

Larvae of the invasive species *Limnoperna fortunei* (Bivalvia) in the diet of fish larvae in the Paraná River, Argentina

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Abstract To assess the trophic impact of the planktonic larvae of the invasive Asian bivalve *Limnoperna fortunei*, introduced in South America around 1990, we investigated the gut contents of fish larvae collected at monthly intervals between October 2000 and March 2001 at three locations along a 600 km stretch of the Paraná River, and during November 2004 in two areas of marginal lagoons connected to the river near the city of San Nicolás, Argentina. Zooplankton was also collected in the lagoons in 2004. In total, 11,956 fish larvae were retrieved, of which

1,511 were used for detailed analyses. Of the 15 fish taxa collected, 11 had veligers of *L. fortunei* in their gut. Fish larvae with empty guts represented 60% (San Nicolás) to 72% (Paraná River) of the total number of fish. Proportions of feeding fish larvae with *L. fortunei* veligers in their guts varied between 20% (San Nicolás) and 56% (Paraná River); in 15% of the guts analyzed, *L. fortunei* was the only food item recorded. For those specimens that had consumed *L. fortunei* larvae and any other food item, *L. fortunei* was the most important item in 55% (Paraná River) to 71% (San Nicolás) of the animals in terms of biomass. No major temporal or spatial changes in the diet were observed along the Paraná River, but the relative biomass contribution of *L. fortunei* larvae differed strongly in fishes of different developmental stage. In protolarvae and mesolarvae, veligers accounted for 30–35% of the gut contents. In metalarvae, veligers accounted for only 3%, indicating enhanced food supply for the earliest fish life stages. Comparison of the relative proportions of the three main zooplankton types (*L. fortunei* veligers, cladocerans, and copepods) in the water and in larval fish guts indicates that *L. fortunei* is always selected positively over the other two prey types. While our results strongly suggest that the expansion of *L. fortunei* results in an enhanced food supply for local fish populations, they do not necessarily imply that

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the overall effect on the ecosystem in general, and on the fish fauna in particular is beneficial.

Keywords *Limnoperna fortunei* · Ichthyoplankton · Prey shift · Ecological impact · Paraná River · Invasive species

Introduction

Limnoperna fortunei (Dunker, 1857), an Asian mytilid bivalve, was first discovered in the Río de la Plata estuary in Argentina around 1990 (Pastorino et al., 1993). At present, it has nearly colonized the entire Río de la Plata basin, and can be found in Argentina, Bolivia, Paraguay, Uruguay, and Brazil, at densities exceeding 200,000 ind. m⁻² (Darrigran, 2002; Brugnoli et al., 2005; Muñiz et al., 2005; Boltovskoy et al., 2006). These sessile bivalves attach to hard substrata by means of a strong byssus, and are readily dispersed as planktonic larvae (Morton, 1979). Larvae are present in the plankton of the lower Paraná River between August and April at densities from 5,000–8,000 ind. m⁻³, with peaks of up to 35,000 ind. m⁻³ (Cataldo & Boltovskoy, 2000).

Predation of *L. fortunei* adults by at least 17 fish species has been recorded in the Río de la Plata basin, indicating that the mussel is an important food item for native fish of ecological and economic importance (García & Protogino, 2005; Boltovskoy et al., 2006). The magnitude of this new trophic resource for large freshwater predators is such that it was suggested to be responsible for the three-fold increase in Argentine freshwater fish landings between ca. 1994 and 2004 (Boltovskoy et al., 2006). However, not only adult fish seem to have benefited from the bivalve: the planktivorous larvae and juveniles of several fish species (Rossi, 1992, 2001; Fuentes & Espinach Ros, 1998) may also benefit from very high densities of *L. fortunei* veligers. This assumption is supported by European and North American surveys on the zebra mussel, *Dreissena polymorpha*, an invasive bivalve that shares several salient biological and ecological traits with *L. fortunei* (Karatayev et al., in press). The free-swimming larvae of the zebra mussel have been found in the digestive tract of at least ten

European and five North American fish species (primarily fry), suggesting that the invasion was associated with dietary shifts, alteration of trophic levels and historical predator-prey roles, and changes in population densities, behaviors, and growth rates of predators (French & Bur, 1996; Molloy et al., 1997).

The objective of the present study was to quantify the impact of *L. fortunei* veligers on larval fish diets in the Paraná River. We compared spatial and temporal differences in prey incidence between fish species. Because some larval fish feed in the main river channel, while others forage in marginal water-bodies of the alluvial plain, data from both environments were analyzed.

Materials and methods

Ichthyoplankton samples were collected monthly in the main channel of the Paraná River, Argentina, near the cities of La Paz, Paraná, and Zárate (Fig. 1), between October 2000 and March 2001 (the only time of the year when fish larvae are present in the water; two samples per site and per month, 36 samples in total). A 0.35 m mouth diameter, 1 m long conical plankton net with 300 µm mesh was used in this study. Stationary horizontal tows were conducted at mid-depth for 5–10 min. Water velocity was generally 0.8 m s⁻¹. In November 2004 seventeen ichthyoplankton (500 µm mesh) and five zooplankton (25 µm mesh) net samples were also collected in the marginal lagoons of El Saco and Laguna Larga, which are connected to the Paraná River near the city of San Nicolás (Fig. 1). Samples were collected in open water areas, and in areas covered by floating macrophytes (chiefly the common water hyacinth, *Eichhornia crassipes*). All samples were fixed with 70% ethanol.

Inclusion of the smaller San Nicolás data set was considered necessary in order to account for the strong environmental - and resulting biological - differences between these two environments. Conditions were generally similar in November 2000 and November 2004 (discharge rates and mean water temperature were within ±5%; Borús et al., 2005), which suggests that

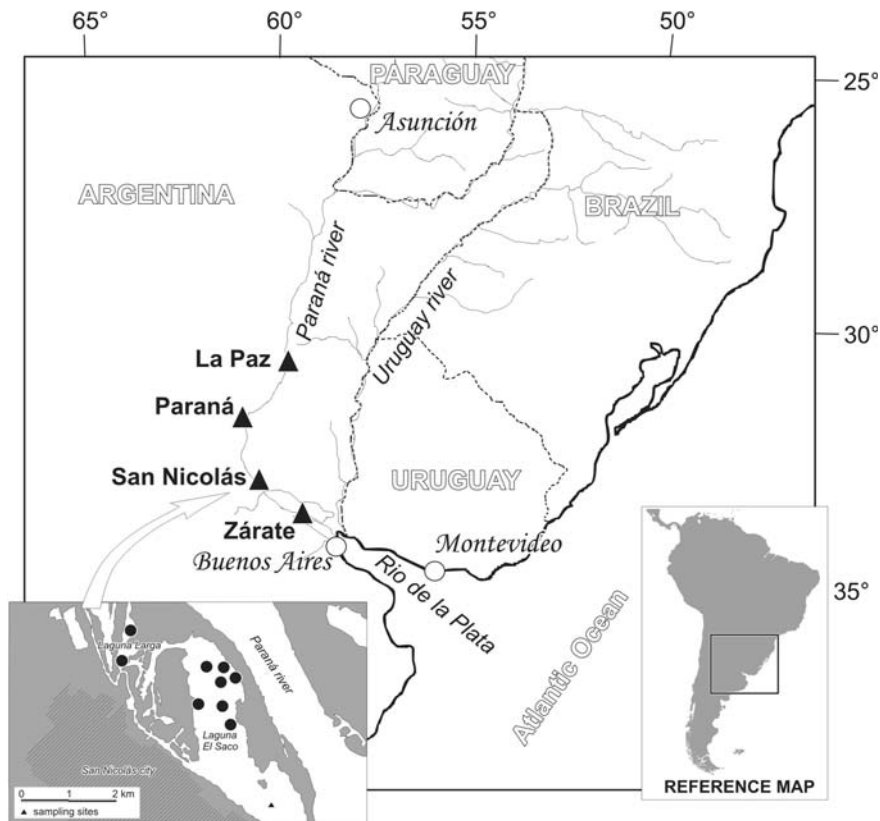


Fig. 1 Sampling sites in the Paraná River (triangles), and in the lagoons of San Nicolás (circles, inset map)

dissimilarities in the ichthyoplankton were not due to environmental year-to-year fluctuations. These marginal lagoons are known to serve as nursery areas for several key fish species, which do not feed in the main Paraná channel, which is reflected by the strong contrasts between these habitats recorded in our survey (see below).

Counts and gut content analyses were based on the entire volume retrieved (when total fish numbers were below 50–100 individuals), or on Folsom splitter subsamples (McEwen et al., 1954) containing at least 50 larvae. Large fish specimens were always removed prior to subsampling, processed, and their relative abundances calculated separately.

Fish were counted, measured, and identified under a binocular microscope provided with a micrometric eyepiece, according to Sverlij et al. (1993) and Nakatani et al. (2001). Developmental stages were assigned to larval fish as follows, protolarvae: no median fins; mesolarvae: with

rays in some median fins; metalarvae: well developed rays in all median fins (Snyder, 1983). Fish larvae were dissected, and their gut contents examined under a binocular microscope. Food items were identified, measured, and quantified. Food items of fish larvae were classified into six categories: *L. fortunei* larvae (trochophores and veligers), cladocerans, copepods, immature insects, fish larvae, and algae. Unidentifiable and unmeasurable remains were lumped into a “unidentified material” category. In total, 11,956 larvae were collected, of which 1,511 were used for detailed analyses.

Frequency of occurrence (FO) of each prey item was estimated as the number of stomachs containing one or more individuals of a given prey item as a proportion of all stomachs with some gut contents (Hyslop, 1980). The biomass (dry weight) of each prey item was assessed; in subsequent analyses both absolute and relative (proportion of the overall gut content) expressions

of prey biomass were used. Dry weights of cladocerans, copepods, and larval insects were calculated according to Dumont et al. (1975), Bottrell et al. (1976), and Masferro et al. (1991). Mean dry weight of the larvae of *L. fortunei* was based on 400 straight-hinged and umboned veligers dried in an oven at 60°C to constant weight. The dry weights of the most abundant fish larvae (*Prochilodus lineatus* and Pimelodidae) found in the stomach contents of other fish larvae were estimated in a similar manner using a total of 383 individuals grouped into 20–0.5 mm length categories.

Between-site, between-month and between-developmental stage differences in mean larval fish length, FO and biomass were compared using one-way Analysis of Variance (ANOVA) following angular transformation of the data (Sokal & Rohlf, 1979). Duncan's multiple contrasts were used as a post-hoc test for all pair-wise comparisons. When the assumptions for parametric tests were not fulfilled the differences were assessed with non-parametric ANOVA techniques (Kruskal-Wallis) (Daniel, 1978). A significance level of 0.05 was used for all statistical testing.

Results

We captured a total of 11,956 fish larvae. Of these, 1,511 larvae were identified, measured, and utilized for gut content analyses (Table 1). We collected more samples from the Paraná River than from San Nicolás, therefore, we had more fish larvae from the Paraná River to perform gut content analysis (10,970) than from San Nicolás (986). The proportion of empty guts was higher in the Paraná River (72%) than in fishes from San Nicolás (60%).

Paraná river

In the Paraná River, over 30% of the fish larvae collected were sábalo (*P. lineatus*). The remaining 70% were unidentified Siluriformes, Doradidae, Pimelodidae and Anostomidae (Table 2). Eight taxa had *L. fortunei* larvae in their guts. Among

these, *Iheringichthys labrosus*, *Luciopimelodus pati* and *Sorubim lima* were by far the most active consumers of the mussel (Table 2). Among the Characiformes only *P. lineatus* consumed *L. fortunei*; however, for all these larvae the mussel was the only identifiable food item recorded.

In the Paraná River, 243 of the 1043 larvae analyzed (23%) had some material in their gut (Table 2). Of these 243 feeding larvae recorded, 37 (15%) fed exclusively on *L. fortunei*, and 40%, (101 fishes) had *L. fortunei* and some other prey item. The occurrence of *L. fortunei* in the diet of these fishes was usually higher than that of any other food item (Table 2). *L. fortunei* biomass represented up to 100% of the gut contents of the fishes that consumed this item. For specimens that consumed the mussel's larvae and any other food item (101 larvae), in terms of biomass *L. fortunei* was the most important in 56 cases (55%).

The spatial distribution of FO and biomass of prey types was uniform along the Paraná River. Numbers of fish larvae with *L. fortunei* in their gut contents were similar at the different sampling sites; the relative biomass of the mussel, as compared with other food items, was somewhat higher (but not significantly different) at the Paraná city site than elsewhere in the Paraná River (Tables 1, 3). The biomass of *L. fortunei* (both in percentage of all food items ingested and in absolute terms) was lower off La Paz than at the other two sampling sites, but these differences were not statistically significant (Tables 1, 3). Copepods and fish were less abundant at the Paraná city site than at the other two sampling sites, and the relative contribution of *L. fortunei* biomass was lower at Zárate (Table 1).

Temporal differences in *L. fortunei* biomass in the diet of the larval fishes followed different patterns at different sites. Off La Paz they were not statistically significant, but off Paraná city and Zárate, *L. fortunei* veligers contributed significantly more to the diet in October than during the remainder of the survey period ($P = 0.005$ and 0.002 , respectively; Table 3). Also the FO of *L. fortunei* peaked in October at the three sites, but differences with other months were not statistically significant.

In absolute terms, the FO and the biomass of *L. fortunei* larvae had similar values in pimelodid

Table 1 General information on the data used for this report. Biomass values are in μg dry weight. [1] Proportion of totals analyzed at each site; [2] proportion of total non-empty guts analyzed at each site; [3] Proportion of total food biomass at each site

Station	La Paz	Paraná	Zárate	San Nicolás, vegetated area	San Nicolás, no vegetation
Total larvae retrieved	6680	3695	595	525	461
Larvae analyzed	430	338	275	161	307
Larvae with gut contents [1]	65 [15]	101 [30]	77 [28]	107 [66]	66 [21]
Guts with <i>L. fortunei</i> [2]	32 [26]	62 [33]	44 [28]	20 [19]	14 [21]
Guts with cladocerans [2]	34 [28]	62 [33]	35 [22]	56 [52]	33 [50]
Guts with copepods [2]	2 [2]	21 [11]	27 [17]	25 [23]	7 [10]
Guts with larval fish [2]	18 [15]	9 [5]	21 [13]	0 [0]	4 [6]
Guts with insects [2]	11 [9]	9 [5]	11 [7]	1 [1]	0 [0]
Guts with algae [2]	0 [0]	0 [0]	0 [0]	5 [3]	1 [1]
Guts with unidentified material [2]	24 [20]	27 [14]	20 [13]	30 [24]	20 [14]
Mean biomass of <i>L. fortunei</i> [3]	122 [5]	239 [49]	227 [7]	48 [13]	11 [8]
Mean biomass of cladocerans [3]	181 [7]	53 [11]	94 [3]	215 [58]	69 [49]
Mean biomass of copepods [3]	7 [0]	10 [2]	63 [2]	96 [26]	11 [8]
Mean biomass of larval fish [3]	2297 [88]	172 [35]	2883 [88]	0 [0]	51 [36]
Mean biomass of insects [3]	18 [1]	14 [3]	17 [1]	9 [2]	0 [0]

Table 2 Diet of ichthyoplankton of the Paraná River. [1] Proportion of all larvae retrieved; [2] Proportion of larvae retrieved; [3] Proportion of larvae analyzed; [4] Proportion of all non-empty guts analyzed. Biomass values are μg dry weight

	Larvae retrieved [1]	Larvae analyzed [2]	Larvae analyzed with gut contents [3]	Guts with <i>L. fortunei</i> [4]	Guts with cladocerans [4]	Guts with copepods [4]	Guts with larval fish [4]	Guts with insects [4]	Guts with unidentified material [4]	Mean biom. <i>L. fortunei</i>	Mean biom. cladocerans	Mean biom. copepods	Mean biom. fish larvae	Mean biom. insects
<i>Characiformes</i>														
<i>Prochilodus lineatus</i>	3603 [32.8]	246 [6.8]	8 [3.3]	6 [75.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	4	0	0	0	0
Unidentif. Anostomidae	1265 [11.5]	105 [8.3]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0	0	0	0	0
Unidentif. Curimatidae	101 [0.9]	9 [8.9]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0	0	0	0	0
<i>Rhaphiodon vulpinus</i>	2 [0.0]	1 [50.0]	1 [100.0]	0 [0.0]	1 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0	0.9	0	0	0
<i>Siluriformes</i>														
Unidentif. Doradidae	1403 [12.8]	242 [17.2]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0	0	0	0	0
<i>Pimelodus</i> spp.	213 [1.9]	73 [34.3]	73 [100.0]	37 [50.7]	56 [76.7]	32 [43.8]	30 [41.1]	15 [20.5]	15 [20.5]	170.9	139.1	632.8	3628.2	0
<i>Iheringichthys labrosus</i>	36 [0.3]	24 [66.7]	22 [91.7]	15 [68.2]	9 [40.9]	1 [4.5]	4 [18.2]	5 [22.7]	9 [40.9]	116.6	19.5	11.6	856.3	8.2
<i>Parapimelodus valenciennis</i>	57 [0.5]	34 [59.6]	34 [100.0]	16 [47.1]	22 [64.7]	7 [20.6]	6 [17.6]	5 [14.7]	5 [14.7]	46.2	80	26.3	219.8	8.8
<i>Pseudoplatystoma</i> spp.	43 [0.4]	43 [100.0]	37 [86.0]	11 [29.7]	8 [21.6]	1 [2.7]	5 [13.5]	2 [5.4]	23 [62.2]	12.1	3	11.5	532.7	3.7
<i>Luciopimelodus pati</i>	1 [0.0]	1 [100.0]	1 [100.0]	1 [100.0]	1 [100.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	4.7	4.4	0	0	0
<i>Sorubim lima</i>	8 [0.1]	7 [87.5]	7 [100.0]	6 [85.7]	2 [28.6]	1 [14.3]	0 [0.0]	1 [14.3]	4 [57.1]	14.1	0.9	0.5	0	0.7
Unidentif. Pimelocidae	1196 [10.9]	116 [9.7]	60 [51.7]	46 [76.7]	30 [50.0]	7 [11.7]	3 [5.0]	3 [5.0]	13 [21.7]	223.1	45.4	28.6	115.6	6.6
Unidentif. Siluriformes	3042 [27.7]	142 [4.7]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0	0	0	0	0

Table 3 ANOVA results for differences in the frequency of occurrence and mean biomass of *L. fortunei* between developmental stages of Pimelodidae from the Paraná River, between sites, and between months for each site, and for vegetated and not vegetated areas in San Nicolás

	ANOVA				Kruskal-Wallis			
	N	d.f.	F	P	H	P	P	
<i>Between-developmental stages of Pimelodidae in the Paraná river</i>								
Guts with <i>L. fortunei</i>	68	66	0.8	0.45	–	–	–	
Mean biomass of <i>L. fortunei</i>	68	66	3.15	0.05*	–	–	–	
<i>Between-sites (La Paz, Paraná, Zárate)</i>								
Guts with <i>L. fortunei</i>	74	72	0.42	0.66	–	–	–	
Mean biomass of <i>L. fortunei</i>	74	72	0.62	0.54	–	–	–	
<i>Between-months for La Paz (October–March)</i>								
Guts with <i>L. fortunei</i>	16	13	–	–	5.19	–	0.16	
Mean biomass of <i>L. fortunei</i>	47	43	0.91	0.44	–	–	–	
<i>Between-months for Paraná (October–March)</i>								
Guts with <i>L. fortunei</i>	28	24	–	–	7.64	–	0.11	
Mean biomass of <i>L. fortunei</i>	84	80	4.04	0.005*	–	–	–	
<i>Between-months for Zárate (October–March)</i>								
Guts with <i>L. fortunei</i>	28	23	–	–	9.91	–	0.08	
Mean biomass of <i>L. fortunei</i>	63	58	4.39	0.002*	–	–	–	
<i>Between vegetated and not vegetated areas in San Nicolás</i>								
Guts with <i>L. fortunei</i>	31	30	–	–	1.99	–	0.16	
Mean biomass of <i>L. fortunei</i>	128	127	0.41	0.52	–	–	–	
Mean length of larval fish	469	468	23.27	<0.001*	–	–	–	
Guts with contents	469	468	71.14	<0.001*	–	–	–	

proto-, meso-, and metalarvae. However, because larger pimelodid larvae consumed significantly more fish larvae than the smaller ones (Table 3), the relative importance of *L. fortunei* in their diets was very dissimilar, decreasing from 48.1% of overall biomass dry weight in protolarvae to 3.0% in metalarvae. Thus, as pimelodid larvae grew their diet shifted from *L. fortunei* veligers to other fish larvae.

San Nicolás lagoons

In San Nicolás, 173 of 468 larvae (37%) had some material in their gut (Table 1). *L. fortunei* was observed in 34 specimens (20% of non-empty stomachs), mostly as the only prey item (Table 4). In terms of biomass, the incidence of *L. fortunei* on the diet of the fishes was the second highest (Table 4). For those specimens that had consumed the mussel's larvae and any other food item, *L. fortunei* was the most important in terms of biomass in five of seven cases (71%). The incidence of *L. fortunei* on the diet of these larvae, particularly FO, was generally lower than in the Paraná River; thus, while in the Paraná over half of the fish larvae with some material in their digestive tract had fed on *L. fortunei*, in San Nicolás less than 20% did.

Seven of the 10 taxa collected in San Nicolás had *L. fortunei* in their guts. Approximately 20% of the Characiformes (Characiformes accounted for approximately 90% of the fishes retrieved) consumed veligers. For the Siluriformes (mostly several species of catfish), the proportion was similar (23%), but these fishes were comparatively scarce in these lagoons (ca. 10% of all larvae collected).

Fish larvae collected in vegetated areas were significantly larger (mean length = 23 mm) and had food in their guts more often (66% with gut contents) than those collected in sites without vegetation (mean length = 6 mm; 21% with gut contents; ANOVA $P < 0.001$ for both parameters; Table 3). The FO and biomass proportion of *L. fortunei* varied slightly between vegetated and unvegetated sites (these differences were not statistically significant; Table 3).

Discussion

The ichthyoplankton of the Paraná River was primarily comprised of Characiformes (45%) and Siluriformes (55%), which agrees with previous information (Fuentes & Espinach Ros, 1998, reported that Characiformes and Siluriformes make up 81% of the fish fauna of the Paraná). In the marginal lagoons, on the other hand, Characiformes were largely dominant (89%).

Our results show that *L. fortunei* veligers are actively consumed by 11 of the 15 fish larvae taxa found in the main channel and in subsidiary marginal lagoons of the Paraná River. *L. fortunei* was recorded in the guts of *P. lineatus*, *I. labrosus*, *Pseudoplatystoma* spp., *L. pati*, *S. lima*, *Pimelodus* spp. and *Parapimelodus valenciennis*, as well as other unidentified Anostomidae, Doradidae, Characiformes, and Pimelodidae. Of all these, only *S. lima* was previously reported to consume *L. fortunei* larvae (Rossi, 2004). Only a few taxa (*Rhaphiodon vulpinus*, *Lycengraulis grossidens*, and some unidentified Curimatidae) were not observed to feed on the mussel.

The proportions of feeding larvae that had *L. fortunei* in their gut varied between 20% (San Nicolás) and 56% (Paraná), showing large differences between fish taxa, sites, and developmental stages (Table 1). This contrast is likely due to differences in the taxonomic makeup of fish larvae at the two sites, rather than to dissimilarities in food availability or predator behavior. In terms of biomass, however, the contribution of the mussel's larvae to the diets analyzed was smaller: 8% (Paraná) to 12% (San Nicolás) (mean weighted values), but figures as high as 100% were recorded for some taxa.

Taxonomic composition of larval fish assemblages, feeding activity, and the incidence of *L. fortunei* on the diet showed several clear differences between the Paraná and San Nicolás. Larvae of the sábalo, *P. lineatus*, which is the most abundant species in the Paraná–Uruguay watershed (Sverlij et al., 1993), were dominant in both environments. However, in the Paraná only 3% of them had some gut contents, while in San Nicolás, almost half of the specimens had food in their stomachs (Tables 2 and 4). This contrast agrees with the known behavior of *P. lineatus*:

Table 4 Diet of ichthyoplankton of San Nicolás lagoons. [1] Proportions of all larvae retrieved; [2] Proportions of larvae retrieved; [3] Proportions of larvae analyzed; [4] Proportions of all non-empty guts analyzed. Biomass values are µg dry weight

	Larvae retrieved [1]	Larvae analyzed [2]	Larvae analyzed with gut contents [3]	Guts with <i>L. fortunei</i> [4]	Guts with cladocerans [4]	Guts with copepods [4]	Guts with fish [4]	Guts with larval fish [4]	Guts with algae [4]	Guts with unidentified material [4]	Mean biom. <i>L. fortunei</i>	Mean biom. cladocerans	Mean biom. copepods	Mean biom. fish larvae
<i>Characiformes</i>														
<i>Prochilodus lineatus</i>	695 [70.5]	264 [38.0]	122 [46.2]	20 [16.4]	70 [57.4]	17 [13.9]	0 [0.0]	0 [0.0]	6 [4.9]	33 [27.0]	34.8	167.5	26.7	0
Anostomidae	148 [15.0]	77 [52.0]	12 [15.6]	5 [41.7]	2 [16.7]	3 [25.0]	0 [0.0]	0 [0.0]	0 [0.0]	3 [25.0]	5.4	1.4	6.2	0
Unidentif.	34 [3.4]	20 [58.8]	12 [60.0]	3 [25.0]	1 [8.3]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	8 [66.7]	2	0.4	0	0
<i>Characidae</i>														
<i>Siluriformes</i>														
Doradidae	2 [0.2]	2 [100.0]	2 [100.0]	1 [50.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	2 [100.0]	0.7	0	0	0
<i>Pimelodus</i> spp.	7 [0.7]	5 [71.4]	5 [100.0]	2 [40.0]	3 [60.0]	2 [40.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	10.1	10	12.2	0
<i>Pseudoplatystoma</i> spp.	13 [1.3]	13 [100.0]	10 [76.9]	2 [20.0]	6 [60.0]	5 [50.0]	0 [0.0]	0 [0.0]	0 [0.0]	2 [20.0]	6.7	7.3	10.4	0
<i>Sorubim lima</i>	7 [0.7]	7 [100.0]	7 [100.0]	0 [0.0]	6 [85.7]	4 [57.1]	4 [57.1]	0 [0.0]	0 [0.0]	1 [14.3]	0	92.9	30.4	51
Unidentif.	11 [1.1]	11 [100.0]	1 [9.1]	1 [100.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	2	0	0	0
<i>Pimelodidae</i>														
Unidentif.	66 [6.7]	66 [100.0]	1 [1.5]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	1 [100.0]	0	0	0	0
<i>Siluriformes</i>														
<i>Clupeiformes</i>														
<i>Lycengraulins grossidens</i>	3 [0.3]	3 [100.0]	1 [33.3]	0 [0.0]	1 [100.0]	1 [100.0]	0 [0.0]	0 [0.0]	0 [0.0]	0 [0.0]	0	4.3	13.2	0

adult sábalo spawn in the Paraná River channel and their larvae migrate toward marginal lagoons while utilizing their vitellum. Active feeding begins once they have reached these lagoons (Welcomme, 1979; Fuentes & Espinach Ros, 1998). On the other hand, catfishes (Pimelodidae), which also reproduce chiefly in the Paraná River channel, start feeding in the channel shortly after hatching. For this group, proportions of non-empty guts in the Paraná were comparable to those in San Nicolás. Thus, when considering the ichthyoplankton as a whole, lower proportions of feeding larvae in the Paraná (23%) compared to San Nicolás (37%) are due to the different taxonomic compositions of the fish fauna in the two environments.

Analysis of spatial variations in *L. fortunei* use was restricted to the Pimelodidae, the only fish family whose larvae were observed to actively feed in the Paraná (Table 2). Proportions of feeding Pimelodidae were 67% (La Paz) to 85% (Zárate), whereas fish larvae with *L. fortunei* in their guts made up 30% (La Paz) to 50% (Paraná) of all Pimelodidae. At all three sites *L. fortunei* biomass accounted for very large proportions of the food consumed by the fish larvae (32–55%), but neither the FO nor the biomass of *L. fortunei* showed a clear spatial pattern. Although a north-south trend could have been expected because many of these species undergo reproductive migrations, these migrations have species-specific traits. For example, *Pseudoplatystoma fasciatum*, *Pseudoplatystoma coruscans*, *Pimelodus albicans*, *Pimelodus maculatus*, *L. pati* and *S. lima* all migrate upstream for spawning, but the extent and timing of these movements are different (Welcomme, 1979; Fuentes & Espinach Ros, 1998). Behavioural heterogeneity is likely responsible for the lack of latitudinal patterns in proportions of the various developmental stages with which foraging on *L. fortunei* is associated.

In the Paraná River, feeding larvae represented between 14% (January 2001) and 38% (February 2001) of all the specimens analysed, whereas *L. fortunei* was present in 56% of the larvae with some material in their digestive tract, but monthly variations did not exhibit a defined pattern. On the other hand, both the mean *L. fortunei* larvae per gut, and the average

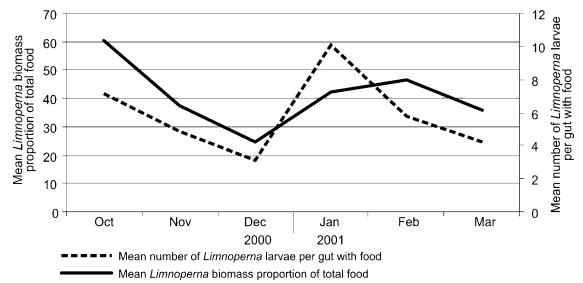
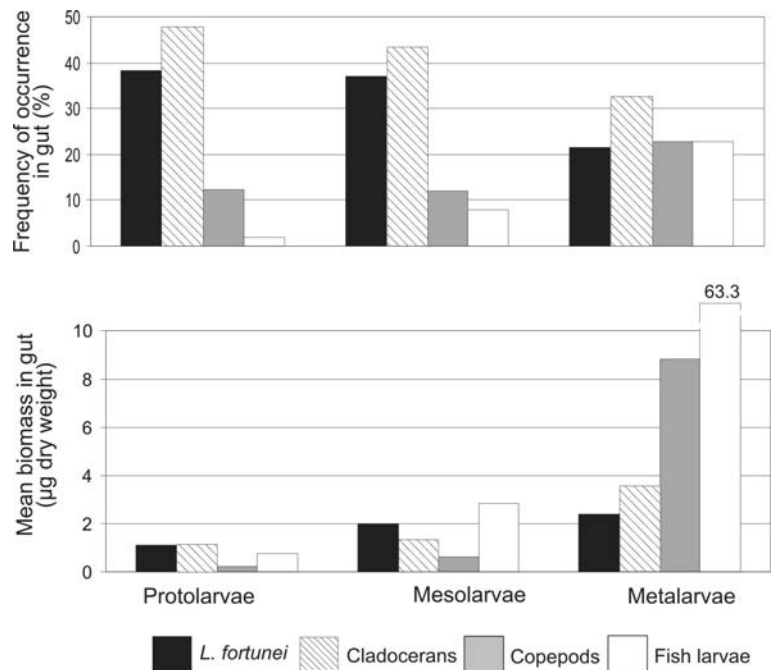


Fig. 2 Monthly changes in the mean numbers of *L. fortunei* larvae recorded in the gut contents of fish larvae, and the mean proportions of *L. fortunei* biomass with respect to overall food in non-empty guts. Pooled data for the Paraná River

proportion of *L. fortunei* biomass with respect to the biomass of all items present in the guts, which showed parallel trends, peaked in October 2000 and in January 2001 (Fig. 2). The January peak in the importance of *L. fortunei* as food for the fishes is consistent with the mussel's reproductive activity, which has been observed to increase strongly during the early summer (Boltovskoy & Cataldo, 1999; Cataldo & Boltovskoy, 2000; Sylvester et al., in press). The October peak is likely associated with the early spring production of *L. fortunei* larvae, which have been observed in northern Argentina (Darrigran et al., 2002).

The relative importance of the biomass of different prey items, as well as the FO of cladocerans, copepods and fish larvae consumed was clearly associated with predator developmental stage. Protolarvae fed chiefly on *L. fortunei* veligers and cladocerans, with fewer copepods and fish larvae (Fig. 3). Mesolarvae consumed veligers, cladocerans and copepods in similar proportions, but exhibited an increased frequency of fish larvae. Finally, metalarvae consumed veligers and cladocerans less often, but exhibited an increased amount of copepods and fish larvae in their diets. Because the biomass of copepods and fish larvae is 5–10 and 50 times greater, respectively, than that of veligers and cladocerans, the relative importance of veliger biomass dropped from 30–35% in protolarvae and mesolarvae, to only 3% in the metalarvae (Fig. 3). Also, cladoceran biomass decreased strongly with increasing fish size, dropping from 20–35% of the

Fig. 3 Average frequency of occurrence and biomass of major prey items found in protolarvae, mesolarvae, and metalarvae (pooled data for the Paraná River and San Nicolás). For *L. fortunei* protolarvae and mesolarvae differed significantly from metalarvae ($P = 0.002$ and $P = 0.02$, respectively, Duncan test)



diet in protolarvae and mesolarvae, to only 5% in the metalarvae (Fig. 3). Conversely, the proportion of fish larvae in the diet increased from 23% in protolarvae, to 41% in mesolarvae, and 81% in metalarvae (Fig. 3). These changes reflect the increased predator-avoidance capabilities of fish larvae as they increase in size. As fish larvae grow they become faster and more agile (Clark et al., 2005), gaining access to copepods and smaller fish larvae, both of which have greater predator-avoidance capabilities. *L. fortunei* larvae are slow, clumsy swimmers (personal observations), and are therefore easy prey for the earliest stage of fish larvae; however, their small size limits the amount of energy that they supply.

In San Nicolás lagoons two different environments were sampled: areas covered with floating aquatic vegetation, and open water areas, barren of vegetation. While the abundance of zooplankton was similar in the two environments, the proportion of feeding larvae was greater in areas with vegetation (66%), than in open waters (21%) (Table 1). The fact that fish larvae feed more actively among submerged vegetation than in open waters contradicts previous results indicating that the predator-avoidance capabilities of cladocerans and copepods is greater in areas where plants offer

refuge and protection (Jeppesen et al., 1997; Stansfield et al., 2004). This conclusion, however, has been challenged by recent studies showing that in subtropical lakes zooplankton strongly avoid macrophytes, especially free-floating ones such as *E. crassipes*, *Pistia stratiotes* and *Salvinia auriculata*, because of higher predation risk among plants than in open waters, due to high densities of zooplanktivorous fish in the former (Meerhoff et al., 2006). Because zooplankton densities did not differ markedly between vegetated and open water areas, our findings do not support the notion that zooplankton avoid vegetated areas. In any case, our results agree with earlier reports on the importance of aquatic plants in waterbodies connected with the Paraná River as places of refuge and feeding for many local fish species (Rossi & Parma de Croux, 1992).

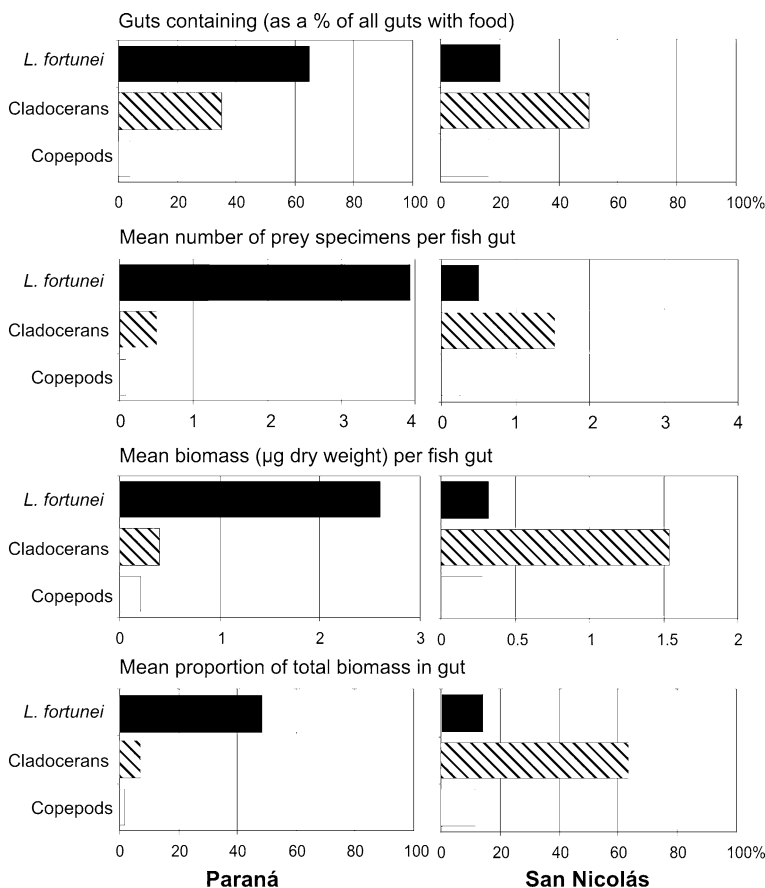
Comparison of the relative proportions of *L. fortunei* veligers, cladocerans, and copepods in the water and in larval fish guts indicates that *L. fortunei* was selected positively over the other two prey types. Thus, on average for all zooplankton samples the ratio of *L. fortunei* veligers:cladocerans:copepods was 1:21:3, whereas in fish stomachs the same ratio was 1:3:1 (San Nicolás data). This pattern is most probably due

the slower swimming and less efficient predator-avoidance behaviour of *L. fortunei* larvae as compared with the other organisms.

Prior to the invasion of *L. fortunei*, fish diets were dominated by cladocerans and copepods, with smaller contribution of rotifers, insect and fish larvae, and plant remains (Rossi, 1992; Makrakis et al., 2005). The same prey items are present after the mussel became established in the area, but now mussel larvae occupy a salient role. Their contribution is particularly important for protolarvae, where *L. fortunei* is either the first (Paraná) or the second (San Nicolás) most important food item, both in terms of numbers and biomass (Fig. 4). These results are in agreement with the only previous study of the diet of larval fishes after the invasion of *L. fortunei* in the Middle Paraná River where Rossi (2001, 2004) concluded that between 1990 and 2002 the diet of the shovelnose catfish (*S. lima*) larvae shifted from cladocerans to *L. fortunei* veligers.

It must be stressed that fish species whose diets rely heavily on *L. fortunei* are among the most abundant and ecologically and economically important in the system (Bonetto et al., 1969; Sverlij et al., 1993; Espinach Ros & Fuentes, 2001). This is especially true of sábalo, *P. lineatus*, which account for over 80% of the fish of the Paraná River (Quirós & Cuch, 1989). In agreement with its numerical dominance, the sábalo is the main food item of several large ichthyophagous species (Sverlij et al., 1993; Iwaszkiw, 2001), and represents over 90% of the fish landings of the lower Paraná and Río de la Plata estuary (Espinach Ros & Fuentes, 2001). Also of major importance may be that *L. fortunei* is especially well suited as food for the youngest developmental stages (Figs. 3, 4) because they are the most vulnerable in the developmental history of fishes (Kamler, 1992). Because *L. fortunei* reproduces continuously between September–October and May–June producing over 30,000 larvae per m³

Fig. 4 Comparative contributions of the three main food items for the protolarvae surveyed



(Boltovskoy & Cataldo, 1999; Cataldo & Boltovskoy, 2000), fish larvae, which are present between October and February–March only (Vazzoler, 1996), have a continuous supply of veligers throughout their early life stages.

Comparison of the ecological impact of *L. fortunei* in South America with that of the zebra mussel, *Dreissena polymorpha*, in Europe and North America, suggests important differences. Although *D. polymorpha* has been intensively investigated for over a century (Schloesser et al., 1994), only 10 European and 5 North American fish species were found to feed on its planktonic larvae, and reported FO and biomass values of *D. polymorpha* larvae in the diets of these species are usually lower than those found in our study (e.g., Mills et al., 1995; Molloy et al., 1997). The moderate trophic impact of *D. polymorpha* veligers on other members of the ecosystem was recently confirmed by stable isotopic studies in estuarine waters (Barnard et al., 2006).

It is probable that this discrepancy results from a combination of traits intrinsic to the invaders, and to environmental settings. Unlike *D. polymorpha*, which is a sequential spawner that produces larvae over a period of 6 to 8 weeks (Nichols, 1996), *L. fortunei* reproduces continuously for up to 10 months (Boltovskoy & Cataldo, 1999; Cataldo & Boltovskoy, 2000). Thus, for potential predators, the availability of *L. fortunei* veligers is greater and more consistent. Environmental conditions in large South American floodplain rivers also differ strongly from most water bodies where *D. polymorpha* has been investigated, especially those in North America. South American rivers are highly turbid (Secchi disk depths around 20 cm) and poor in plankton. Phytoplankton densities are usually below 500 cells ml⁻¹, and zooplankton densities, including rotifers, cladocerans and copepods, are usually below 30 ind. l⁻¹ (Boltovskoy et al., 1995; de Cabo et al., 2003). Filter feeding organisms are therefore scarce in these waters (Boltovskoy et al., 2006), and planktophagous fishes are restricted to a few species, some of which prey on plankton only during their juvenile phases (Iwazskiw, 2001). Thus, it is improbable that the positive effects of an enhanced food supply could be offset by *Limnoperna's* competitive impact on

filter-feeding organisms, including fishes, as has been noted for *Dreissena* (MacIsaac et al., 1996; Bridgeman et al., 1995; Bartsch et al., 2003).

The invasion of Western Europe and North America by the zebra mussel has been the subject of hundreds of investigations (Schloesser et al., 1994). This wealth of information and the fact that *D. polymorpha* shares several salient traits with *L. fortunei* (Karatayev et al., in press) results in *D. polymorpha* being used as a proxy for forecasting the impacts of *L. fortunei* in South America. Our results suggest that similarities between the two species do not warrant unconstrained extrapolations on ecosystem-wide effects. Just as not all non-indigenous species have large effects (Byers et al., 2002), very similar invaders can have different effects in different areas. However, while our results strongly suggest that the expansion of *L. fortunei* results in an enhanced food supply for local fish populations, they do not necessarily imply that the overall effect on the ecosystem in general, and on the fish fauna in particular, is beneficial. Trophic relationships with fishes are only one of the many new interactions that the invasion of this mussel has brought about. While consumption of veligers by larval fish may indeed have positive effects on the predators involved, there may be other direct or indirect consequences that can offset these benefits. Among these are disruptions of the historical balance between fish species, increased water transparency, enhanced macrophyte growth, modifications in the composition and abundance of planktonic and benthic assemblages, introduction of new parasites, etc. (Botts et al., 1996; Karatayev et al., 1997; Strayer et al., 1999; Ogawa et al., 2004).

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