

Macrophytes as dispersal vectors of zooplankton resting stages in a subtropical riverine floodplain

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Abstract The resting stages of freshwater zooplankton constitute a special mechanism for passive dispersal, often displaying a variety of adaptations so as to ease transport. In floodplain systems, macrophytes are one of the most representative biotic groups showing interactions with the zooplankton community. The annual fluctuations in the hydrometric level of the Paraná River favour the displacement of this aquatic vegetation in floodplain environments. This paper hypothesizes that the roots and submerged portions of different macrophytes contain zooplankton resting stages which are able to hatch when environmental conditions are favourable. In turn, this contributes to the dispersal of zooplankton by plants when they are displaced by the flood pulse. Six macrophyte species were sampled (*Eichhornia crassipes*, *Azolla filiculoides*, *Limnobium spongia*, *Pistia stratiotes*, *Eichhornia azurea* and *Nymphoides indica*) from lakes within the Paraná River floodplain. Roots and

submerged portions of vegetation were stored (90 days) at 4 °C then incubated at 25 °C for 90 days. Hatching emergence was recorded at 2-day intervals during this period. In total, 70 zooplankton taxa were recorded in all macrophyte samples; rotifers were the most representative group (69%) followed by cladocerans (28%) and copepods (3%). The roots and submerged parts of aquatic vegetation house viable zooplankton resting stages. This phenomenon allows the dispersal of resting stages and therefore colonization of new habitats during the displacement of macrophyte species.

Keywords Flood pulse · Connectivity · Diversity · Egg banks

Introduction

The most interesting strategy developed by freshwater zooplankton to survive under adverse environmental conditions is the production of dormant stages (Hairston and Cáceres 1996; Cáceres 1998; García-Roger 2006) which usually accumulate in the bottom sediment (De Stasio 1989; Duggan et al. 2002) Although little is known about it, they could also be fixed on substrates (Fryer 1972).

Dormant stages are also part of a special mechanism for population dispersal and often evidence a variety of adaptations for easy transport (Havel et al.

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2000; Bohonak and Jenkins 2003). The resting stages often represent a sufficient inoculum for the colonization of a new habitat (Havel and Stelzl-Schwent 2000).

Experimental and field studies suggested that the passive dispersal of freshwater organisms should work well at least over short distances (Maguire 1963), as for example, due to the movement of waterfowl as a vector (Proctor and Malone 1965). On the other hand, transport by flowing water (Michels et al. 2001; Havel and Shurin 2004) boats and other human transport vectors provide mechanisms for dispersing freshwater organisms over long distances (Carlton 1992; Havel et al. 2000; Havel and Stelzl-Schwent 2000). Moreover, it has been shown that many zooplankton resting stages are able to hatch after passing through the digestive tract of filter-feeding fish capable of extensive migrations along rivers of the La Plata basin and, which therefore act as a vector of long-distance dispersal (Battauz et al. 2015).

Macrophytes are one of the most representative biotic groups in floodplain systems, constituting the major biomass component (Sabattini et al. 1983). The aquatic vegetation often displays high taxonomic and ecological diversity (Burkart 1957). It shows complex interactions with several groups of organisms, including the zooplankton community (Inger et al. 2004; Poi de Neiff and Neiff 2006; Gonz ales 2007). This is one of the main factors promoting high biodiversity in wetlands (Burks et al. 2006; Dudgeon et al. 2006), affecting structural features such as presence, diversity and composition of aquatic assemblages (Jeppesen et al. 1998; Thomaz and Da Cunha 2010; Yu et al. 2016). Both zooplankton species richness and the occurrence of species preferring littoral habitats are favoured by the presence of macrophytes (Villabona-Gonz alez et al. 2011). However, what happens to the passive assembly of zooplankton community that can inhabit these submerged structures of macrophytes is not yet known.

The annual fluctuations (flood-drought) of the hydrometric level of the Paran  River (Neiff 1997) favour the displacement and redistribution of macrophytes in the floodplain environment (21,000 km²) (Sabattini and Lallana 2007). During periods of high hydrological connectivity, many macrophytes inhabiting the floodplain are pushed into the main and secondary courses by the flow of water. Fernandez

et al. (1990) estimated a daily flow of 4.51 ha day⁻¹ of free-floating aquatic vegetation.

The aims of this work were: (1) to determine whether the roots and submerged parts of macrophytes are able to house zooplankton resting stages, (2) to determine which of the resting stages present were viable, (3) to estimate species richness from the hatching of the resting stages.

The hypothesis here is that the roots and submerged portions of the different species of macrophytes house zooplankton resting stages, which are able to hatch when conditions are favourable. Therefore, zooplankton is dispersed by plants displaced by the flood pulse.

Materials and methods

This study was carried out in 13 shallow lakes of the Middle Paran  River floodplain: Santa Fe 1 Lake (SF1L) (31°39'S, 60°36'W), La Sandia Lake (SAL) (31°41'S, 60°31'W), La Guardia Lake (GUL) (31°38'S, 60°38'W), Ram rez Lake (RAL) (31°38'S, 60°37'W), Aislada Lake (AIL) (31°40'S, 60°32.05'W), Mini 1 Lake (MN1L) (31°40'S, 60°33'W), Gendarmer a Lake (GEL) (31°40'S, 60°34'W), Mini 2 Lake (MN2L) (31°41'S, 60°32'W), Puente Lake (PUL) (31°38'S, 60°40'W), Santa Fe 2 Lake (SF2L) (31°39'S, 60°36'W), Vialidad Lake (VIL) (31°39'S, 60°35'W), Refulado Lake (REL) (31°38'25S, 60°40'W) and El Mirador Lake (MIL) (31°38'S, 60°40'W), in the period March–April 2012.

These lakes are mostly shallow, 1.60 m deep or less, and some of them are temporary. All of them have some degree of connection with the Paran  River at a certain period of the year. Some environmental parameters were measured in situ: temperature ( C), pH, dissolved oxygen (ppm) and conductivity ($\mu\text{S cm}^{-1}$), by means of a HANNA multi-parameter sensor.

Hatching experiments on the resting stages present in macrophytes

Vegetation was obtained from lakes under similar limnological conditions and in monospecific assemblages: free-floating macrophytes, *Eichhornia crassipes* (Mart.) Solms, *Azolla filiculoides* Lam., *Limnobium spongia* (Bosc), *Pistia stratiotes* L. and

floating-leaved macrophytes *Eichhornia azurea* (Sw.) Kunth and *Nymphoides indica* (L.) Kuntze. Sometimes the last two species showed a free-floating period with intertwined stems in the case of *E. azurea*, and in the case of *N. indica* during periods of high water (>3 m) roots can be released from the substrate (Neiff et al. 2000).

The aquatic vegetation was sampled using a quadrat (784 cm²). In each case, one quadrat sample of the dominant species in lakes was taken, placed in polyethylene bags, labelled and carried to the laboratory.

Aiming at accessing the resting stages in roots and submerged macrophytes portions, the emergence assessment method ex situ was used to estimate the number of animals contributing to population recruitment from the “egg bank” in sediment (Brendonck and De Meester 2003; García-Roger et al. 2008; Battauz et al. 2014).

In the laboratory, roots and submerged portions were dried at 21 °C for 72 h. Then, they were stored in a refrigerator in darkness at 4 °C for 90 days (Hagiwara and Hino 1989a, b). After the storage period, 22 samples (7 samples of *E. crassipes*, 3 samples of *A. filiculoides*, 2 samples of *L. spongia*, 3 samples of *N. indica*, 2 samples of *P. stratiotes* and 5 samples of *E. azurea*) were placed on plastic trays (surface: 165 cm², each tray) and covered with 250 cc of dechlorinated water (Table 1).

Dry weight of macrophyte tissue was quantified by lakes. The number of samples per macrophyte species

was proportional to its presence in the corresponding sample lake.

Finally, trays were placed in an incubator at 25 °C with a dark/light photoperiod of 8:16 h. Hatchlings were checked at 2-day intervals for 90 days; supernatant water of all trays was filtered using a 25- μ m mesh net and mixed in a single sample per macrophyte and their respective lake. The material was fixed with formalin 10%, stained with erythrosine and analysed using an optical Nikon Eclipse (E100) microscope. Analyses of sub-samples were carried out in a 1-ml Kolwicz cell. A total of 990 sub-samples (for all macrophytes) were analysed.

Taxonomic determinations were made mainly using these keys: Koste (1978) and Segers (1995) for rotifera, Korovchinsky (1992) and Koříněk (2002) for cladocera and Battistoni (1995), Alekseev (2002) for copepoda.

Data analysis

Species richness was assessed as the total number of taxa among the hatchlings identified in each sub-sample. One-way analysis of variance was used to analyse differences among the taxonomic composition of hatchlings. The similarity of the taxonomic compositions of hatchlings among aquatic macrophytes was calculated using the Jaccard similarity index (Magurran 1988). For the purpose of this analysis, copepod larvae unidentified to the species level were excluded. The frequency rate of hatching species was calculated per macrophyte.

Table 1 Dry weight (in grams) of macrophyte tissue per quadrat

	GUL	SF1L	SF2L	VIL	MN1L	SAL	MN2L
<i>Eichhornia crassipes</i>	22.07	25.55				31.76	14.16
<i>Azolla filiculoides</i>							
<i>Nymphoides indica</i>					13.27		15.66
<i>Limnium spongia</i>			6.13				
<i>Pistia stratiotes</i>							
<i>Eichhornia azurea</i>			27.49	16.87	5.98		
	GEL	RAL	PUL	MIL	AIL	REL	
<i>Eichhornia crassipes</i>	18.53	8.70				7.67	
<i>Azolla filiculoides</i>		7.61	8.11			6.73	
<i>Nymphoides indica</i>						11.33	
<i>Limnium spongia</i>						9.66	
<i>Pistia stratiotes</i>					9.02		8.19
<i>Eichhornia azurea</i>		5.95				6.22	

La Guardia lake (GUL), Santa Fe 1 lake (SF1L), Santa Fe 2 lake (SF2L), Vialidad lake (VIL), Mini 1 lake (MN1L), La Sandia lake (SAL), Mini 2 lake (MN2L), Gendarmería lake (GEL), Ramírez lake (RAL), Puente lake (PUL), El Mirador lake (MIL), Aislada lake (AIL), Refulado lake (REL)

In order to study hatching patterns during the test, the cumulative curve of species hatched was drawn. Discrimination between limnetic and littoral species was performed (Shiel et al. 1982 and our own experience in regional fauna) to evaluate the relationship between root architecture and the number of hatched littoral and limnetic species, using averages.

Statistical analyses were performed using Past 2.14 statistical package (Hammer et al. 2001).

Results

Mean water temperature in lakes was 24.8 °C (SD = 3.45), and mean conductivity was 386 ($\mu\text{S cm}^{-1}$), (SD = 338.15); the mean pH was weakly acidic (pH 5.61) (SD = 0.97), and the mean value of dissolved oxygen concentration was 1.77 ppm (SD = 0.92) (Table 2).

The mean hydrometric level of the Paraná River during the sampling period was 3.92 m, registered in the harbour of Santa Fe (Data provided by the Instituto Nacional del Agua 2012).

A total of 70 zooplankton taxa were registered in all macrophyte samples; rotifers were the best represented group (69% of the total richness) (48 taxa), followed by microcrustaceans, within which cladocerans contributed 28% of the taxa richness (20 taxa) and copepods, 3% (2 taxa). Figure 1 shows the

hatched resting stages of zooplankton, associated with macrophytes. There was no evidence of differences in zooplankton hatchling total among macrophytes ($F = 1.704$, $p = 0.190$).

The recorded diversity of rotifer species hatched was represented by the genera *Lecane* (21 spp.), *Euchlanis* (4 spp.), *Lepadella* (4 spp.), *Epiphanes* (3 spp.), *Trichocerca* (3 spp.), *Cephalodella* (2 spp.), *Colurella* (2 spp.), *Anuraeopsis* (1 sp.), *Brachionus* (1 sp.), *Dipleuchlanis* (1 sp.), *Keratella* (1 sp.), *Mytilina* (1 sp.), *Platyonus* (1 sp.), *Platyias* (1 sp.), *Scaridium* (1 sp.), *Testudinella* (1 sp.), *Tripleuchlanis* (1 sp.) and Bdelloidea (unidentified at lower level). Cladocerans were represented by *Alona* (3 spp.), *Chydorus* (3 spp.), *Macrothrix* (3 spp.), *Diaphanosoma* (2 spp.), *Ceriodaphnia* (1 sp.), *Euryalona* (1 sp.), *Ephemeroporus* (1 sp.), *Kurzia* (1 sp.), *Moina* (1 sp.), *Moinodaphnia* (1 sp.), *Leydigopsis* (1 sp.), *Oxyurella* (1 sp.) and *Simocephalus* (1 sp.). Finally, copepods were represented by the genera *Paracyclops* (1 sp.) and *Harpacticoida* (1 sp.).

The diversity of the hatched assemblages from different species of macrophytes showed greater similarity between *E. crassipes*—*A. filiculoides* (Jaccard: 0.53) followed by *E. crassipes*—*N. indica*, *E. crassipes*—*L. spongia* and *A. filiculoides*—*N. indica* (Jaccard: 0.5) (Fig. 2).

With regard to the frequency of hatching throughout the experiment, rotifers were the most common

Table 2 Environmental data for target lakes. For lake names see Table 1

Lakes	Temperature (°C)	pH	Conductivity ($\mu\text{S cm}^{-1}$)	Dissolved oxygen (ppm)
GUL	22.6	6.37	114	1.55
SFIL	20.5	6.34	187	0.52
SF2L	23	6.05	422	1.39
VIL	26.8	6.44	910	2.58
MN1L	22.5	6.41	910	3.36
SAL	22.5	6.95	860	2.01
MN2L	24.4	4.8	96	1.54
GEL	25.9	4.49	124	2.58
RAL	28.3	4.65	135	0.93
PUL	30.2	4.52	51	0.83
MIL	26.4	4.5	553	0.71
AIL	18.91	6.59		3.06
REL	28.7	4.85	271	1.93

Fig. 1 Number of zooplankton hatching species per macrophyte (macrophytes species) discriminated by zooplankton group (rotifera, cladocera and copepoda). The dotted line indicates the total number of zooplankton hatching

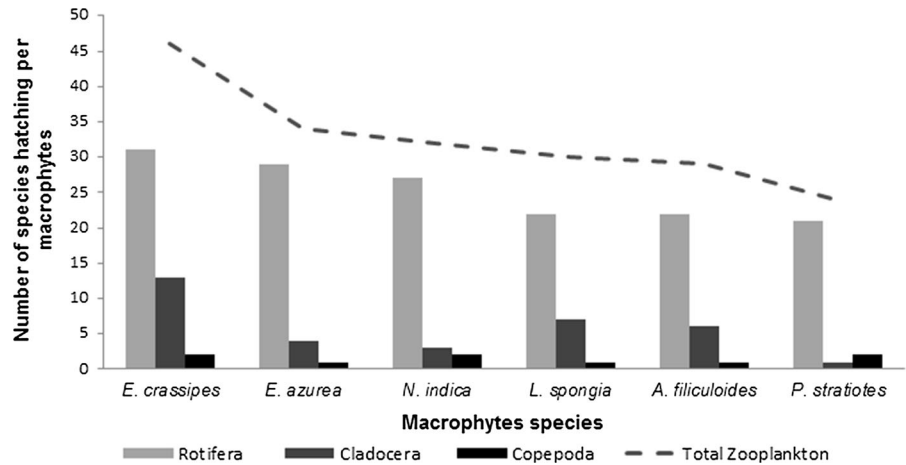
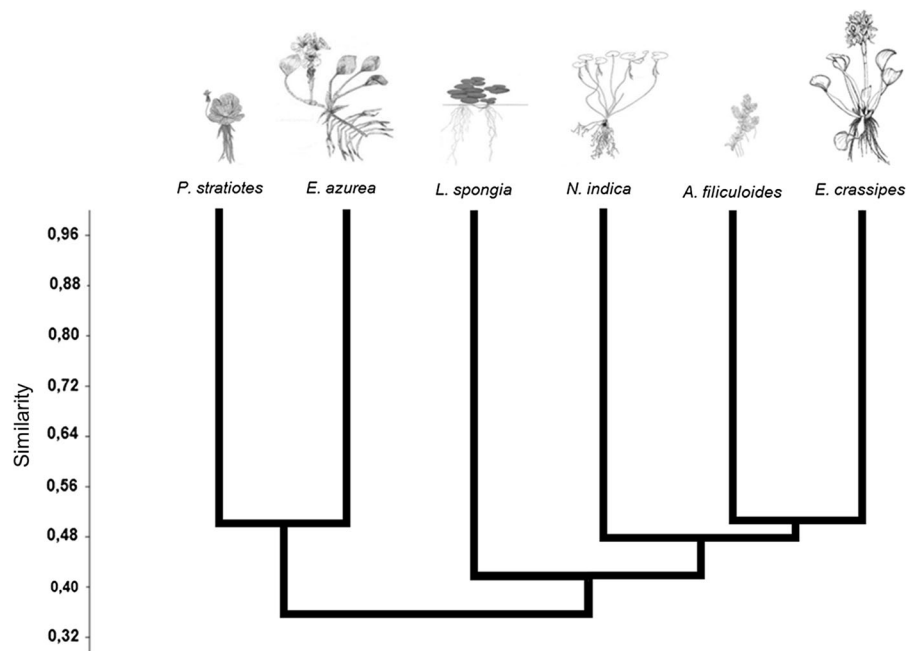


Fig. 2 Faunistic similarity among macrophytes. *Eichhornia crassipes*, *Azolla filiculoides*, *Limnobium spongia*, *Nymphoides indica*, *Pistia stratiotes* and *Eichhornia azurea*



among all macrophyte species, ranging from 72 to 98%, followed by cladocerans 0.3–20% and copepods 0.2–15%.

The most frequent rotifers were Bdelloid except in *L. spongia*. The second most frequent rotifer species were *Lecane hamata* in *E. crassipes*, *P. stratiotes* and *E. azurea*, *Lecane bulla* in *A. filiculoides* and *Trichocerca* sp. in *N. indica* (Fig. 3).

With reference to cladocerans recorded in macrophytes, the most frequent ones in *E. crassipes* and *A. filiculoides* were *Euryalona occidentalis* and *Macrothrix* sp. In *N. indica* and *L. spongia*, *Chydorus eurynotus* was most frequently observed, followed by

Euryalona occidentalis and *Macrothrix squamosa*, respectively. In *P. stratiotes*, only *Leydigiopsis ornata* was recorded and in *E. azurea* *Alona* cf. *guttata* and *Ceriodaphnia* cf. *quadrangula* were the most frequent species (Fig. 4).

Regarding the copepods group, the most frequent species was *Paracyclops chiltoni*, nauplii and adults, for all macrophytes except in *A. filiculoides*, where harpacticoid copepods were the most frequently found.

If the cumulative number of hatching species by macrophyte and by lake is analysed, a similar hatching pattern may be observed. In almost all cases, more

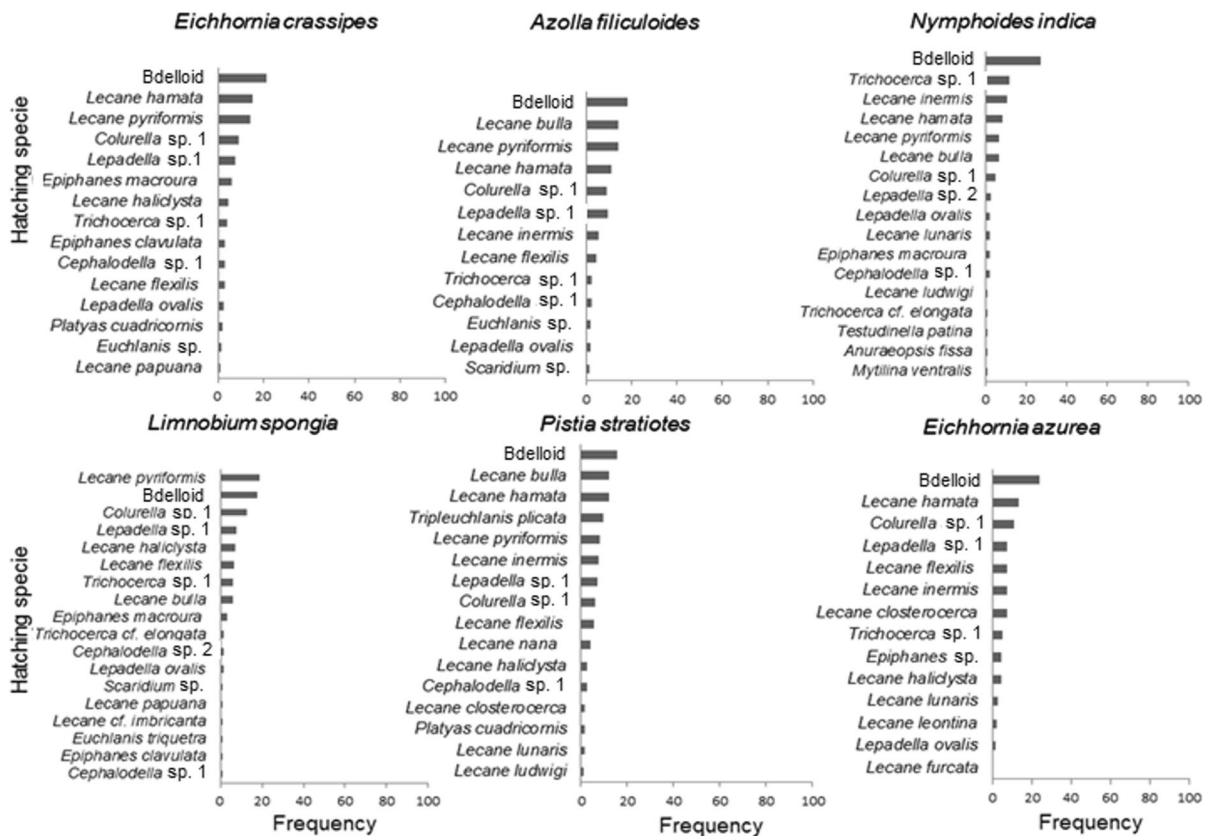


Fig. 3 Frequency of hatching rotifera species (>1) per macrophyte

species become active during the early stages of incubation from day 3–30 approximately, with some oscillations, with the incorporation of fewer species until day 90. Figure 5 shows a more detailed analysis of these cumulative curves of hatchings.

In all macrophytes, hatching of littoral species was higher compared with limnetic ones. This difference in relative richness is statistically significant ($p = 0.005$) (Fig. 6).

Discussion

Our results indicate that macrophyte species are able to house numerous viable resting stages of zooplankton in their submerged parts. This is relevant considering biomass and transport ability by means of macrophytes.

Not arbitrarily, zooplankton resting stages may be seen as the counterpart of the vegetation seed bank. Lallana (1990) recorded 2000–5000 seeds per m^2 ,

belonging to 19 species, in studies of transport and dispersal of seed over great distances by macrophytes such as *E. crassipes*, *P. stratiotes* and *Salvinia* spp., in the Paraná River floodplain.

Although no information was found in the literature on resting stages of zooplankton present on the roots of macrophytes, studies performed on active aquatic invertebrates populations associated with macrophytes in the Middle Paraná floodplain recorded a variety of taxa present, such as nematodes, oligochaetes, cladocerans, copepods, ostracods, amphipods and decapods (Poi de Neiff 1977; Bonetto 1986). The density of this associated fauna was highly variable according to season and the plant species sampled. For example, the density of faunal populations associated with the genera *Azolla*, *Pistia* and *Salvinia* fluctuated seasonally from 5000 to 20,000 ind m^{-2} , and *E. crassipes* showed densities of over 100.00 ind m^{-2} of macrophytes (Poi de Neiff 1977). Hatchling richness, except among copepods, found in this study is consistent with that recorded for active populations.

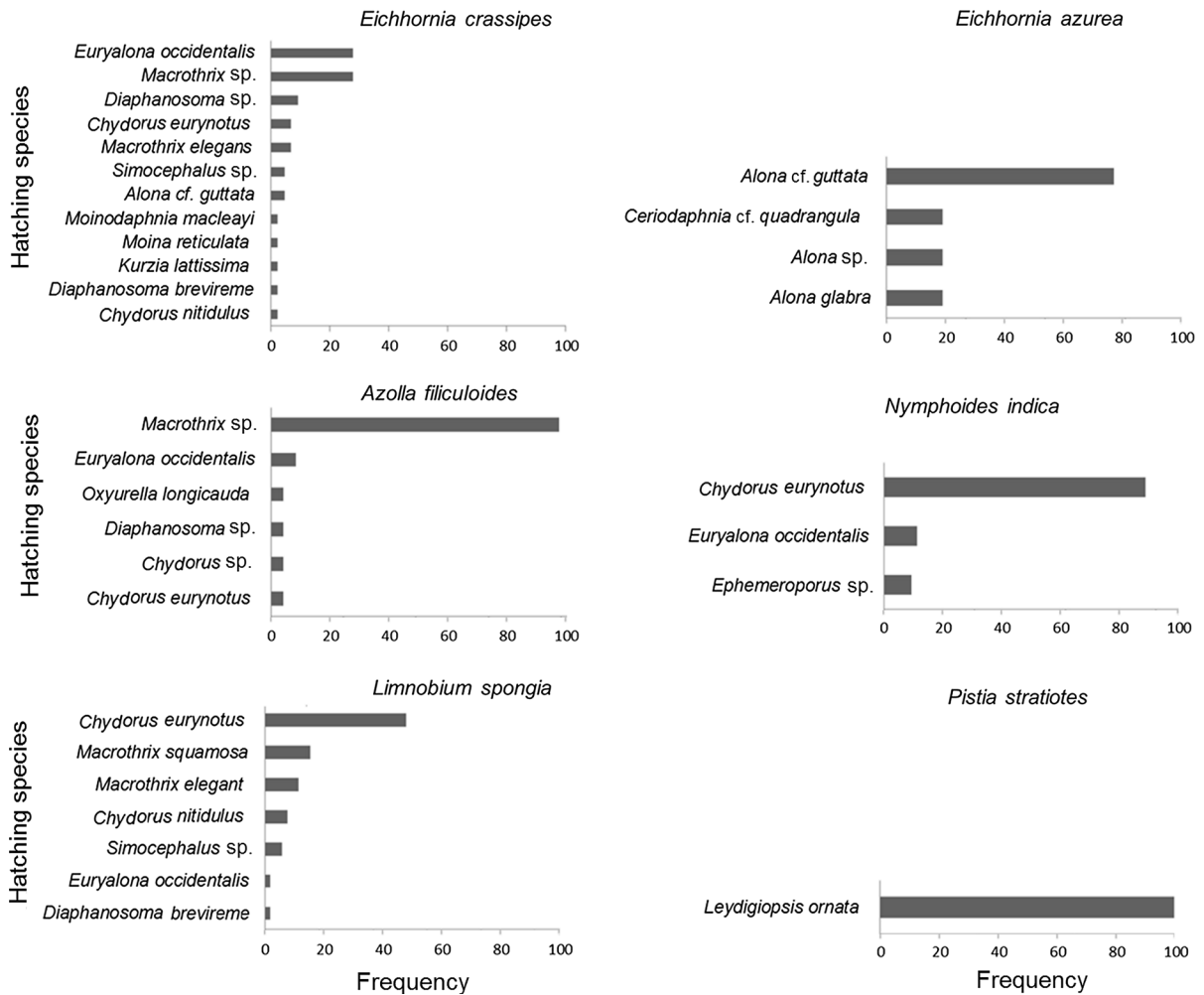


Fig. 4 Frequency of hatching cladocera species per macrophyte

In line with what is mentioned above, a study to test the effects of macrophytes on zooplankton distribution in a shallow subtropical lake (Brazil) showed that zooplankton densities were higher in free-floating plants (Gazulha et al. 2011).

The high density of invertebrates associated with *E. crassipes* may explain the presence of zooplankton resting stages, which is evidenced in the hatchlings. Nevertheless, it is also shown that the faunal composition is quite similar to that of *A. filiculoides*.

Moreover, the high frequency of the emergence of Bdelloidea in all macrophytes could be related to their dominance in littoral areas. Ricci (1987) recorded that in littoral vegetated areas Bdelloidea accounted for 20–30% of total rotifers. Villabona-González et al.

(2011) reported Bdelloidea rotifers showing high densities in experiments with active zooplankton associated with *Eichhornia heterosperma* Alexander, *E. crassipes*, *E. azurea* and *Oxycarium cubense* in eight sampling sites in the San Jorge River floodplain (Colombia).

The high richness of hatchling rotifers of *Lecane* (21 spp.) is consistent with the results of hatching tests performed in lake sediments by Santangelo et al. (2015) in Brazil and by our research group in Argentina (Battauz et al. 2014) where the family with the highest species richness was Lecanidae. This genus is very frequent in the vegetated littoral areas of water bodies because its species are substratum dwellers (Segers 1995).

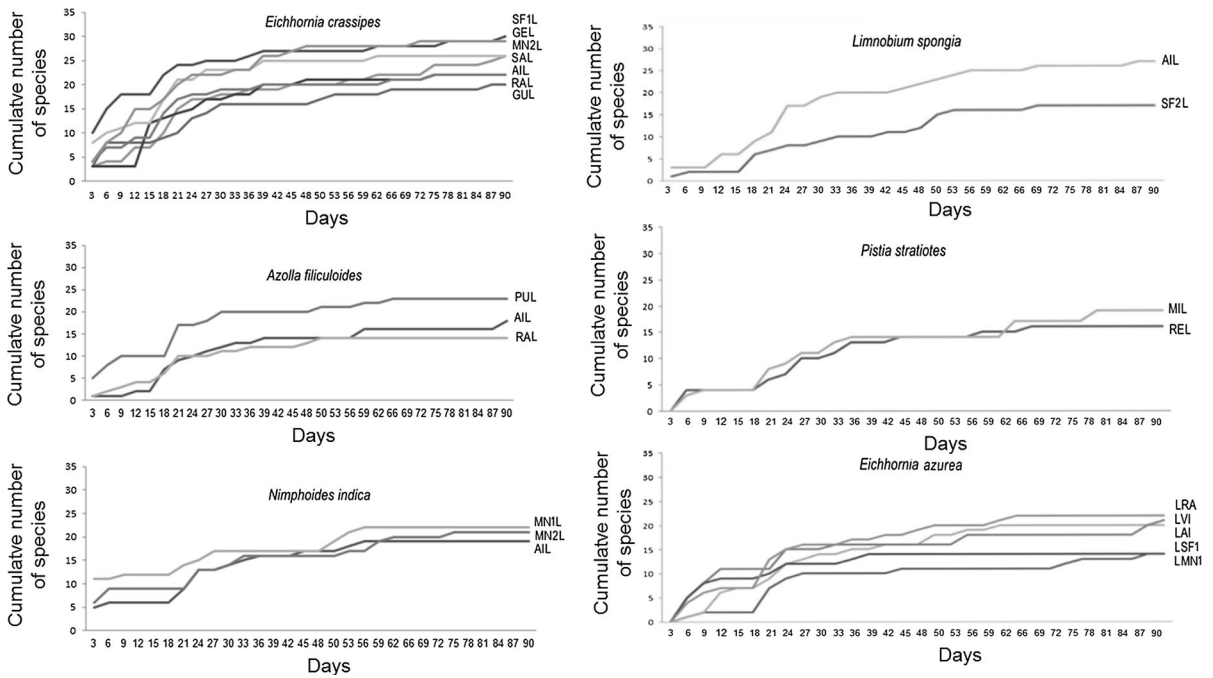


Fig. 5 Cumulative richness of hatched species per lake and species macrophyte

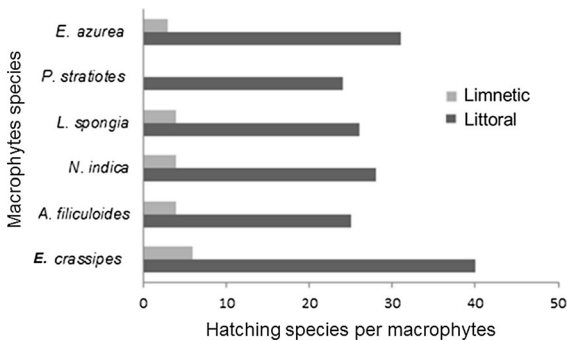


Fig. 6 Number of the zooplankton (littoral and planktonic species) hatched from macrophytes

Our results suggest that rotifers may be the most favoured ones to be dispersed by the movement of aquatic vegetation. Regarding the richness of hatching of cladocerans and macrophytes, Villabona-González et al. (2011) and Gazulha et al. (2011) recorded a high diversity of taxa belonging to the family Chydoridae associated with aquatic vegetation. In our study, a high frequency of emergence of species of the genus *Chydorus* was recorded.

The timing of hatching recorded in this work and the cumulative species curve results are fairly similar to those obtained in previous studies on the dry

sediments of the Mirador lake, in the Paraná River floodplain (Santa Fe), where a significant number of species broke their inactivity stage during the first 30 days (Battauz et al. 2014).

The predominance of littoral species hatchlings is apparently related to the great number of species of zooplankton assemblage that inhabit the water column under macrophytes, favoured by the conditions of these microhabitats, such as structural complexity, sheltered breeding area and substrate for abundant production of food for many aquatic animals (Lodge 1991; Rennie and Jackson 2005; Kuczyńska-Kippen and Joniak 2015). Furthermore, species show their own characteristics to respond to hatch stimuli to which they were subjected.

The methodology used to deposit resting stages on the roots of macrophytes is poorly known and represents a line of work for future research. However, there is one work by Fryer (1972), which describes the way the ephippia of four macrothricid cladocerans, *Lathonura rectirostris*, *Acantholeberis curvirostris*, *Streblocerus serricaudatus* and *Ophryoxus gracilis*, are attached to a substratum.

Macrophytes have traditionally been considered filters that prevent displacement of active zooplankton populations during periods of flooding (Hamilton et al.

1990). Nevertheless, this work allows us to show for the first time that macrophytes can be a major source of zooplankton re-population. It is interesting to notice that the richness of local habitats could be very important in regulating the richness levels of zooplankton at a regional scale.

Our results complement what Sabbatini and Lallana (2007) suggested that drift vegetation contributes to the transport of organic matter, insects or other organisms, in our case as resting stages, from one place to another in the ecological system.

As it can be seen, many of the records of zooplankton associated with vegetation were obtained in floodplain lakes. Gaining knowledge of the dynamics of such lakes is of considerable interest, but aquatic vegetation present in these water bodies is affected by flood pulse and the hydrological connectivity that controls the distribution of plants (Neiff 1997). This phenomenon might not only mobilize the aquatic vegetation into the main course, carrying it downstream over long distances, but also disperse *egg banks* present on submerged stems and roots, resulting in an interesting strategy for zooplankton to avoid critical periods of flood or drought by ensuring their displacement in space and permanence in time.

It may be concluded that the roots and submerged parts of aquatic vegetation house viable stages of resistance zooplankton. This phenomenon allows the dispersion of resistance stages and therefore colonization of new habitats during the displacement of macrophytes species. On present evidence, *Eichhornia crassipes* and rotifers are the organisms which are most likely to participate in this dispersal mechanism.

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