller), followed by Bdelloidea, *Cephalodella paggiae* Koste and Robertson, *Cephalodella cf. tenuior* (Gosse) and cladocerans *Anthalona verrucosa* (Sars), and *Alona glabra* Sars (Fig. 2).

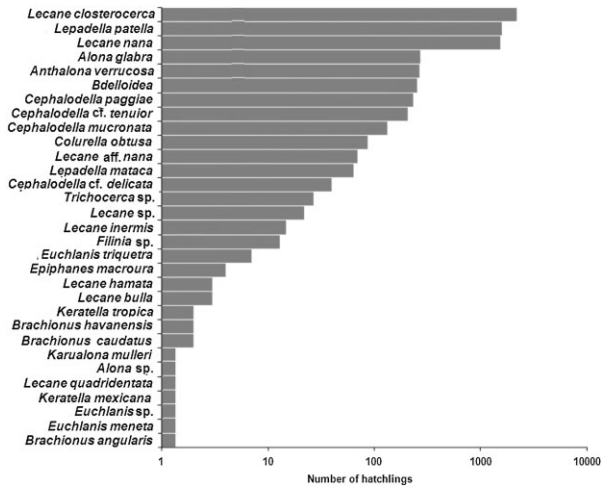


Figure 2. Taxonomic composition and abundance (log) of the hatchlings.

3.2 Richness and hatching timing

The number of hatched species increased significantly, but with some oscillations, from day 4 to day 30, then began to decrease until day 67 when there were no new species. The richness had an average of 7.6 species per sampling (CV=0.27). As it is shown by the beta diversity values (Fig. 3), the species turnover rate was higher at the beginning and the end of the experiment (49 and 43) and lower during the intermediate periods (28 and 23).

Species recorded during the experiment showed varied timings and patterns of hatching. Rotifers were the first to enter in active state; on day 4 hatched a single species hatched, on day 7, seven species. Cladocerans exhibited the first emergence at 15 days into the experiment. A small group of species (*L. patella*, *L. nana*, and *L. closterocerca* and *Bdelloidea*) were present in 69–92% of the samples, and other four species in 38–50% while a half of the total species were recorded on less than four occasions (Fig. 4). 60% species hatched in the E period, 28% in ME, 3% in ML and finally 9% in L.

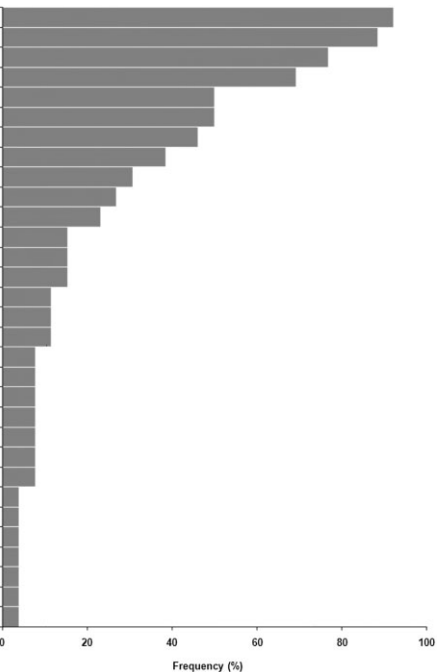
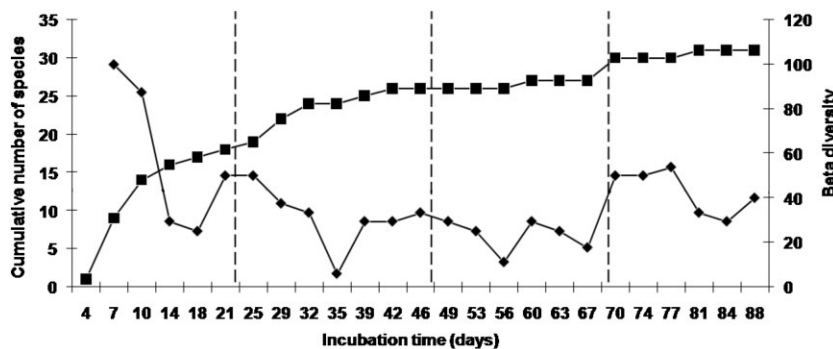


Figure 4. Taxonomic composition and frequency of the hatchlings.

Most of the recorded species, perhaps with exception of *L. patella* with values of abundance and frequency, exhibits moderately well defined monomodal trends with the highest values at different times. Notwithstanding the number of hatchlings of each species these patterns, schematically adjusted to the time periods established in this work, can be perceived in Fig. 5. These patterns can be better visualized in those species with more abundant hatchlings (Fig. 6). The tendency to hatch in the early period, though with some differences, is shown by *Cephalodella mucronata*, *L. closterocerca* and *A. glabra*. A similar situation may be seen for *Cephalodella cf. tenuior*, *L. nana* and *Bdelloidea* for the middle periods and *C. paggiae*, *A. verrucosa*, and *L. patella* for the late period. Even though the last one species was abundant in all the experimental time, it was more abundant in the late period.

Figure 3. Cumulative richness of hatched species and Beta diversity.

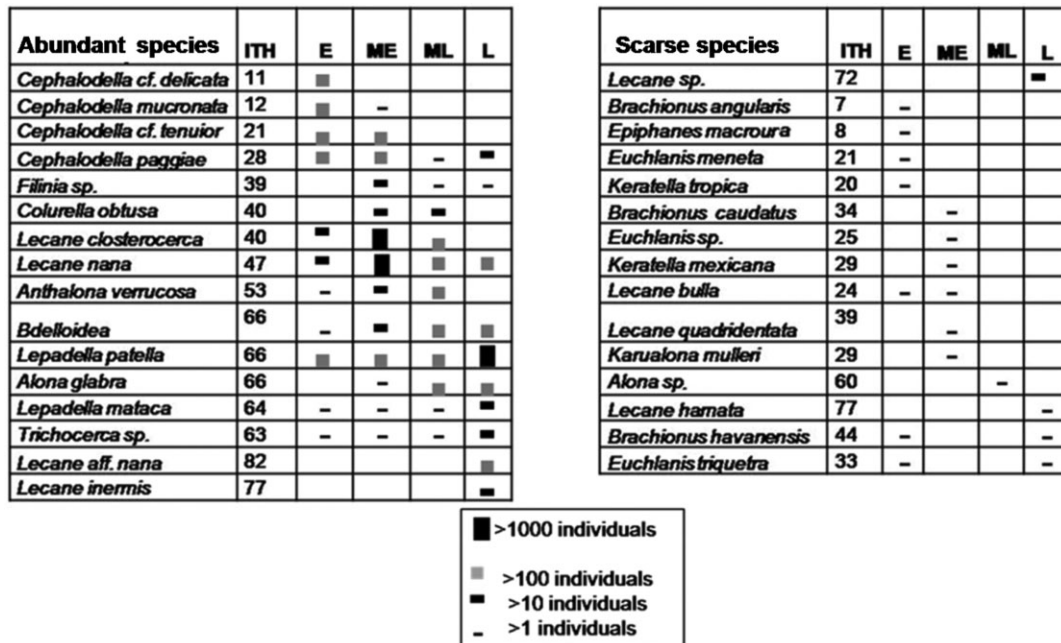


Figure 5. Timing and emergence E, early; ME, middle early; ML, middle late; L, late; ITH, Index for timing of hatching.

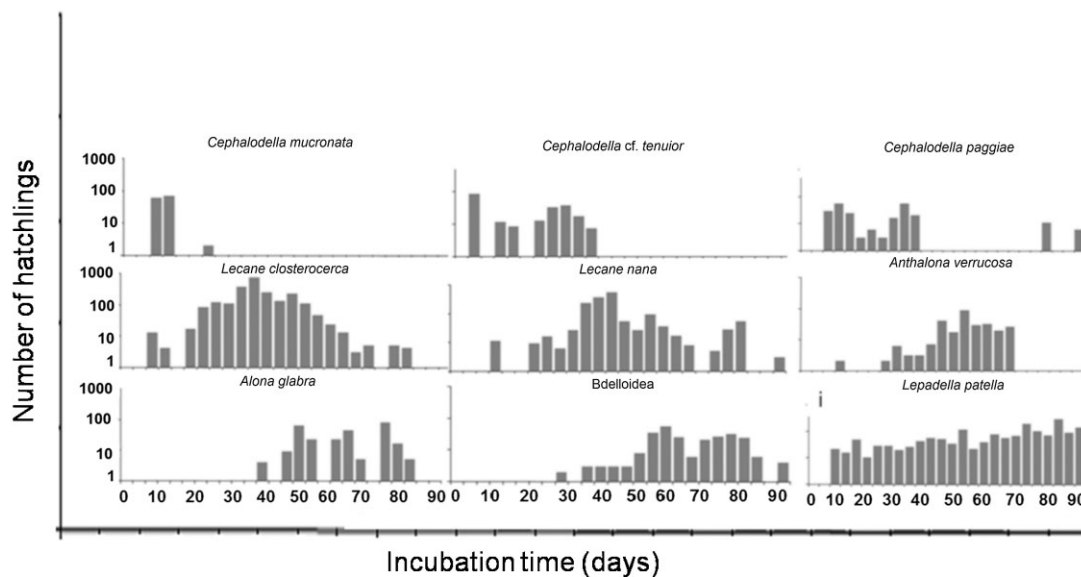


Figure 6. Hatching timing of the most representative species.

3.3 Hatched species assemblage versus active population

The taxonomic composition of the active zooplankton of the lake included 110 species of rotifers, cladocerans, and copepods. The similarity between these and the composition of hatchling assemblages was very low (Jaccard: 0.07) considering the dominant group: The similarity between species of rotifers recorded of the littoral region in the water column and the composition of hatching in the sediment

also was very low (Jaccard: 0.08) (Table 1). Thirty percent of hatched species were unrecorded species, not found in the lake and also in the region. These were: *Lecane inermis* (Bryce), *Lepadella mataca* José de Paggi, *Keratella mexicana* Kutikova and Silva-Briano, *C. paggiae* Koste and Robertson, *Cephalodella cf. tenuior* (Gosse), *Cephalodella cf. delicata* Wulfert.

Of the most common species recorded in the active zooplankton only *L. closterocerca* (Schmarda), *Keratella tropica* (Apstein), *Filinia sp.*, and *Epiphanes macroura*

Table 1. Comparative list of rotifer species recorded from littoral region of the lake (LR) and hatched from sediment (SR)

	LR	SR		LR	SR
<i>Anuraeopsis fissa</i> Gosse	x		<i>Lecane acuminata</i> (Ehrenberg)	x	
<i>Anuraeopsis navicula</i> Rousselet	x		<i>Lecane arcula</i> Haring	x	
<i>Anuraeopsis urawensis</i> Sudzuki	x		<i>Lecane bulla</i> (Gosse)	x	x
<i>Ascomorpha</i> sp.	x		<i>Lecane closteroerca</i> (Schmarda)	x	x
<i>Asplanchna sieboldi</i> (Leydig)	x		<i>Lecane curvicornis</i> (Murray)	x	
<i>Brachionus angularis</i> Gosse	x	x	<i>Lecane elsa</i> Hauer	x	
<i>Brachionus austrogenitus</i> Ahlstrom	x		<i>Lecane furcata</i> (Murray)	x	
<i>Brachionus budapestinensis</i> Daday	x		<i>Lecane hamata</i> (Stokes)	x	x
<i>Brachionus calyciflorus</i> Pallas	x		<i>Lecane inermis</i> (Bryce)		x
<i>Brachionus caudatus</i> Barrois & Daday		x	<i>Lecane inopinata</i> Haring and Myers	x	
<i>Brachionus chelonis</i> Ahlstrom	x		<i>Lecane leontina</i> (Turner)	x	
<i>Brachionus falcatus</i> Zacharias	x		<i>Lecane ludwigi</i> (Eckstein)	x	
<i>Brachionus havanaensis</i> Rousselet		x	<i>Lecane nana</i> (Murray)		x
<i>Brachionus mirabilis</i> Daday	x		<i>Lecane</i> aff. <i>nana</i> (Murray)idem 1		x
<i>Brachionus</i> cf. <i>quadridentatus</i> Hermann	x		<i>Lecane papuana</i> (Murray)	x	
<i>Cephalodella</i> cf. <i>delicata</i> Wulfert		x	<i>Lecane pyriformis</i> (Daday)	x	
<i>Cephalodella mucronata</i> Myers		x	<i>Lecane quadridentata</i> (Ehrenberg)	x	
<i>Cephalodella paggiae</i> Koste & Robertson		x	<i>Lepadella donneri</i> Koste	x	
<i>Cephalodella</i> cf. <i>tenuior</i> (Gosse)		x	<i>Lepadella elongata</i> Koste	x	
<i>Cephalodella</i> sp.	x		<i>Lepadella mataca</i> Jose de Pagi		x
<i>Colurella obtusa</i> (Gosse)		x	<i>Lepadella ovalis</i> (Muller)	x	
<i>Colurella</i> cf. <i>sinistra</i> Carlin	x		<i>Lepadella patella</i> (Muller)	x	x
<i>Colurella</i> sp.	x		<i>Lepadella rhomboides</i> Gosse	x	
<i>Dicranophorus caudatus</i> (Ehrenberg)	x		<i>Lepadella</i> sp.	x	
<i>Epiphanes clavulata</i> (Ehrenberg)	x		<i>Mytilina bisulcata</i> (Lucks)	x	
<i>Epiphanes macroua</i> (Barrois & Daday)		x	<i>Platyias quadricornis</i> (Ehrenberg)	x	
<i>Euchlanis dilatata</i> Ehrenberg	x		<i>Platyionus patulus</i> (Daday)	x	
<i>Euchlanis meneta</i> Myers		x	<i>Polyarthra platensis</i> (Jose de Paggi & Paggi).	x	
<i>Echlanis triquetra</i> Ehrenberg		x	<i>Synchaeta</i> sp.	x	
<i>Euchlanis</i> sp. 1		x	<i>Testudinella patina</i> (Hermann)	x	
<i>Euchlanis</i> sp. 2	x		<i>Trichocerca bicristata</i> (Gosse)	x	
<i>Filinia novaezealandiae</i> Shiel & Sanoamuang	x		<i>Trichocerca similis</i> (Wierzejski)	x	
<i>Filinia</i> sp. 2		x	<i>Trichocerca similis grandis</i> Hauer	x	
<i>Hexarthra mira</i> (Hudson)	x		<i>Trichocerca</i> sp. 1	x	x
<i>Hexarthra</i> sp.		x	<i>Trichocerca</i> sp. 2	x	
<i>Horaella thomassoni</i> Koste	x		<i>Trichocerca</i> sp. 3	x	
<i>Keratella lenzi</i> Hauer	x		<i>Trichotria tetractis</i> Ehrenberg	x	
<i>Keratella mexicana</i> Kutikova & Silva-Briano		x	<i>Trochosphaera aequatorialis</i> Semper	x	
<i>Keratella tecta</i> (Gosse)	x		<i>Bdelloideos</i>		x
<i>Keratella tropica</i> (Apstein)	x	x			
<i>Lecane</i> cf. <i>abanica</i> Segers		x			

(Barrois and Daday) were recorded in the hatched assemblage.

In terms of species composition, we observed that while the majority of emergences of the littoral species had significant hatchling abundance during all the trials, planktonic species hatched mainly in the early periods of the trial (Fig. 7a). The ratio of limnetic and littoral species, in the active zooplankton composition and species hatched composition was similar (Fig. 7b).

4 Discussion

The number of species hatched from the dry sediments was low in comparison with that assessed in a similar environment, like the Murray River, Australia, where 54 species hatched in 35 days [37]: Also Segers and Shiel [38], by examining the Rotifera hatching experiment on dried sediments of two billabongs of the River Murray floodplain recorded 48 spp., including several new or

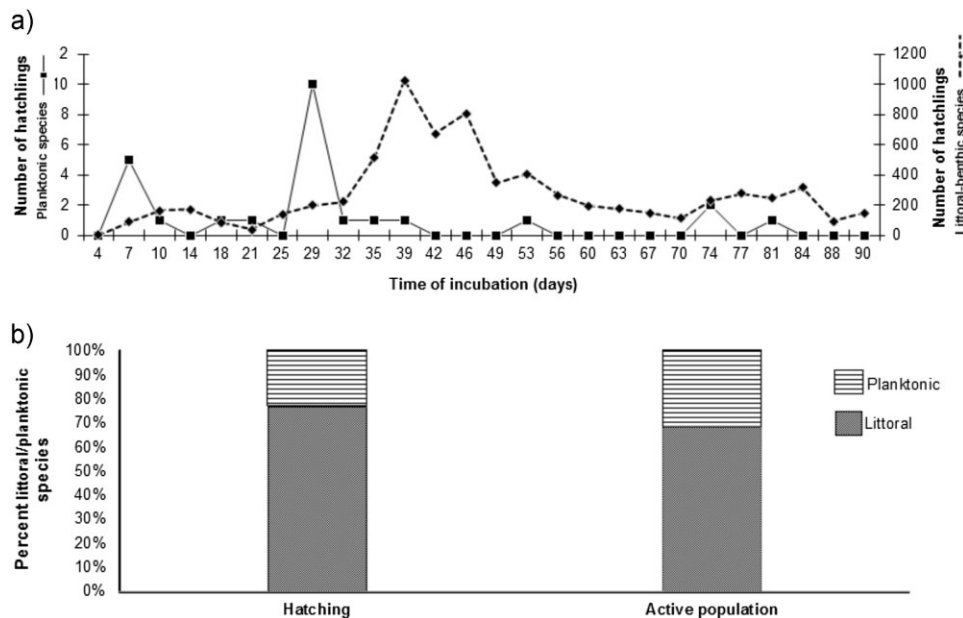


Figure 7. (a) Hatched species and numbers of hatchlings of littoral and planktonic species. (b) composition of the zooplankton (littoral and planktonic species) hatched from sediment and active populations in the lake.

previously unrecorded taxa. However, it was higher than that found in Brazil in the sediments taken in a shallow lake by Panarelli et al. [39], 14 spp.; or 20 spp. in a pool of nine water bodies [40]. Likewise, in dry littoral sediments from Thailand, Chitapum et al. [26] recorded 14 species in a 68-day trial and 17 species in 2 years of experiment, respectively. Our data show that the diversity of potentially available species for dispersion in surface sediments is high considering that it has been suggested that the horizontal egg banks show a patchy distribution and a gradient with highest densities in the deeper parts of the lakes (several authors in Brendonck and De Meester [2]), although this distribution may vary depending of flooding frequency [41]. The high abundance of rotifers hatching during the experiment may be due to in situ reproductive events that take place over a period of 3 days at 25°C [42].

Rotifers and cladocerans represented 87 and 13%, respectively of all the hatched species. Rotifers became active first responding successfully to applied temperature and photoperiod. In contrast the hatches of cladocerans were low considering their significant regional diversity [43]. Studies performed in Brazil by Maia-Barbosa et al. [44] on the hatching rate of rotifers and cladocerans in tropical littoral exposed sediments, using the same pre-incubation treatment, reported a hatching rate of 60–80% for rotifers and <10% for cladocerans. Similarly, Panarelli et al. [39] also found only four species in Cavalos Lake, Brazil; Palazzo et al. [45] found five cladocerans species in the littoral of a shallow lake of Brazil, also. In another study using eggs isolated, only 18% of *Moina micrura* Kurz and 6% of *Diaphanosoma birgei* Kofínek hatched successfully, it has been suggested that a low hatching rate can be caused by the pre-incubation treatment of drying and

exposure to low temperature [46]. Although some studies also show the importance of the photoperiod duration of the emergence [47]. We could infer that this low hatching would be related to the hatching-stimuli factors employed during pre-incubation, mainly temperature, since in the area under study winters are mild and, consequently, frost periods are short. However, regarding the adequate temperature of cladocerans incubation, there are contradictory results. Some authors in the Northern Hemisphere found that the emergence of most species occurred with temperatures of 10 and 15°C. Likewise, with incubation temperature (20 and 25°C) hatching decreased [21].

Regarding copepod hatching, Maia-Barbosa et al. [44] in littoral sediments in Pampulha Reservoir (Brazil) also reported the absence of copepod eggs hatching in 20 days of study. However, Frisch and Green [48] in 72 sediment samples of six ponds (Spain) in only seven days of incubation at 15°C reported cyclopoid copepods (*Metacyclops minutus* Claus) and calanoid nauplii; also Frisch [49] found that the copepods were the dominant first colonist in a floodplain pond in Germany. The reason for the lack of hatching of the copepod resting stages in this study is unknown. However, it is important to conduct further studies to obtain a suitable methodology for the emergence of cladocerans and copepods in subtropical zones.

The analysis of the hatching dynamics showed a trend interpreted as a strategy to avoid overlap in hatching time, species groups E, ME, ML, and L being identified. Studies by Lindholm et al. [50] with cladocerans in Africa also found that species such as *M. micrura*, *Daphnia laevis*, and *Chydorus sphaericus* (O. F.Müller) hatched exclusively

during a specific time period. Studies by Tan and Shiel [51], with plankton in Australia they sampled during pre-flooding and post-flooding periods, three population responses were evident for most common taxa of 63 rotifer species recorded: marked collapses indicative of dilution or deleterious effects of inundation (e.g. *Brachionus budapestinensis*); maintenance of pre-flooding levels in populations (e.g. *Asplanchna asymmetrica*) and population pulses exceeding pre-flood densities (e.g. *Brachionus falcatus*). This behavior support the hypothesis proposed by Hairston and Kearns [52] that in some cases the egg bank may play a fundamental role in maintaining the coexistence of species. Moreover, species of the same genus, for example, *Cephalodella*, *Lecane*, or *Alona*, behaved similarly in terms of timing of hatching emerging in the same period. We could assume that by exposing the sediments to fixed conditions of incubation (photoperiod, temperature), behavioral hatching responses may be due to selection pressure by biological interactions as predation or competition, indicating the result of a long co-evolutionary process between species, but as Cáceres and Schwalbach [53] suggested one must be cautious when applying these laboratory data to the dynamics of natural populations, studies are needed to verify these timing of hatching in situ in the lake.

Vandekerckhove *et al.* [54] analyzing cladocerans, suggested that the propagule banks integrate at least part of the temporal variation in active community structure. In our study, the diversity of hatched eggs was lower than the active zooplankton, probably according with the number of samples of sediments or their localization, only the littoral area, and stimuli specific for each taxon; Duggan *et al.* [6] showed that at only one site of sampling sediments it is not enough to detect all rotifer species in the active community. However, an interesting contribution of this study is having found species rarely found or not found at all in this region, e.g. *L. inermis*, is a rare record in Argentina (José de Paggi unpublished). This species was an abundant taxon in the sediments from Brazil, but it was not found in the composition of active zooplankton [39], the species is also abundant in the hygropsammon interstitial [55]; *L. mataca* was recorded for the first time after its original description in the Pilcomayo river, Argentina [56]; *K. mexicana* was recorded for the first time in the Paraná River Basin after having been found only in the Paraguay River Basin, (José de Paggi unpublished); *C. paggiae*, described by Koste and Robertson [57] from Amazon River basin was recorded for the first time in Argentina and for the second time after its original description. *Cephalodella cf. tenuior* and *Cephalodella cf. delicata* have not been previously recorded in Argentina. All this show the value of littoral eggs bank as archives of local diversity. The ex situ incubation technique in dry littoral sediment, as was suggested by other authors [21, 22, 58], is an efficient

complementarity method for assessment of the biological diversity.

The proportions of hatched species classified by their life habit (planktonic, littoral) are similar to those obtained in the active population. Thus, we can observe that the structure, but not the composition, of plankton in the lake is reflected in the hatches. The absence of hatching of species present in the water column may be because they were not present in the littoral zone, thereby indicating a marked spatial heterogeneity of the egg bank of the lakes or the lack of appropriate stimuli in both storage phase and in the incubation.

Our results provide information about the dynamics of hatching of common species in the region, at 25°C. The shore sediments constitute an important potential source of resting forms available for recruitment to the water body itself and dispersal to other water bodies of the floodplain. Taking into account the abundance of hatching, the species with higher probability of dispersal through exozoochory are Monogononta rotifers *L. closteroerca*, *L. nana*, and *L. patella*, followed by cladocerans *A. glabra*, *A. verrucosa*, and *Bdelloidea*.

This study was supported by Universidad Nacional del Litoral (CAI+d 2009-14-78) and Provincia de Santa Fe (SECTeL 2010-037-11). We thank Cristian De Bonis for field assistance and two anonymous reviewers for very helpful comments.

The authors have declared no conflict of interest.

5 References

- [1] García-Roger, E. M., Carmona, M., Serra, M. J., Deterioration patterns in diapausing egg banks of *Brachionus* (Muller, 1786) rotifer species. *J. Exp. Mar. Biol. Ecol.* 2005, 314, 149–161.
- [2] Brendonck, L., De Meester, L., Egg banks in freshwater zooplankton: Evolutionary and ecological archives in the sediment. *Hydrobiologia* 2003, 491, 65–84.
- [3] De Stasio, B. T., The seed bank of a freshwater crustacean: Copepodology for the plant ecologist. *Ecology* 1989, 70, 1377–1389.
- [4] Hairston, N. G., Jr., Van Brunt, R. A., Kearns, C. M., Engstrom, D. R., Age and survivorship of diapausing eggs in a sediment egg bank. *Ecology* 1995, 76, 1706–1711.
- [5] Brock, M. A., Nielsen, D. L., Shiel, R. J., Green, J. D., Langley, J. M., Drought and aquatic community resilience: The role of eggs and seeds in sediments of temporary wetlands. *Freshwater Biol.* 2003, 48, 1207–1218.
- [6] Duggan, I. C., Green, J. D., Shiel, R. J., Rotifer resting egg densities in lakes of different trophic state, and their assessment using emergence and egg counts. *Arch. Hydrobiol.* 2002, 153, 409–420.
- [7] Cáceres, C. E., Hairston, N. G., Jr., Benthic–pelagic coupling in planktonic crustaceans: The role of the benthos. *Arch.*

- Hydrobiol. Spec. Issues. Advances Limnol.* 1998, 52, 163–174.
- [8] Gyllström, M., Hansson, L. A., Dormancy in freshwater zooplankton: Induction, termination and the importance of benthic-pelagic coupling. *Aquat. Sci.* 2004, 66, 274–295.
- [9] Ishida, S., Ohtsuki, H., Awano, T., Tsugeki, N. K. et al., DNA extraction and amplification methods for ephippial cases of *Daphnia* resting eggs in lake sediments: A novel approach for reconstructing zooplankton population structure from the past. *Limnology* 2012, 13, 261–267.
- [10] Proctor, V. W., Malone, C. R., De Vlaming, V. L., Dispersal of aquatic organisms: Viability of disseminules recovered from the intestinal tracts of captive Killdeer. *Ecology* 1967, 48, 672–676.
- [11] Mellors, W. K., Selective predation of ephippial *Daphnia* and the resistance of ephippial eggs to digestion. *Ecology* 1975, 56, 974–980.
- [12] Duffy, M. A., Perry, L. J., Kearns, C. A., Weider, L. J. et al., Paleogenetic evidence for a past invasion of Onondaga Lake, New York, by exotic *Daphnia curvirostris* using mtDNA from dormant eggs. *Limnol. Oceanogr.* 2000, 45, 1409–1414.
- [13] Cohen, G. M., Shurin, J. B., Scale-dependence and mechanisms of dispersal in freshwater zooplankton. *Oikos* 2003, 103, 603–617.
- [14] Martinez, M., Las Aves y la Limnología, in Boltovskoy, A., Lopez, H. (Eds.), *Conferencias de Limnología Instituto de Limnología “Dr. R. A. Ringuelet”*, La Plata 1993, 127–142.
- [15] Iriondo, M., Paggi, J. C., Parma, J. (Eds.), *The Middle Parana River: Limnology of a Subtropical Wetland*, Springer, Berlin 2007, 229–245.
- [16] Tockner, K., Malard, F., Ward, J. V., An extension of the flood pulse concept. *Hydrol. Process* 2000, 14, 2861–2883.
- [17] Junk, W. J., Bayley, P. B., Sparks, R. E., The flood pulse concept in river floodplain systems. *Can. Spec. Publ. Fish. Aquat. Sci.* 1989, 106, 110–127.
- [18] Schröder, T., Colonising Strategies and Diapause of Planktonic Rotifers (Monogononta, Rotifera) during Aquatic and Terrestrial Phases in a Floodplain (Lower Oder Valley, Germany). *Int. Rev. Hydrobiol.* 2001, 86, 635–660.
- [19] Beltzer, A. H., Quiroga, M. A., Birds, in Iriondo, M., Paggi, J. C., Parma, J. (Eds.), *The Middle Parana River: Limnology of a Subtropical Wetland*, Springer, Berlin 2007, 363–377.
- [20] Beltzer, A. H., Quiroga, M. A., Bertoluzzi, A. L., Variación estacional de la comunidad de aves en un ambiente lenítico del valle de inundación del río Paraná. *Nat. Neotrop.* 2004, 35, 33–37.
- [21] Vandekerckhove, J., Declerck, S., Brendonck, L., Conde-Porcuna, J. M. et al., Uncovering hidden species: Hatching diapausing eggs for the analysis of cladoceran species richness. *Limnol. Oceanogr. Methods* 2005, 3, 399–407.
- [22] Garcia-Roger, E. M., Armengol, X., Carmona, M. J., Serra, M., Assessing rotifer diapausing egg bank diversity and abundance in brackish temporary environments: An ex situ sediment incubation approach. *Fundam. Appl. Limnol.* 2008, 173, 79–88.
- [23] José de Paggi, S., Paggi, J. C., Zooplankton, in Iriondo, M., Paggi, J. C., Parma, J. (Eds.), *The Middle Parana River: Limnology of a Subtropical Wetland*, Springer, Berlin 2007, 229–245.
- [24] Pautasso, A., Aves de la Reserva Urbana de la Ciudad Universitaria Universidad Nacional del Litoral El Pozo, Santa Fe, Argentina. *Comunicación Museo Provincial de Ciencias Naturales Florentino Ameghino* 2002, 8, 1–12.
- [25] José de Paggi, S. B., Muñoz, S., Frau, D., Paggi, J. C., Horizontal distribution of rotifers in a subtropical shallow lake (Paraná floodplain, Argentina). *Fundam. Appl. Limnol.* 2012, 180, 321–333.
- [26] Chittapun, S., Pholpunthin, P., Segers, H., Restoration of tropical peat swamp rotifer communities after perturbation: An experimental study of recovery of rotifers from the resting egg bank. *Hydrobiologia* 2005, 546, 281–289.
- [27] Koste, W., *Die Rädertiere Mitteleuropas*, Borntraeger, Berlin, 1978, 1–82.
- [28] Korovchinsky, N. M., Sididae & Holopediidae (Crustacea: Daphniiformes). Guides to the Identification of the Microinvertebrates of the Continental Waters of the World, III, SPB Academic Publishing, Amsterdam 1992, pp. 82.
- [29] Battistoni, P., Copepoda, in Lopretto, E., Tell, G. (Eds.), *Ecosistemas de Aguas Continentales. Metodologías Para su Estudio, Tomo III, Ediciones Sur*, La Plata 1995, 953–971.
- [30] Segers, H., Rotifera, in Dumont, H. J. (Ed.), *Guides to the identification of the Microinvertebrates of the Continental Waters of the World*, Backhuys Publishers, Leiden 1995, 1–226.
- [31] Alekseev, V. R., Copepoda, in Fernando, C. H. (Ed.), *A Guide to Tropical Freshwater Zooplankton*, Backhuys Publishers, Leiden 2002, 123–188.
- [32] Kořínek, V., Cladocera, in Fernando, C. H. (Ed.), *A Guide to Tropical Freshwater Zooplankton*, Backhuys Publishers, Leiden 2002, 69–122.
- [33] Vandekerckhove, J., Niessen, B., Declerck, S., Jeppesen, E. et al., Hatching rate and success of isolated versus non-isolated zooplankton resting eggs. *Hydrobiologia* 2004, 526, 235–241.
- [34] Magurran, A., *Ecological Biodiversity and its Measurement*, Princeton University Press, Nueva York 1988.
- [35] Shiel, R. J., Walker, K. F., Williams, W. D., Plankton of the lower River Murray South Australia. *Aust. J. Mar. Freshwater Res.* 1982, 33, 301–327.
- [36] Hammer, Ø., Harper, D. A. T., Ryan, P. D., 2001, PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia*. Online at: http://palaeo-electronica.org/2001_1/past/past.pdf
- [37] Langley, J. M., Shiel, R. J., Nielsen, D. L., Green, J. D., Hatching from the sediment egg-bank, or aerially dispersed? – the use of mesocosms in assessing rotifer biodiversity. *Hydrobiologia* 2001, 446/447, 203–211.
- [38] Segers, H., Shiel, R. J., Diversity of cryptic Metazoa in Australian freshwaters: A new genus and two new species of sessile rotifer (Rotifera, Monogononta, Gnesiotrocha, Flouculariidae). *Zootaxa* 2008, 1750, 19–31.
- [39] Panarelli, E. A., Casanova, S. M. C., Henry, R., The role of resting eggs in the recovery of zooplankton community in a marginal lake of the Paranapanema River (São Paulo, Brazil), after a long drought period. *Acta Limnol. Bras.* 2008, 20, 73–88.
- [40] Fernandez, A. P. C., Braghin, L. S. M., Nedli, J., Palazzo, F. et al., Passive zooplankton community in different environments of a neotropical floodplain. *Acta Sci. Biol. Sci.* 2012, 34(4), 413–418.
- [41] Shiel, R. J., Green, J. D., Tan, L. W., Microfaunal and resting stage heterogeneity in ephemeral pools, upper River Murray floodplain. *Verh. Int. Ver. Limnol.* 2001, 27, 3738–3741.
- [42] Edmondson, W. T., Reproductive rate of planktonic rotifers as related to food and temperature. *Ecol. Monogr.* 1965, 35, 61–111.

- [43] Paggi, J. C., Importancia de la fauna de "Cladóceros" (Crustacea, Branchiopoda) del Litoral Fluvial Argentino. *INSUGEO Miscelanea* 2004, 12, 239–246.
- [44] Maia-Barbosa, P. M., Eskinazi-Santanna, E. M., Valadares, C. F., Pessoa, G. C. D., The resting eggs of zooplankton from a tropical, eutrophic reservoir (Pampulha Reservoir, south-east Brazil). *Lakes Reserv. Res. Manage.* 2003, 8, 269–275.
- [45] Palazzo, F., Costa Bonecker, C., Fernandez, A. P. C., Resting cladoceran eggs and their contribution to zooplankton diversity in a lagoon of the Upper Paraná River floodplain. *Lakes Reserv. Res. Manage.* 2008, 13(3), 207–214.
- [46] Santangelo, J. M., Rabelo Araújo, L., Esteves, F. A., Manca, M., Method for hatching resting eggs from tropical zooplankton: Effects of drying or exposing to low temperatures before incubation. *Acta Limnol. Bras.* 2011, 23, 42–47.
- [47] Shan, R. K. C., Influence of light on hatching resting eggs of Chydorids (Cladocera). *Int. Revue ges. Hydrobiol. Hydrogr.* 1970, 55, 295–302.
- [48] Frisch, D., Green, A. J., Copepods come in first: Rapid colonization of newly built temporary ponds. *Fundam. Appl. Limnol. Arch. Hydrobiol.* 2007, 168(4), 289–297.
- [49] Frisch, D., Dormancy, dispersal and the survival of cyclopoid copepods (Cyclopoida, Copepoda) in a lowland floodplain. *Freshwater Biol.* 2002, 47, 1269–1281.
- [50] Lindholm, M., Hessen, D. O., Ramberg, L., Diversity, dispersal and disturbance: Cladoceran species composition in the Okavango Delta. *Afr. Zool.* 2009, 44, 24–35.
- [51] Tan, L. W., Shiel, R. J., Responses of billabong rotifer communities to inundation. *Hydrobiologia* 1993, 255/256, 361–369.
- [52] Hairston, N. G., Jr., Kearns, C. M., Temporal dispersal: Ecological and evolutionary aspects of zooplankton egg banks and the role of sediment mixing. *Integr. Comp. Biol.* 2002, 42, 481–491.
- [53] Cáceres, C. E., Schwalbach, M. S., How well do laboratory experiments explain field patterns of zooplankton emergence? *Freshwater Biol.* 2001, 46, 1179–1189.
- [54] Vandekerkhove, J., Declerck, S., Jeppesen, E., Conde-Pocurna, J. M. et al., Dormant propagule banks integrate spatio-temporal heterogeneity in cladoceran communities. *Oecologia* 2005, 142, 109–116.
- [55] Turner, P. N., Palmer, M. A., Notes on the species composition of the rotifer community inhabiting the interstitial sands of Goose Creek, Virginia with comments on habitat preferences. *Quekett J. Microsc.* 1996, 37, 552–565.
- [56] José de Paggi, S., A new species of *Lepadella* (Rotifera: Monogononta: Colurellidae) from the Rio Pilcomayo National Park, *Argentina Hydrobiol.* 2001, 455, 223–228.
- [57] Koste, W., Robertson, B. A., Taxonomic studies of the rotifera (phylum Aschelminthes) from a Central Amazonian varzea lake, Lago Camaleão (Ilha de Marchantaria, Rio Solimões, Amazonas, Brazil). *Amazoniana* 1983, 8, 225–254.
- [58] Segers, H., Shiel, R. J., Tale of a sleeping beauty: A new and easily cultured model organism for experimental studies on bdelloid rotifers. *Hydrobiologia* 2005, 546, 141–145.