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Zooplanktophagy in the natural diet and selectivity of the invasive mollusk *Limnoperna fortunei*

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Abstract Since the 1990s the Río de La Plata basin has been widely colonized by the invader mollusk *Limnoperna fortunei*. In spite of a relatively well-developed knowledge of the biology and ecology of this mollusk, not much is known about its natural diet and possible food selectivity. Stomach contents of 120 specimens attached to the roots of *Eichhornia crassipes*, and available planktonic food sources, taken from seven representative environments of the Paraná River floodplain, were analyzed. The diet consisted of 156 taxa with a wide size range (2–1,178 μm) and representing a great variety of organisms. Phytoplankton was dominant in abundance (98.6% of the total diet), while zooplankton, mainly small cladocerans, was dominant in volume (67% of the total diet). *L. fortunei* showed a positive food selectivity for organisms with limited escape ability and low to moderate size (Euglenophyta, Rotifera, Chydoridae and Bosminidae), and a negative selectivity for many algae. Therefore, the plankton community structure would be changed due to this differential predation pressure. These are the first observations about the feeding of *L. fortunei* upon zooplankton. The results of the present study agree, in general, with those of descriptive field studies and laboratory experiments on the effect of *Dreissena polymorpha* on zooplankton, but differ in some aspects. The differences suggest the possibility of different impacts on the ecosystem, and a probable complementary coexistence in potentially 'invadable' environments. Ecological interaction between *L. fortunei* and the invasive hydrophyte *Eichhornia crassipes* suggests a possible synergistic effect on the distributional efficiency of the mollusk.

Keywords Golden mussel · Invasive species · Plankton · Selective feeding · *Dreissena* · *Eichhornia*

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Introduction

Limnoperna fortunei (Dunker 1857) (Bivalvia, Mytilidae), also called "golden mussel", is a bivalve mollusk native to estuarial waters of China and southeastern Asia and also found inland (Morton 1973, 1977). This mollusk was discovered in the Río de La Plata Estuary (Argentina) (Pastorino et al. 1993) where it probably entered while still in larval or young adult form, introduced in ballast water released by transoceanic vessels in the early 1990s (Darrigran and Pastorino 1995). Since then, this mollusk started invading several environments of the Río de La Plata basin reaching other countries such as

Uruguay, Brazil, Paraguay and Bolivia (Dreher Mansur et al. 1999). It has also widely colonized the basin of the Paraná River, the main tributary of the Río de la Plata, thus inhabiting the principal and secondary channels, alluvial plain, and several other tributaries (Darrigran and Ezcurra de Drago 2000; Di Persia and Bonetto 1997; García Solá et al. 2000; Villar et al. 1997).

Among their most negative aspects, invading species may be accountable not only for the extinction of native species (Gurevitch and Padilla 2004) but also for great economic losses (Pimentel et al. 2000). Byers et al. (2002) highlight the fact that despite their similarities, invading species may exert widely different impacts depending on the characteristics of the receptor environments. In accordance with these authors, Boltovskoy et al. (2006) emphasize the risks taken when presupposing that due to the biological and ecological similarities with *Dreissena polymorpha* (Pallas), the impact exerted by *L. fortunei* on the aquatic ecosystems must be similar; noting that from various points of view, in particular environmental ones, South America is considerably different from North America and Europe. In the comparative analysis of the biological and ecological features of the two most conspicuous invader mollusks of recent times, Karatayev et al. (2007a, b) cite numerous similarities but also some differences, particularly regarding the trophic aspect, since whereas *D. polymorpha* feeds on detritus, phytoplankton, bacterioplankton and zooplankton, *L. fortunei* would only feed on detritus and phytoplankton.

Data resulting from experimental laboratory and field tests indicate that *L. fortunei*, with a high filtering rate, has a strong impact on nutrient recycling, phytoplankton and aquatic plant growth, and water transparency (Cataldo et al. 2006; Sylvester et al. 2005). In spite of the existing background knowledge of the biology and ecology of the golden mussel (Boltovskoy and Cataldo 1999; Cataldo and Boltovskoy 2000; De Oliveira et al. 2006; Maroñas et al. 2003), not much is known about its natural diet. Data on the feeding spectrum of the mussel on natural phytoplankton were presented by Cataldo et al. (2006) but nothing is known about grazing on zooplankton. Recent studies performed in secondary channels of the Middle Paraná River show a decrease in the current chlorophyll-a concentrations and zooplankton abundance compared to periods prior to this

mollusk invasion (Rojas Molina and José de Paggi 2008). In this work it is suggested that the likely negative effect of *L. fortunei* is due not only to the indirect consequence of the consumption of primary zooplankton food source (phytoplankton), but also to direct predation on some zooplankton components. Therefore, our objective is to analyze the diet and possible feeding selectivity of the invasive mollusk *Limnoperna fortunei* in environments of the Middle Paraná River.

Study area

The Paraná River, the second largest hydrographical system in South America and fifth in the world, drains an area of 26,106 km^2 along its 3,800 km length. The middle stretch is classified as a large floodplain river with a slight slope (3–5 cm/km) and 16,000 m^3/s of average annual discharge. The wide floodplain (13,000 km^2) is located along its right bank comprising thousands of permanent and temporary bodies of water, a great number of islands and banks of loose sediment (Drago 1989; Ramonell et al. 2000).

The selected sampling unit constitutes a broadened region of the Paraná River where the secondary channel Colastiné River originates, which after a course of 53 km, drains back into the main channel. The study area is delimited by the Paraná main stem, the Colastiné and Colastinecito rivers. It corresponds to the geomorphological unit "meander plain" composed of numerous meander scrolls partially or totally inactive during most of the year (Iriondo 1972).

Samples were collected from seven representative environments of the Paraná River floodplain located at Timbó Island (Fig. 1). Samplings were carried out on October 11–12, 2006, during a medium–low water period (2.6 m level at Santa Fe harbor). This is the reason why the area was hydrologically inactive, constituting a set of low-depth lentic bodies of water with their surface mostly covered with floating and rooted aquatic vegetation, mainly *Eichhornia crassipes* (Mart.), and *Paspalum repens* Bergins, followed by *Pistia strationes* Linn., *Polygonum acuminatum* Martius, *Salvinia herzogii* de la Sota, *Ludwigia peploides* (Kunth), *Cyperus digitatus* Roxb, *Scirpus cubensis* Kurtz and several other plants of lesser frequency. Environmental factors were quite similar
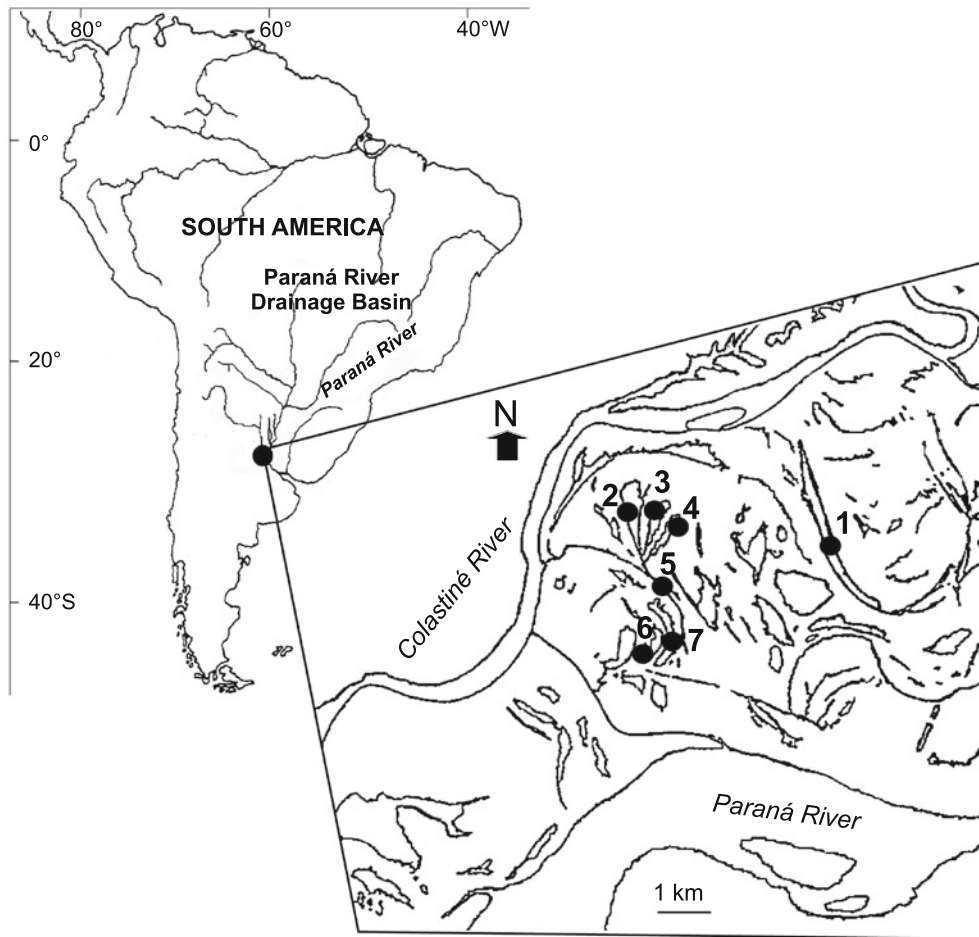
Fig. 1 Map showing the location of the Paraná River and the studied sites: (1) Colastinecito River, (2) La Ferranda Pond, (3) La Horqueta Pond, (4) La Horqueta II Pond, (5) El Mini Pond, (6) El Paso Pond, (7) Mini Pond

among the studied bodies of water, showing low variability. Mean temperature: 23.6°C (22–31°C), mean conductivity: 108.3 µs/cm (63–151 µs/cm), mean pH: 7.7 (7.68–7.79), mean dissolved oxygen: 6.2 ppm (5.24–7.01 ppm) and mean transparency: 62.7 cm (52–78 cm).

Materials and methods

In order to study the potential feeding resource, phytoplankton samples were taken with a 2-l Ruttner bottle and fixed with acidified lugol. Simultaneously, 100 l of water from the environment for zooplankton samples were filtered using a 20-l Schindler-Patalas trap fitted with a 50 µm mesh net. Samples were fixed in situ with 10% formaldehyde. The quali-

quantitative analysis of the zooplankton samples was performed under a binocular microscope. Rotifers and nauplii were counted and identified in a 1 ml Sedgwick-Rafter chamber, and microcrustaceans in a 5 ml Bogorov chamber. At least 100 individuals of the first dominant species were counted per sample. The total number of individuals counted per sample ranged between 275 and 782 (mean = 577) and the mean counting error was 22.9%. Algae quantification was carried out under an inverted microscope in sedimentation chambers, following the Utermöhl method (1958).

Limnoperna fortunei adult specimens were found only in the roots of *E. crassipes*, they were manually collected and placed in containers with 10% formaldehyde solution. The mollusks for which stomach content analyses were performed were selected among

those of greater size so that their handling and dissection in the laboratory were facilitated. Therefore, results were comparable among sampling sites, minimizing the possibility of error caused by varying sizes. In order to establish an acceptable number of stomachs to be analyzed per site, the Chao2 mean index (richness estimator) was used (Chao et al. 2009). The valve lengths of 140 selected mollusks (20 specimens from each sampling site) were measured with a 0.02 mm precision vernier caliper. The general mean size of the organisms studied was 16.8 mm (coefficient of variation = 13.46%). The mean range per body of water was 15.3–18.2 mm and their coefficients of variability ranged between 9 and 16%.

The stomach contents of the mollusks studied were extracted under a stereo binocular microscope by means of dissection needles. It should be noted that all the stomachs were included in the study, regardless of their degree of completeness. Once open, each stomach content was placed individually on a slide with some drops of a mixture of distilled water and 10% glycerol and then slightly pressed under a 24 mm × 40 mm cover slip. Counts and measurements were performed under a compound binocular microscope. "Animal" organisms—a group in which protozoans are included arbitrarily—of each stomach were identified and counted in full. In the case of algae, total stomach contents were estimated by counting the organisms found in fields at random, until reaching 100 individuals of the dominant taxa. In most cases, identifications were performed at the species level. Even though some organisms were partially destroyed or distorted by digestive processes, most of them were able to be identified at least to genus or family levels.

In order to represent and specify the importance of various-sized taxa within the diet of the studied mollusk, the biovolume was calculated. Volumes of

food items and potential food organisms were determined by approximation to regular geometric shapes, or by converting weight data of the organisms cited in the literature to volume (Dumont et al. 1975; Hillebrand et al. 1999; Ruttner-Kolisko 1977). On the basis of such measures, five size groups were established: two for algae (I and II) and three for animals (III, IV and V) (Table 1).

Feeding selectivity was calculated as the linear index of food selection proposed by Strauss (1979), using the formula: $Li = ri - pi$ (where ri = relative abundance of the feeding item i in the diet and pi = relative abundance of item i in the environment). Li ranges from -1 to $+1$ and when $Li = 0$, selective feeding does not occur. When $Li < 0$, less food item i occurs in the diet than expected from random feeding, indicating negative selection (avoidance or inaccessibility). When $Li > 0$, more food item i occurs in the diet than expected, indicating positive selection (preference). According to Strauss (1979), Li distribution is approximately normal, therefore statistical comparisons between a calculated value and a null hypothesis are allowed. The mean selectivity index was compared to zero (H_0) using Student's one sample t-test, two-tailed (Zar 1984).

With the aim of comparing abundances and organisms' biovolume of the stomach content among the studied sites, a non-parametric Kruskal–Wallis test was applied. A significance level of 95% was used for all statistical analyses.

Results

The organisms identified were assembled into 14 groups. Algae were grouped according to morphological and taxonomical characteristics: solitary and

Table 1 Size groups (#) of the food items recorded in the *L. fortunei* stomach and in the studied sites

Sizes (μm^3)	#	Taxa
$<10^3$	I	Cyanobacteria, Chlorococcales, most Volvocales, most Bacillariophyceae Centrales, Chrysophyceae and Cryptophyceae
10^3 to 57×10^3	II	Some Chlorococcales, filamentous Chlorophyceae, most Zygnematales, most Bacillariophyceae Pennales, Euglenophyta, and Dinophyceae
35×10^3 to $<16 \times 10^5$	III	Protozoa, Rotifera, Nematodo and *L. fortunei* larvae
16×10^5 to 10^7	IV	Chydoridae, Bosminidae, *Ceriodaphnia cornuta*, nauplii larvae and Ostracoda
$>10^7$	V	Copepoda and Cladocera (Sididae, Moinidae, Daphnidae, Macrothricidae, Chydoridae)

cenobial algae, colonial algae, filamentous algae, Euglenophyta, Dinophyta and Cryptophyta. Animal organisms were grouped into: Protozoa, Rotatoria, Cladocera, Copepoda (nauplii, copepodid larvae and adults), Ostracoda, Nematoda, *L. fortunei* larvae and "others".

Potentially available feeding resource

A total of 168 taxa were recorded in the environments. Algae were characterized by 70 taxa belonging to Cyanobacteria, Chlorophyceae, Ulotrichales, Xantophyta, Zygnematales, Bacillariophyceae, Chrysophyceae, Euglenophyta Dinophyta and Cryptophyta. The "Animal" group was composed of: Rotifera (52 taxa), Cladocera (30 taxa), Copepoda (11 taxa), Ostracoda, Nematoda, *Limnoperna fortunei* larvae and Protozoa.

An average of 4,900 ind./ml was recorded. Algae constituted the highest abundance (99% of the organisms) dominated by Cryptophyta (*Cryptomonas* sp.), solitary and cenobial algae (Bacillariophyceae Pennales, Chlorophyceae Chlorococcales and Volvocales) (Table 2). Animal organisms were represented principally by Rotifera, Cladocera, and Copepoda, though dominated by the former (58% of the animals) and in a smaller proportion by the latter (30% of the animals, mainly nauplii larvae) (Table 2). Among Rotifera, the most abundant genera were *Keratella, Lecane, Colurella, Polyarthra, Synchaeta* and *Lepadella*. Among microcrustaceans Chydoridae and nauplii larvae were dominant.

When taking into consideration the size structure of organisms (Fig. 2), smaller sizes (I and II) exhibited greater density, and size II made an important volumetric contribution. Densities of other
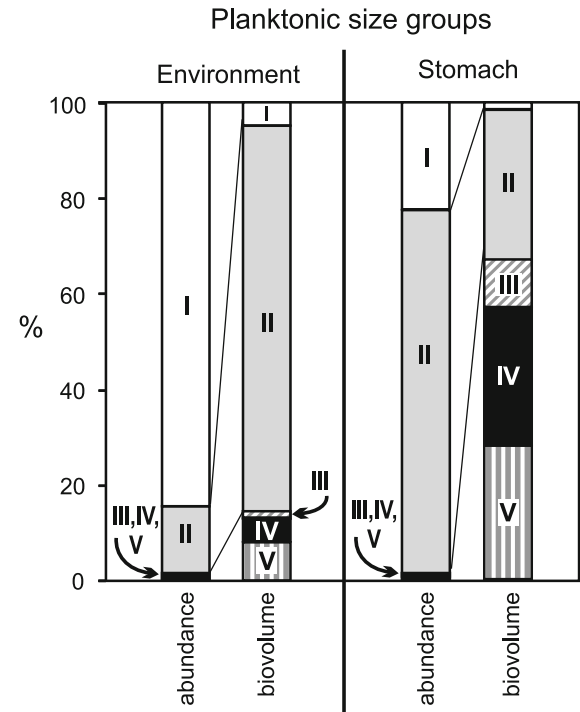

Fig. 2 Relative abundance and biovolume (%) of the size groups (*I*: $<10^3$, *II*: 10^3 to 57×10^3, *III*: 35×10^3 to $<16 \times 10^5$, *IV*: 16×10^5 to 10^7 and *V*: $>10^7$ μm³) of food items recorded in the *L. fortunei* stomach and in the environment

Taxa	Mean	SD	Min	Max
Solitary and cenobial algae	1,917 (ind./ml)	1942.8	600.3	4825.5
Colonial algae	92 (ind./ml)	66.5	28.2	161.8
Filamentous algae	312 (ind./ml)	383.2	26.9	958.9
Euglenophyta	405 (ind./ml)	273.9	112.9	943.8
Dinophyta	71 (ind./ml)	62.3	13.5	164.9
Cryptophyta	2,103 (ind./ml)	1896.8	431.4	6104
Protozoa	1,389 (ind./l)	193.9	17.5	362.5
Rotatoria	175 (ind./l)	242.2	15.7	678.7
Cladocera	26 (ind./l)	30.3	4	88.3
Copepoda	90 (ind./l)	54.7	3.2	163.75
Ostracoda	1 (ind./l)	0.9	0.2	2.5
Nematoda	8 (ind./l)	2.6	6.25	10
Limnoperna fortunei (larvae)	0.6 (ind./l)	0.3	0.3	1

Table 2 Potentially available feeding resource for *L. fortunei* found in the studied sites

SD standard deviation, *min* minimum value, *max* maximum value

sizes were very low. However, size V biovolume was important, mainly because of Cyclopoida. It is important to mention that among larger zooplankton sizes, individuals which were not present in the mollusk diet were recorded: adult copepods (Calonoida and Cyclopoida), *Alona glabra* Sars, *Ceriodaphnia dubia* (Richard), *Ceriodaphnia reticulata* (Jurine), *Diaphanosoma* sp., *Ilyocryptus spinifer* Herrick, *Moina* sp., and *Simocephalus* sp., among others.

Diet composition

As to the stomachs analyzed, a total of 156 taxa represented by the same groups present in the environment, except Cryptophyta which was not found in the stomachs, were recorded in the diet. Algae were characterized by 81 taxa, while animals presented 46 Rotifera, 17 Cladocera and 4 Copepoda. Protozoa, Ostracoda, Nematoda and *L. fortunei* larvae were also identified. Very infrequently, remnants of other organisms such as insect antenna parts, probably digested as detritus rather than complete live organisms, were found. This diversity of organisms implies a wide range of size: from 4 μm to slightly over 1 mm length. Abundance and biomass of the different animals and algae groups did not present significant differences among sites (Kruskal–Wallis test).

Phytoplankton was numerically dominant in the mollusk diet, with an average of 1,825 ind./stomach (98.6% of the organisms), Euglenophyta being the most frequent (99% of the stomachs) and abundant (1,502 ind./stomach, 74% of the organisms), mainly species of *Trachelomonas*. Solitary and cenobial algae (mainly Bacillariophyceae and Chlorococcales) followed in importance with an average of 230 ind./stomach (17% of the organisms) and a frequency of occurrence of 96% of the total stomachs. Animal organisms were represented by an average of 18 ind./stomach, with a very low contribution to total density (1.4%). Rotifers were among the animal organisms of the highest frequency (96% of the stomachs) and relative abundance in all sites (mean = 15 ind./estomach, 1% of the organisms). They represented 81% of the animals, mainly the genera *Keratella* and *Lecane* (up to 56 and 47% of the rotifers, respectively). With a lesser frequency (64% of the stomach), cladocerans constituted 9.5% of the animals

(especially Chydoridae and Bosminidae individuals) and copepods were represented exclusively by nauplii and copepodids larvae whose frequency (24% of the stomachs) and proportion were very low (mean = 0.3 ind./estomach, 1.7% of the animals). Protozoa, Ostracoda, Nematoda and larvae of *L. fortunei* accounted for 0.1% of the total abundance.

Taking the size groups into account (Fig. 2), smaller sizes (I and II) represented by the phytoplankton were the ones of a greater density in the diet of this mollusk (22 and 77% of the organisms, respectively). The rest of the sizes made a minimum contribution, where size III that gathered the smallest animal organisms presented the greatest proportion among them. Contrarily, if the biovolume of the different groups is considered, animals made the greatest contribution to the diet (67% of the organisms), fundamentally size IV (mainly small cladocerans) and V (especially large cladocerans and copepodit larvae). However, size II made an important contribution mainly due to euglenoids (Fig. 2).

Feeding selection

According to Strauss' linear index (*L*) applied to the abundance of the taxonomic groups, in the case of phytoplankton, the feeding item with the highest positive selection was Euglenophyta (Fig. 3), which would be included within the size II group (Fig. 4a). Solitary, cenobial algae, and Cryptophyta were not positively selected as food (Fig. 3), this coinciding with the negative selection of the size I group whose main components were the aforementioned algae (Fig. 4a).

Regarding animal organisms, they all had a positive selection, Rotifera and Cladocera being the most selected ones (Fig. 3). This might indicate a positive selection clearly biased toward smaller animals (size group III) (Fig. 4a), comprising principally Rotifera, followed by size IV represented mainly by Bosminidae and small Chydoridae, the dominant Cladocera.

Among the main rotifers and cladocerans in the environment (Fig. 5), a clear positive selection for *Keratella*, *Lecane*, Bosminidae and Chydoridae and a clear negative selectivity for *Polyarthra* and *Synchaeta* were exhibited. With the exception of *Keratella*, all selectivity values were significant.

Fig. 3 Strauss's linear index of selectivity (L) applied to the abundance of phytoplankton (**a**) and zooplankton (**b**) taxa. $L > 0$: positive selection, $L < 0$: negative selection, $L = 0$ absence of selectivity (* $P < 0.05$)
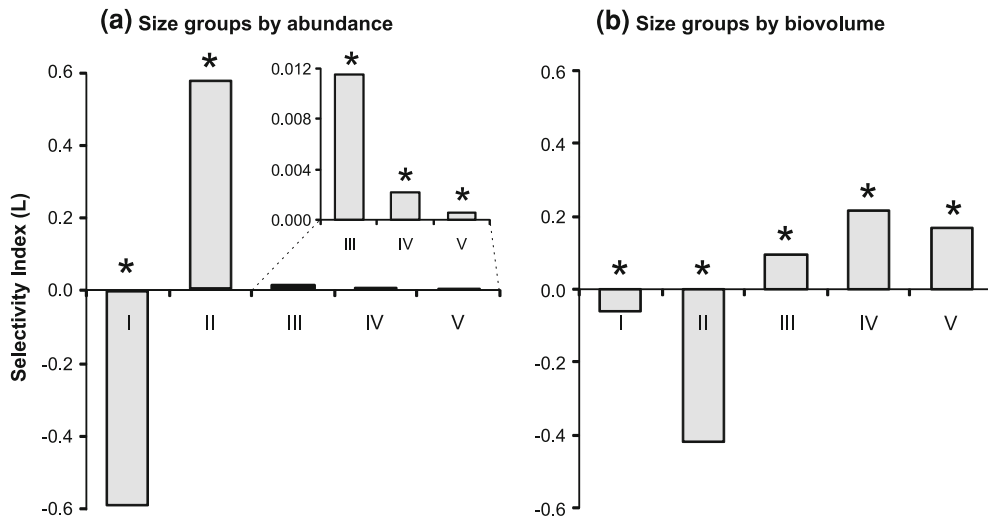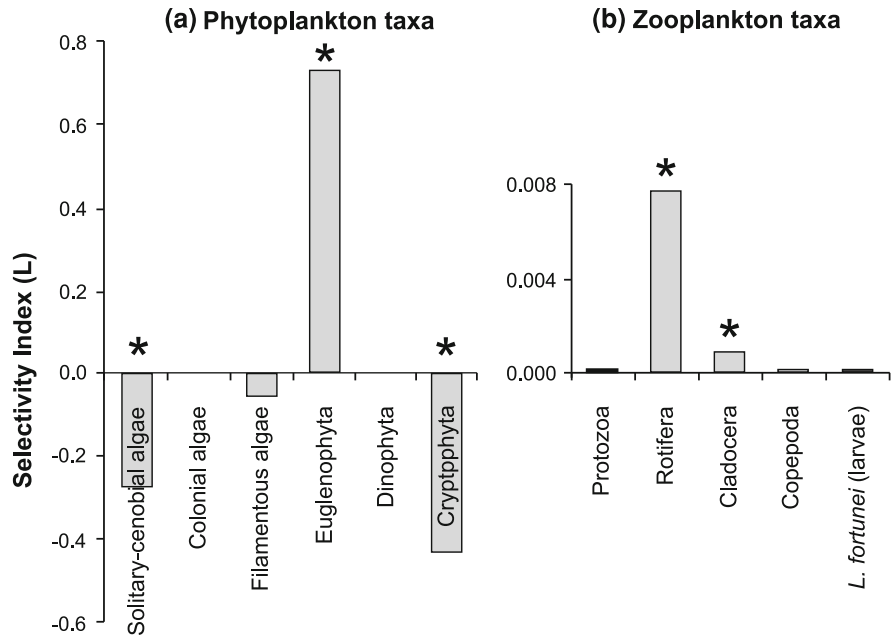

Fig. 4 Strauss's linear index of selectivity (L) applied to the abundance (**a**) and biovolume (**b**) of planktonic size groups (I: $<10^3$, II: 10^3 to 57×10^3, III: 35×10^3 to $<16 \times 10^5$, IV:

16×10^5 to 10^7 and V: $>10^7$ μm^3). $L > 0$: positive selection, $L < 0$: negative selection, $L = 0$ absence of selectivity (* $P < 0.05$)

Considering size groups by volume (Fig. 4b), the selectivity pattern was different. Smaller sizes (I and II) were negatively selected in the diet, contrary to what is shown for density of size II (Fig. 4a). Biggest sizes (III, IV and V) continued having a positive selection which was even higher. Sizes IV and V stood out with the highest values.

Discussion

Considering the resources available in the environment, it would be reasonable to expect the *L. fortunei* diet to be dominated by solitary and cenobial algae and mainly Cryptophyta due to their higher concentrations. However, our findings show the absence of
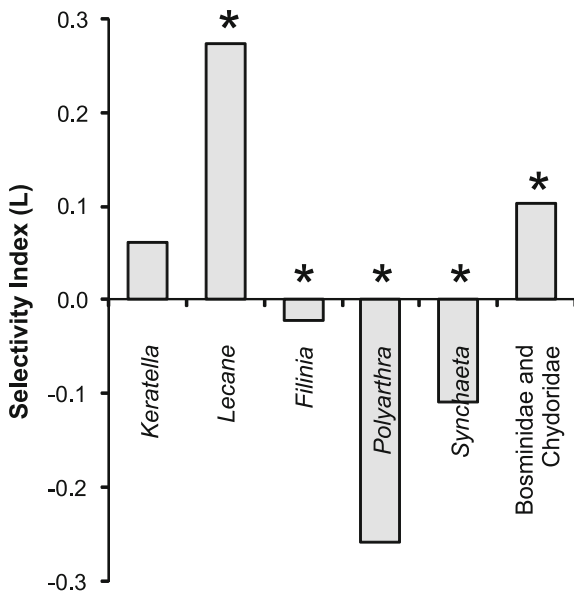
Fig. 5 Strauss's linear index of selectivity (L) applied to the abundance of the main rotifers and cladocerans. ($L > 0$: positive selection, $L < 0$: negative selection, $L = 0$ absence of selectivity) (* $P < 0.05$)

this last group in the diet and its consequent negative selectivity. At a first glance, it is not easy to understand this absence taking into account its small size (about 10 μm) and poor mobility. Moreover these algae seemingly do not possess mechanisms preventing them from being captured such as negative palatability, thorns, which make their digestion more difficult (Gladyshev et al. 1999). It could also be inferred that the filtration mechanism of the mollusk gills does not have the ability to retain so minute particles. However, in the experience of Sylvester et al. (2005) with determining the filtering rate of this bivalve, *Chlorella vulgaris* monocultures of small cellular diameter were used (5–10 μm). Similarly, experiences with other mytilids such as *Dreissena polymorpha* were carried out on algae cultures of greatly reduced cellular diameters (*Synechococcus elongates*: 1 μm; *Chlamydomonas reinhardii*: 6 μm; *Chlamydomonas noctigama*: 12 μm; *Cryptomonas* sp.: from 0.7 μm; *Scenedesmus obliquus*: 4.7 μm) (Dionisio Pires et al. 2004; Sprung and Rose 1988). It could also be mentioned that field studies have shown the preference for *D. polymorpha* over *Cryptomonas* sp. (Naddafi et al. 2007; Ten Winkel and Davids 1983). Other possible reasons for the absence of these algae among the stomach

contents of *L. fortunei*, which is manifested as apparent negative selection, might be that they are rapidly digested. Another reason for their absence might be the effect of the fixative, since formaldehyde has been frequently reported to cause harm to algal cells and protozoans of weak consistency (Leakey et al. 1994).

Gliwicz and Pijanowska (1989) pointed out that prey selection as a function of prey body size is common for size-dependent predators (exclusively invertebrates), which rely mainly on tactile information rather than vision for detecting and locating prey. Regarding organisms of animal origin, mollusks are capable of selecting them, at least because of their size, since organisms of sizes larger than those contained in the digestive tract were recorded in the environment. Among the large-sized organisms recorded in the environment, Cladocera and adult Copepoda [*Alona glabra*, *Ceriodaphnia dubia*, *Ceriodaphnia reticulata*, *Diaphanosoma* sp., *Moina* sp., *Simocephalus* sp., *Macrocyclops albidus* (Jurine), *Microcyclops anceps* (Richard), *Argyrodiaptomus furcatus* (Sars), *Notodiaptomus conifer* Sars, *Notodiaptomus inconpositus* Brian, *Notodiaptomus spiniger* (Brian), among others] ranging from 300 to 1,600 μm long were found. The majority of these organisms, particularly calanoids, followed by cyclopoids and large-sized cladocerans, mainly *Diaphanosoma*, show high escape ability due to their relatively high-speed locomotion. Kerfoot et al. (1980) suggested that the morphological characteristics of copepods (four pairs of thoracic appendages modified for locomotion, a flexible and hydrodynamic body, two pairs of long and mobile antennae, an abdomen articulated with the thorax and thin exoskeleton) allow them to maneuver quickly and accelerate rapidly, reaching speeds of up to 20–35 cm/s. Several authors (Caparroy et al. 2000; Fields and Yen 1997; Yen et al. 1992) have demonstrated through experiments with copepods that they are capable of detecting deformations in the flow field as hydrodynamic signals generated by the predator movements, provoking an escape reaction in order to avoid being captured. Such arguments might support in the present work the absence of selectivity for these organisms ($L = 0.00015$, for copepodids).

In general, planktonic cladocerans have limited locomotive abilities, at least as an escape mechanism, owing to the fact that they depend on a single pair of

appendages for locomotion (second pair of antennae) adapted to maintain a more or less stable position in the water column rather than for lateral translocation (Kerfoot et al. 1980; Williamson 1983). Some cladocerans like *Diaphanosoma*, provided with large antennae, are capable of moving around with sudden and quick jumps with the aim of avoiding being captured by predators. In the presence of a suction flow that simulates fish capture actions, *Diaphanosoma*'s probability of capture is lower than that of other planktonic cladocerans such as *Daphnia* and *Ceriodaphnia*, but larger than that of a copepod (Drenner and McComas 1980). In our study, *Diaphanosoma* (with a maximum of 3.7 ind./l) was recorded in four out of seven environments. However, it was not found in any of the 80 stomachs from the mollusks of the four sites mentioned.

Smaller cladocerans (mainly individuals of Bosminidae and Chydoridae), belonging to size IV group, were the most abundant in the environment and also presented a significant positive selection ($P = 0.03$) among zooplankton organisms. They are about 300 μm long, have a relatively hard carapace, and exhibit slow locomotion. These organisms present a passive escape response called akinesis ("playing dead" or "becoming motionless"), which consists of stopping any kind of movement, retracting their antennae, closing the valves and letting themselves fall passively, sinking through water (Kerfoot et al. 1980; Williamson 1983). Such strategy, which evolved in the presence of active predators with mechanoreceptors and which, jointly with post-contact defenses (thick exoskeleton for difficult capture in the case of *Chydorus*, and sharp mucrons in the case of *Bosmina*), would, however, not be efficient in front of the filtering mollusk.

Euglenoids and rotifers showed a high positive selectivity, certainly favored by their relatively low mobility among the mobile plankton organisms. The former use the emergent flagella as a motor system and the forward thrust in swimming is achieved by accelerating a small volume of water rapidly backward with the flagellum (Cosson et al. 2001). Rotifers' swimming movements are in general weak and regular and they also have a limited ability to accelerate and get away from danger (Kerfoot et al. 1980). These low mobility and anti-predation post-contact strategies (presence of spines, thick body walls, gelatinous cover, etc.) (Kerfoot et al. 1980)

would not be enough to avoid being captured by the mollusks. These considerations would be valid to explain the high proportion of individuals of the genera *Keratella* and *Lecane* consumed by the mollusks. Nevertheless, some rotifers like *Polyarthra*, *Synchaeta* (which were very abundant in the environment but not in the stomachs) and *Filinia* (recorded in the environment only) exhibit pre-contact strategies as escape responses when facing a predator. *Synchaeta* shows rapid translocation (3.19 mm/s, Walton 1988), and both *Polyarthra* and *Filinia* have mobile swimming appendices (paddles and bristles, respectively) which allow evasive escape. This happens whenever they perceive the movement of the predator or when they enter the feeding currents of larger suspension feeder organisms (Gilbert 1987; Walton 1988; Williamson 1987). It is reasonable to assume that this behavior might be the reason for the absence of such rotifers in the mollusk diet. Other loricate soft-bodied rotifers lacking a specific escape mechanism (*Conochilus, Epiphanes, Monnomata, Cephalodella*), were also not recorded in the diet. To explain this finding, we might resort to other reasons including their rapid digestion. On the other hand, in the case of *Conochilus*, thanks to studies by Diéguez and Balseiro (1998) and Gilbert (1988), it is known that species of this genus are capable of developing a defensive strategy in the presence of an invertebrate predator [*Parabroteas sars* Daday, *Daphnia pulex* (Leydig)] by forming colonies and increasing their size by enlarging the number of constituent individuals, which would make it difficult for the predator to handle and ingest the prey.

The results of the present study agree in general with those of descriptive field studies and laboratory experiments about the effect of *Dreissena polymorpha* on zooplankton, but differ in some aspects. In field experiments in the Ohio River and in the St. Lawrence River, zebra mussels caused a significant decline in density of rotifers *Keratella crassa* Ahlstrom and *Polyarthra vulgaris* (Carlin) through predation and competition (Jack and Thorp 2000; Thorp and Casper 2002). The population growth of crustacean zooplankton was significantly negatively affected by the mollusk 'because its high filtration rate could reduce food availability to these macro-zooplankton' (especially for *Diacyclops*, *Bosmina* and *Diaphanosoma*, Jack and Thorp 2000), or none of

the microcrustaceans showed a significant mollusk effect (Thorp and Casper 2002). Laboratory experiments (MacIsaac et al. 1991, 1995; Mikheyev in Sprun and Rose 1988; Wong and Twining 2003) proved that *D. polymorpha* preys directly on small zooplankton organisms such as rotifers and *D. polymorpha* veliger larvae, but large zooplankton, mainly copepod nauplii and Cladocera, were not affected. Moreover, ciliated tintinnids, rotifers and nauplii decreased significantly in the Hudson River after the invasion of *D. polymorpha*, while copepod and cladoceran densities were decreased (especially *Bosmina*), but not significant (Pace et al. 1998). Horgan and Mills (1997) pointed out that the largest particles that this mollusk can collect are *Gleotrichia echinulata* colonies (1,200 μm) but most of them were subsequently ejected, and it is not mentioned whether the remaining colonies or part of them are finally ingested. In this sense, it is important to emphasize the differences between the collection of algal aggregations and the ingestion of invertebrates with greater or lesser escape capability. In this study, relatively large organisms with different locomotion methods, such as copepodids of *Tropocyclops* sp. and nematods (717.5 and 1,178 μm, respectively), were found in the stomachs of several specimens of *L. fortunei*. Indeed, *L. fortunei* showed a strong tendency to capture zooplankton organisms such as rotifers, nauplii of copepods and small cladocerans like Bosminidae and Chidoridae.

Rojas Molina and José de Paggi (2008) suggested a likely negative effect of *L. fortunei* on zooplankton and pointed out a decrease in rotifers, mainly the genus *Keratella*, which is one of the most frequent and abundant rotifers in the environments of the Middle Paraná River system (José de Paggi 1981, 1984; José de Paggi and Paggi 2007). Our results likewise support the hypothesis of these authors, providing information about filtration feeding of *L. fortunei* populations, which might tend to diminish and change the composition of phytoplankton and zooplankton, either directly by predation on the resource or indirectly by competing for the feeding resource. Selective feeding is recognized as an important mechanism through which planktonic communities are structured by predation (Fields and Yen 1997).

Boltovskoy et al. (2006) and Karatayev et al. (2007a, b) suggested that *L. fortunei* could colonize a great part of the Northern Hemisphere already invaded by *D. polymorpha* and to coexist taking into account their ecological differences. It is likely that the morphological differences that *Limnoperna fortunei* presents when compared to *D. polymorpha*, such as the larger size of the inhalant siphon opening (Morton 1973), would allow the former to collect and presumably swallow larger prey. In any case, the consequences of such a capture mechanism would have a more negative impact on the zooplankton than in the case of *D. polymorpha*. Moreover, since it seems that the trophic niche of *L. fortunei* is broader than that of *D. polymorpha* we could consider the possibility of a complementary coexistence in the same environment.

Though it is not the main goal of this study, it is also interesting to emphasize the fact that the environmental characteristics of floodplain bodies of water like the ones studied, where the scarcity or absence of firm solid substrata seems not to be an obstacle for colonization by this mollusk. *L. fortunei* is capable of utilizing the seemingly inadequate support offered by the thin and flexible roots of *Eichhornia crassipes*. In this sense, it is valid to reflect upon the possible future consequences of the association of an old and a new successfully invasive species. *E. crassipes*, commonly called water hyacinth and often termed 'a perfect invader' (Ashton and Mitchell 1989), is a free-floating hydrophyte native to lowland tropical South America having probably originated in the Amazon and La Plata basins (Barrett 1977; Barrett and Forno 1982; Holm et al. 1977). Over the past 150 years *E. crassipes* has invaded, mainly anthropogenically, aquatic ecosystems in almost every continent, having been reported from most countries between 40° N and 45° S (Gopal 1987; Holm et al. 1977). *E. crassipes* would favor the *L. fortunei* colonization providing an alternate attachment surface and hence a likely effect of invasional meltdown sensu Simberloff and Von Holle (1999).

Both species are known to have wide ranges of tolerance for most environmental factors (François 1970; Karatayev et al. 2007a, b; Kikuchi et al. 1997; Oki et al. 1978; Ruiz Téllez et al. 2008). It is also interesting to point out the existence of a remarkable coincidence between them. So, it is possible to infer that the presence of water hyacinth would increase the potential invasibility of freshwater environments currently free of *L. fortunei*.

Due to the presence of *E. crassipes*, local changes in ecological conditions have already been associated with the transmission of human diseases because it provides a favorable habitat for increased populations of snails that transmit schistosomiasis (Plummer 2005).

Conclusions

In South American floodplain lakes *L. fortunei* feeds upon both animal and vegetable matter, which are siphoned and swallowed as suspended particles.

Zooplanktic organisms are extensively consumed by *L. fortunei* and constitute an important part of the total volume of its diet.

Limnoperna fortunei shows a positive selectivity for organisms with limited escape abilities and low to moderate size and a negative selectivity for many algae. Therefore, the plankton community structure may change due to this differential predation pressure.

Morphological and ecological differences between *L. fortunei* and *D. polymorpha* suggest different impacts on the ecosystem and the probability of complementary coexistence in potentially 'invadable' environments.

Ecological interaction between *L. fortunei* and the well-known invasive hydrophyte *Eichhornia crassipes* suggests a possible synergistic effect on the spread efficiency of the mollusk.

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