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Veligers of the invasive bivalve *Limnoperna fortunei* in the diet of indigenous fish larvae in a eutrophic subtropical reservoir

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Abstract Larval fish development depends largely on their ability to capture and ingest food items, and on food availability. In this context, invasive species, eutrophication and river impoundments have complex impacts on fish larvae. Using samples collected in 2005–2009 in the Salto Grande reservoir (Argentina–Uruguay), periodically affected by cyanobacterial blooms, we studied the impact of the larvae of the exotic bivalve *Limnoperna fortunei* (Dunker, 1857) (Bivalvia) on larval fish diets. Compared with other nearby waterbodies, the abundance of fish larvae was scarcer in the reservoir, especially during algal bloom periods. Only 20% of the larval fish with gut contents fed on *L. fortunei* veligers. Seven fish taxa (of a total of 12) consumed veligers of *L. fortunei*, but only two showed a preference for this prey. Taxonomic changes in the larval fish assemblages due to the river's impoundment, and temporal uncoupling between veliger densities (affected by the toxigenic effects of *Microcystis* spp.) and ichthyoplankton could account for the comparatively low trophic importance of the invasive bivalve's veligers. These results reflect the complexity of interactions brought about when the same invasive species invades different environments, underscoring that the impacts involved depend as much on the invader, as on the regional and ecological settings of the area invaded.

Key words: Ichthyoplankton, cyanobacterial blooms, feeding impact, invasive species, prey selection, fish assemblage.

INTRODUCTION

Food-web disruptions are one of the most significant impacts of invasive species, with both positive and negative consequences for the native fauna (Karatayev *et al.* 2007; Davis 2009). These changes are frequently modulated by anthropogenic alterations, in particular the eutrophication of aquatic environments (Byers 2002). The start of exogenous feeding is a vital period in the life of fishes, during which survival is determined by food availability and the ability of the larvae to capture and ingest prey (Nunn *et al.* 2012). The larval planktonic stages of invasive bivalves may have a positive impact on native fish larvae when they are successfully included in their diet (Molloy *et al.* 1997; Nack *et al.* 2015; Paolucci & Thuesen 2015). Factors that may negatively affect the survival of larval river fishes include, among others, river impoundment (Humphries & Lake 2000), and the concomitant increase in cyanobacterial blooms, often enhanced by the presence of invasive mussels (Vanderploeg *et al.* 2001; Knoll *et al.* 2008; Sarnelle *et al.* 2010; Boltovskoy *et al.* 2013). Cyanobacterial blooms may not only reduce prey availability (Boltovskoy *et al.* 2013) but also reduce fish feeding activity and affect embryonic development and survival (Ojaveer *et al.* 2003; Engström-Öst *et al.* 2006; Palíková *et al.* 2007; Ghazali *et al.* 2009).

Since its introduction into the Río de la Plata estuary (Argentina) around 1990 (Pastorino *et al.* 1993), the Asian golden mussel (*Limnoperna fortunei*) has colonized almost all of the Río de la Plata basin, as well as other smaller watersheds in Argentina, Brazil, Bolivia, Paraguay and Uruguay (Boltovskoy *et al.* 2006; Oliveira *et al.* 2015). In South America, its range includes an array of natural and man-made environments, where very high densities of adult sessile mussels (up to over 200 000 ind. m^{-2}; Correa *et al.* 2015) and their planktonic larvae (up to ~70 veligers L^{-1}; Boltovskoy *et al.* 2013) are frequent. The widespread distribution and high abundance of

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this introduced bivalve have made it a common food item of many local fishes: at least 50 fish species feed on adult mussels, and 18 larval fish species feed on *Limnoperna* veligers (Boltovskoy & Correa 2015; Cataldo 2015; Paolucci & Thuesen 2015). Significantly, up to 85% of the individuals of the earliest larval fish stages, in particular among the most abundant Characiformes and Siluriformes, consume *Limnoperna* veligers (Paolucci & Thuesen 2015).

Laboratory and field studies indicate that the impact of *Limnoperna* veligers on larval fish diet depends on the relative abundance of veligers (Paolucci *et al.* 2010a,b, 2015), which varies greatly in time and space (Boltovskoy *et al.* 2009, 2015; Darrigran *et al.* 2011; Oliveira *et al.* 2011). Veliger densities depend on those of adult mussels, which in turn are associated with the time elapsed since initial colonization (Boltovskoy *et al.* 2015), as well as with various environmental factors, such as availability of suitable substrata and food, dissolved oxygen and water temperature, among others (Boltovskoy *et al.* 2009; Oliveira *et al.* 2010; Correa *et al.* 2015). In the Salto Grande reservoir, veliger densities are negatively affected by toxic cyanobacterial blooms (which, paradoxically, are enhanced by the filtration activity of adult mussels; Boltovskoy *et al.* 2013; Cataldo *et al.* 2012).

In this study we analyse the impact of *Limnoperna* veligers on the diet and feeding preferences of native larval fishes in a large reservoir that is strongly affected by recurrent cyanobacterial blooms. Our objectives were as follows: (1) to assess the importance of *Limnoperna* veligers and indigenous prey in the diet of fish larvae; (2) to study temporal changes in the trophic selectivity of larval fishes as a function of the availability of veligers, ichthyoplankton composition and cyanobacterial blooms, under the hypothesis of that a combination of these factors may reduce veliger impact on larval fish diets and (3) to compare the diet of larval fishes in Salto Grande reservoir with those recorded in other nearby lotic environments characterized by contrasting environmental settings (Paolucci 2002; Paolucci *et al.* 2007, 2015; Rossi 2008).

METHODS

Regional setting

The sampling sites were located in the Salto Grande reservoir, a long (ca. 130 km) and narrow water body (~800 km^2) created in 1979 by damming of the Uruguay River. The Uruguay River is the second most important tributary of the Río de la Plata basin, discharging around 4600 m^3 s^{-1} into the Río de la Plata estuary (Fig. 1). The reservoir hosts ~60 fish species (Menni 2004). Mature adults of several migratory species, such as *Prochilodus lineatus*, *Leporinus obstusidens, Salminus maxillosus, Luciopimelodus pati* and *Raphiodon vulpinus*, migrate upstream to spawn, chiefly between October and March (Paolucci 2002; de Resende 2003). Larval fish drift downstream until they reach nursery grounds in marginal wetlands or the Salto Grande reservoir where they feed and grow for 1–2 years

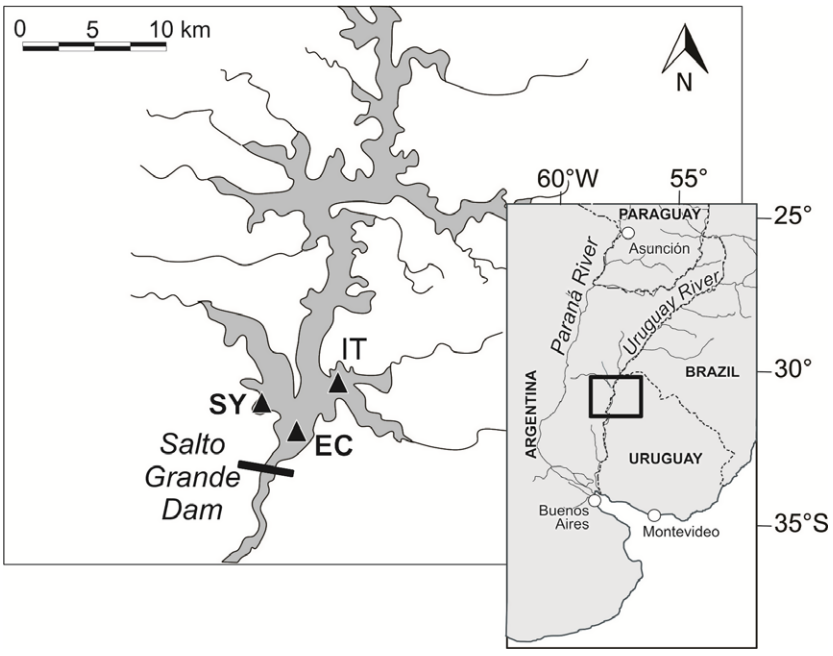

Fig. 1. Location of sampling sites in the main channel (EC) and in the coastal areas SY (Seno Yacaré) and IT (Itapebí) of the Salto Grande reservoir.

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(Paolucci 2002). After damming, some relic populations of other species (e.g. *Pachyurus bonariensis*, *Lycengraulis grossidens* and *Iheringichthys westermanni*) managed to successfully reproduce in the reservoir and even became more abundant than in the pre-existing river, which substantially changed the reservoir's fish assemblage (Menni 2004).

Limnoperna fortunei was first detected in the Salto Grande reservoir in 2001 (Oliveira *et al.* 2015). Veliger densities in the water column, monitored weekly since 2006, peak between October–November and March–April reaching >20 000 larvae m^{-3}, but interannual fluctuations are very strong (Boltovskoy *et al.* 2013; see below).

Despite its high flushing rates and low water-retention time (2–9 weeks), toxic blooms of *Microcystis* spp. and *Dolichospermum* spp., with microcystin concentrations in the water in excess of 200 $\mu g\ L^{-1}$, are a recurrent summer–autumn phenomenon in the reservoir, especially in its lower section during dry summers (Chalar 2006; O'Farrell *et al.* 2012; Boltovskoy *et al.* 2013).

Sample collection and analysis

Ichthyoplankton and zooplankton samples were collected at weekly intervals between October and March 2005 to 2009 (fish larvae are almost absent between April and September), covering four fish reproductive periods. Samples were collected at three sites in the lower part of the reservoir: at the centre, in the vicinity of the dam (where flow rates are greatest; station EC, 31°15.99′S, 57°55.91′W, in 2005–2009), and at two shallow coastal environments located in the lateral arms (stations SY, 31°14.99′S, 57°57.54′W, in 2005 and 2006; and IT, 31°11.23′S, 57°50.36′W, in 2007 to 2009; Fig. 1).

Ichthyoplankton samples were collected with a conical plankton net (three-point bridle, 0.50-m mouth diameter, 1 m long, 500 μm mesh) towed by a boat below the surface (2–3 m depth) for 10 min at 0.8–1.0 m s^{-1}. All ichthyoplankton tows were performed using the same protocol, and therefore their yields are roughly comparable (net clogging of the 500 μm mesh was negligible); however, because the net was not equipped with a flowmeter, in our estimates we opted for using relative values (i.e. proportions of the total number of fish larvae retrieved throughout the entire survey), rather than absolute densities.

On the same dates, zooplankton samples were obtained by filtering 100 L of bucket-collected surface water through a 25-μm-mesh net. Immediately after collection, samples were fixed with 5% formaldehyde. In total, we analysed 95 pairs of ichthyoplankton–zooplankton samples. Due to its strong flushing rates and low water residence times, vertical stratification in this river-like reservoir is weak and the distribution of zooplankton throughout the water column is homogeneous (De León & Chalar 2003; O'Farrell *et al.* 2012). Thus, we can reasonably assume that our near-surface samples are representative of the entire water column. For most analyses, we used monthly averages of these weekly data.

Cyanobacterial concentrations at the sites sampled and surface water temperature were provided by the Salto Grande Joint Technical Commission (CTM-SG), and the Uruguay River Management Commission (CARU). Additional data of veliger densities for the period spanned by our survey were supplied by the long-term monitoring programme of *L. fortunei* based on weekly samples from 2006 (see Boltovskoy *et al.* 2013 for details).

Fish larvae and zooplankton (*L. fortunei* larvae, cladocerans, copepods and rotifers) were counted and measured under a binocular microscope equipped with a micrometric eyepiece. When total numbers of organisms per sample were below ~100, the entire sample was counted. Larger samples were subsampled with the aid of a Folsom splitter (McEwen *et al.* 1954) using splits with at least 50 organisms. Fish species were identified following Nakatani *et al.* (2001). Developmental stages were assigned on the basis of the median fins (protolarvae: no median fins, mesolarvae: rays in some median fins, metalarvae: well-developed rays in all median fins; Snyder 1983).

A binocular microscope (80×) was used to dissect fish larvae and examine their gut contents. Food items were identified, counted, measured (maximum dimension) and assigned to one of five categories: *L. fortunei* larvae, cladocerans, copepods, rotifers and algae. Unidentifiable remains were combined into an "Unidentified material" category.

Frequency of Occurrence (FO) was used to describe the importance of each prey category for each fish species based on the number of stomachs containing one or more individuals of the corresponding prey item as a proportion of all stomachs with some gut contents (Hyslop 1980). For size to biomass conversions, we used the expressions proposed by Paolucci *et al.* (2007) (veligers), Dumont *et al.* (1975) (cladocerans), Bottrell *et al.* (1976) (copepods) and González *et al.* (2008) (rotifers). Mean densities of the zooplankton available for larval fish are based on samples collected together with feeding larval fish only (rather than on the extended series of weekly samples collected since 2006 by Boltovskoy *et al.* 2013).

Selectivity values for each prey item were assessed using a Chi-square-based index (Pearre 1982):

$$C = \pm\left[\frac{(|a_d \times b_e - a_e \times b_d| - (n/2))^2}{(a \times b \times d \times e)}\right]^{1/2}$$

and:

$a = a_d + a_e$; $b = b_e + b_d$; $d = a_d + b_d$; $e = a_e + b_e$ and $n = a + b$

Where a, b, d and e are the sum of the number of specimens of prey a in the diet (a_d) and the environment (a_e), the total number of specimens of other preys in the diet (b_d), and in the environment (b_e), and the combination of both numbers for the diet and the environment, respectively. This index is not affected by the relative abundance of rare prey items and allows statistical estimates of significance for any sample size (Pearre 1982; Lazzaro 1987), which is particularly important for the scarcest prey items. When the expected frequency of a given prey item was above 5%, the statistical significance of the corresponding selectivity value was assessed with the χ^2 test using Yate's correction for continuity (Pearre 1982; Zar 1999). This index varies between −1 and 1; positive values which are significantly different from zero indicate preference for the prey item, whereas negative values indicate that the prey item is avoided. Values non-significantly different from zero indicate lack of selectivity.

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Differences in zooplankton densities, frequency and biomass of prey items between environments (centre of the reservoir, station EC, vs. coastal areas, and western – SY vs. eastern – IT coasts; see Fig. 1) were tested using t-tests after angular transformation of the frequency data (Sokal & Rohlf 1979). When the assumptions for parametric tests were not fulfilled, the differences were assessed with non-parametric techniques (Mann–Whitney or Kruskal–Wallis/ Mann–Whitney pairwise contrasts). The software Statistica 7.0 at a significance level of 0.05 was used for all tests.

RESULTS

Of the 95 ichthyoplankton samples collected during 2005–2009, 61 (64.2%) contained larval fishes, yielding a total of 577 fish larvae (mean ± SD: 6.3 ± 14.2 individuals per sample). Fifty-four (9%) of the fish larvae collected were feeding endogenously and were excluded from further diet analyses (Table 1). Of the remaining 523 specimens, 278 (53%, mostly protolarvae) had empty guts, whereas 245 (47%) had gut contents. Larvae with gut contents comprised 91% protolarvae, 7% mesolarvae and 2% metalarvae. Because almost all differences in zooplankton densities, biomass and FO of prey items, between the two coastal stations were non-significant (*t*-test, $P > 0.05$), for all subsequent analyses we pooled the data from these two sampling sites (SY and IT in Fig. 1).

Larval fish abundance, diversity and the proportion of individuals with gut contents did not differ between the centre of the reservoir (EC) and the coastal area (SY and IT; Table 1). However, the feeding ratio, expressed as the average number of food items per fish stomach (overall mean ± SD: 2.3 ± 3.1, with a maximum of 8 items per stomach), was significantly greater in the main channel (EC, 2.8 ± 2.2), than at the coastal stations (1.8 ± 1.5; Table 1).

Of the 245 larval fish with gut contents, veligers were found in 49 individuals (20%), whereas

Table 1. General information on the diet of the fish larvae and zooplankton recorded in the main channel and in the coastal area (pooled data from stations SY and IT, see Fig. 1) of the Salto Grande reservoir. Zooplankton densities are based on data when the paired ichthyoplankton sample yielded fish larvae with gut contents only. Biomass values are in μg dry weight. (1) Proportion of the totals analysed at each site; (2) Proportion of all feeding fish larvae; (3) Proportion of all non-empty guts analysed at each site; (4) Proportion of total food biomass at each site.

	Salto Grande Reservoir			
Variable	Main channel (%)	Coastal area (%)		
Larvae analysed	339	238		
Total larvae with yolk sac (1)	46 (13.6)	8 (3.4)		
Total feeding fish larvae	293 (86.4)	230 (96.6)	***t*-test (d.f. = 22)**	
Larvae without gut contents (2)	171 (58.4)	107 (46.5)	***t*-value**	***P*-value**
Larvae with gut contents (2)	122 (41.6)	123 (53.5)	0.66	0.5144
Feeding ratio (number of items per stomach ± SD)	2.8 ± 2.2	1.8 ± 1.5	***t*-test (d.f. = 243)**	
			2.29	0.0227
Zooplankton density (ind. L^{-1} ± SD)			***t*-test (d.f. = 28)**	
			***t*-value**	***P*-value**
Limnoperna fortunei	3.5 ± 3.5	3.6 ± 4.3	−0.0972	0.9233
Cladocera	2.2 ± 1.5	2.4 ± 1.8	−0.2851	0.7777
Copepoda	3.0 ± 2.3	2.7 ± 1.9	0.4348	0.6671
Rotifera	1.5 ± 2.4	1.6 ± 2.1	−0.0515	0.9593

			Mann–Whitney *U*-test	
Larval fish diet	Main channel	Coastal area	Z-value	*P*
Frequency of occurrence (%)				
L. fortunei (3)	28 (22.9)	21 (17.1)	−1.04	0.2998
Cladocera (3)	62 (50.8)	73 (59.3)	0.84	0.3999
Copepoda (3)	6 (4.9)	6 (4.9)	−0.23	0.8178
Rotifera (3)	12 (9.8)	3 (2.4)	−1.00	0.3180
Unidentified	28 (22.9)	36 (29.3)	1.55	0.1200
Algae (3)	8 (6.5)	8 (6.5)	0.19	0.8475
Mean Biomass (μg dry weight, %)				
L. fortunei (4)	73.7 (44.1)	22.1 (25.5)	−0.83	0.4039
Cladocera (4)	67.7 (40.5)	58.1 (67.0)	2.56	0.0106
Copepoda (4)	15.6 (9.3)	6.2 (7.1)	−0.19	0.8496
Rotifera (4)	10.2 (6.1)	0.3 (0.4)	−1.51	0.1323

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cladocerans were recorded in 135 larvae (55%; Table 1). For both frequency of occurrence and biomass, differences in gut contents between the coastal stations and the centre of the reservoir were minor and statistically non-significant, with the only exception of the biomass of cladocerans, which was significantly greater in the coastal area (Table 1; Mann–Whitney, $P < 0.05$). In terms of biomass, cladocerans and veligers dominated the diet at both sites, followed by copepods and rotifers (Table 1). Of the 49 larval fish with veligers in their guts, 23 (47%) fed on *L. fortunei* only; whereas the other 26 (53%) had veligers and some other prey, mostly cladocerans. For specimens that consumed mussel larvae and other food items (26 larval fish), the biomass of veligers was greatest in 18 cases (69%).

Mean values based on all the zooplankton samples collected for this survey yielded greater densities of veligers (mean ± SD: 3.1 ± 2.7 ind. L^{-1}) and rotifers (1.9 ± 1.5 ind. L^{-1}), than of cladocerans (0.6 ± 0.5 ind. L^{-1}) and copepods (0.7 ± 0.4 ind. L^{-1}). However, when zooplankton samples were limited to those paired with ichthyoplankton samples where feeding larvae were recorded (i.e. to the data points that more closely reflect the availability of prey items to the fish larvae), the dominance of veligers and rotifers in the plankton was much lower (Table 1). This indicates that cladocerans, veligers and copepods were available to feeding fish larvae in similar proportions, but only cladocerans and veligers were abundant in the gut contents.

Proportions of fish larvae that had some gut contents varied widely between species, ranging from around 50–80% (*Catathyridium jenynsii, Apareiodon affinis, P. bonariensis*, Pimelodidae larvae) to 20–30% (*L. grossidens*, *P. lineatus*, Anostomidae and other small unidentified Characiformes and Siluriformes) (Table 2). Eight of the ten larval fish taxa had a diet composed mostly of cladocerans and occasionally veligers, copepods and rotifers (Table 2). Most of these taxa showed positive selectivity values for the cladocerans, seven of which were significant (Chi-square test $P < 0.01$; Fig. 2). In terms of biomass, only two taxa (*C. jenynsii* and Pimelodidae), consumed chiefly larvae of *L. fortunei*, and occasionally cladocerans. For these fishes, veligers accounted for up to 83% of the total biomass consumed. However, the selectivity values were positive and significantly different from zero only for *C. jenynsii* and Siluriformes (Chi-square test $P < 0.01$; Fig. 2).

Seasonal variation

Although larval fish abundances differed greatly between years (in 2007–2008 their relative densities were significantly greater than during the other breeding periods covered; $P < 0.05$, Kruskal–Wallis/mean ranks tests), the seasonal pattern was generally similar throughout the four reproductive periods surveyed (Fig. 3a). Larval fish abundance was significantly higher in October–November, dropping sharply in December–March ($P < 0.05$, Kruskal–Wallis/mean ranks tests; Fig. 3a). These differences in relative abundance did not affect the proportions of the different feeding stages. Yolk-sac larvae seemed to be most common in October and February, being almost totally replaced by feeding larvae (with and without gut content) in November–December and March (Fig. 4), but statistically these differences were not significant ($P > 0.05$, Kruskal–Wallis). Again, proportions of larval fish with gut content and the numbers of food items per gut seemed to increase from October to December, decreasing gradually thereafter until the end of each sampling season, in March (Fig. 4); however, month-to-month differences were not significant ($P > 0.05$, Kruskal–Wallis). At both sampling sites (coastal and main channel), the taxonomic diversity of feeding larvae decreased evenly from October to March, but again month-to-month differences were not significant ($P > 0.05$, Kruskal–Wallis; Fig. 5).

Crustacean seasonal patterns were very similar throughout the study period and varied little between years and from month to month. Veliger densities were also similar between years, but monthly changes were significant ($P < 0.01$, Kruskal–Wallis/mean ranks tests), with greatest values in October–December and lowest values in January–March (Fig. 6a). Rotifers tended to peak towards the end of the summer, from January to March, but these increases were not significant ($P > 0.05$, Kruskal–Wallis; Fig. 6a). To draw closer comparisons between the prey available and the prey consumed, we calculated zooplankton abundances and proportions using only those zooplankton samples which were collected simultaneously with larval fish samples that yielded feeding larvae with gut contents (61 of the 95 zooplankton samples retrieved). This analysis showed smaller and non-significant differences ($P > 0.05$, Krukal–Wallis; Fig. 6b), indicating that during periods of most intensive feeding, all prey items were available to the larvae in roughly similar numbers.

Based on their diet, the larval fish taxa investigated can be ascribed to two categories: those that selectively consumed *Limnoperna* veligers (Siluriformes and *C. jenynsii*), and those that did not. Among the latter (8 taxa), only three showed significant levels of avoidance of *Limnoperna* veligers (*A. affinis, P. bonariensis* and *L. grossidens*; Chi-square test $P < 0.001$; Fig. 2). Pooled data for these two categories show that although the proportions of food types available to these larvae were generally similar throughout the breeding season (Fig. 6b), their gut contents were dominated by either veligers (Fig. 7a) or cladocerans

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Table 2. Diet of ichthyoplankton sampled from the Salto Grande reservoir, absolute numbers and (percentages)

Ichthyoplankton taxa	Larvae analysed (%)†	Total feeding larvae (%)‡			Guts with *Limnoperna fortunei* (%)‡	Guts with Cladocera (%)‡	Guts with Copepoda (%)‡
		Total	Main channel	Coastal Area			
Prochilodus lineatus	28 (5)	7 (25)	7 (27)	0 (0)	0 (0)	4 (57)	0 (0)
Anostomidae	61 (11)	16 (26)	7 (16)	9 (56)	0 (0)	5 (31)	0 (0)
Luciopimelodus pati	4 (1)	1 (25.0)	1 (25)	0 (0)	0 (0)	1 (100)	0 (0)
Pachyurus bonariensis	27 (5)	19 (70)	9 (69)	10 (71)	1 (5)	19 (100)	2 (11)
Lycengraulis grossidens	221 (38)	70 (32)	43 (33)	27 (30)	3 (4)	40 (57)	6 (9)
Siluriformes	20 (3)	5 (25)	4 (21)	1 (100)	1 (20)	3 (60)	0 (0)
Apareiodon affinis	89 (15)	58 (65)	13 (54)	45 (69)	8 (14)	26 (45)	4 (7)
Characiformes	30 (5)	8 (27)	3 (13)	5 (71)	1 (13)	6 (75)	0 (0)
Catathyridium jenynsii	41 (7)	21 (51)	7 (41)	14 (58)	16 (76)	11 (52)	0 (0)
Pimelodidae	51 (9)	40 (78)	28 (78)	12 (80)	21 (52)	22 (55)	0 (0)

(Fig. 7b). Larvae that did not show a preference for veligers invariably selected cladocerans as their preferred food (Fig. 7d), whereas larvae that favoured veligers had a more variable behaviour, with negative selectivity values in October and March, and positive values in November through January (Fig. 7c). Copepods were always consumed in lower proportions than those available in the plankton, whereas for rotifers the proportions in the guts were generally similar to those in the plankton (Fig. 7c and d).

DISCUSSION

In the lower section of the Salto Grande reservoir, the importance of veligers as food for larval fishes was among the lowest recorded in the Río de la Plata basin (Table 3). This contrast can stem chiefly from differences in the abundance and composition of the ichthyoplankton of the reservoir as compared with the other nearby waterbodies investigated and, to a lesser extent, from the frequent mid-summer drops in veliger densities due to the toxic effects of *Microcystis* spp. blooms (Boltovskoy *et al.* 2013).

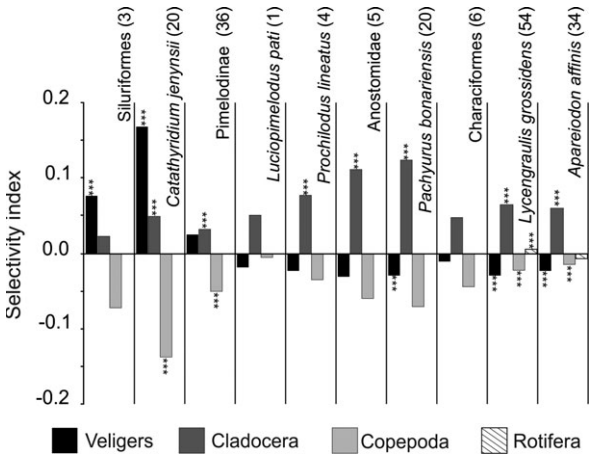

Fig. 2. Mean monthly selectivity indices for the prey items assessed by the fish taxa present in the Salto Grande reservoir. Asterisks denote significant differences between the proportions of the corresponding prey in the water column and in the gut content at $P < 0.05$ (*), $P < 0.01$ (**) or $P < 0.001$ (***) (Chi-square tests). Values in parentheses denote the numbers of larvae analysed.

Previous work showed that the very high consumption rates of veligers by larval fishes of the Río de la Plata basin rivers are largely due to the abundance of larvae of *P. lineatus*, a dominant characid (Sverlij *et al.* 1993), whose larvae feed actively on the veligers (Paolucci *et al.* 2007, 2010b). *Prochilodus lineatus* is typically a lotic, migratory, species, scarce or absent altogether in lakes and reservoirs. In the Salto Grande reservoir, *P. lineatus* hardly reached 5% of the fish larvae collected, and although other species, like *A. affinis* (15% of all larvae), *L. grossidens* (38%) and *P. bonariensis* (5%), are more abundant in Salto Grande than in the rivers of this basin (Paolucci *et al.* 2007, 2015), none of them consumes veligers as frequently as *P. lineatus* (only 14% of their larvae were found with veligers in their guts). Larvae of the flatfish *C. jenynsii*, which feed of veligers actively (72% with veligers in their guts), were also more abundant in the reservoir than in the rivers, but their abundance in the reservoir was too low (7%) to significantly offset the generally low importance of veligers for the diet of Salto Grande's fish larvae. Thus, in agreement with some previous results for the northern hemisphere (Molloy *et al.* 1997; Harding 1999), we conclude that differences in the composition of fish species are largely responsible for the lower importance of *Limnoperna* veligers in the diet of the fish larvae of the Salto Grande reservoir, as compared with lotic waterbodies of the Paraná and Uruguay rivers.

Temporal mismatches between fish breeding periods and abundance changes in the populations of their prey may have negative consequences for fish

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Table 2. Continued

Ichthyoplankton taxa	Guts with Rotifera (%)‡	Guts with NI (%)‡	Guts with algae % (%)‡	Mean biom. *L. fortunei* (%)§	Mean biom. Cladocerans (%)§	Mean biom. Copepoda (%)§	Mean biom. Rotifera (%)§
Prochilodus lineatus	0 (0)	4 (57)	0 (0)	0.00 (0)	0.07 (100)	0.00 (0)	0.00 (0)
Anostomidae	0 (0)	7 (44)	4 (25)	0.00(0)	0.34 (100)	0.00(0)	0.00(0)
Luciopimelodus pati	0 (0)	0 (0)	0 (0)	0.00 (0)	0.08 (100)	0.00 (0)	0.00 (0)
Pachyurus bonariensis	0 (0)	0 (0)	0 (0)	0.05 (2)	1.65 (70)	0.67 (28)	0.00 (0)
Lycengraulis grossidens	11 (16)	13 (19)	9 (13)	0.04 (5)	0.50 (72)	0.09 (13)	0.07 (10)
Siluriformes	0 (0)	1 (20)	1 (20)	0.18 (10)	1.56 (90)	0.00 (0)	0.00 (0)
Apareiodon affinis	3 (5)	34 (59)	0 (0)	0.19 (24)	0.47 (59)	0.08 (10)	0.05 (7)
Characiformes	0 (0)	2 (25)	0 (0)	0.10 (35)	0.18 (65)	0.00 (0)	0.00 (0)
Catathyridium jenynsii	0 (0)	1 (5)	0 (0)	1.51 (69)	0.67 (31)	0.00 (0)	0.00 (0)
Pimelodidae	1 (3)	2 (5)	2 (5)	1.92 (83)	0.37 (16)	0.00 (0)	0.02 (1)

†Based on pooled data from the main channel and the two coastal stations. ‡Proportions of all feeding larvae. §Biomass values are in μg dry weight and as a proportion of total biomass. NI denotes non-identified prey items.

recruitment (Cushing 1990; Fortier *et al.* 1995). Although veligers are generally abundant in Salto Grande (Fig. 3b), their presence varies widely, both seasonally and interannually, thus they represent an unpredictable and often scarce food source. Seasonally, lowest veliger availability occurred around January–March, in association with the occurrence of massive cyanobacterial blooms (Fig. 6a), at which time golden mussel larvae disappear altogether from the water column, most

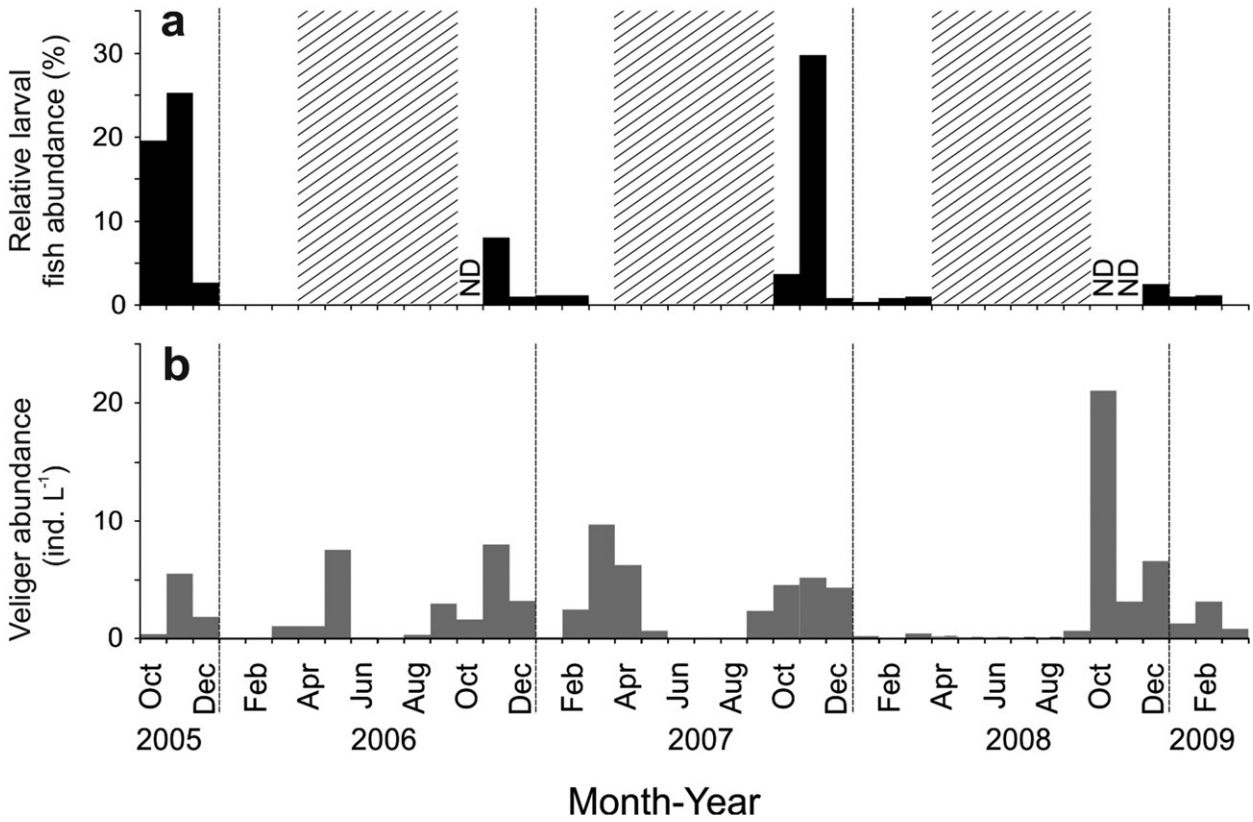

Fig. 3. (a) Monthly means of relative abundance of fish larvae, as a percentage of all larvae retrieved throughout the entire survey, and (b) absolute veliger densities (ind. L^{-1}; data from Boltovskoy *et al.* 2013). Hatched areas denote periods without fish larvae in the water column (Paolucci 2002; de Resende 2003) (not sampled). ND: No data.

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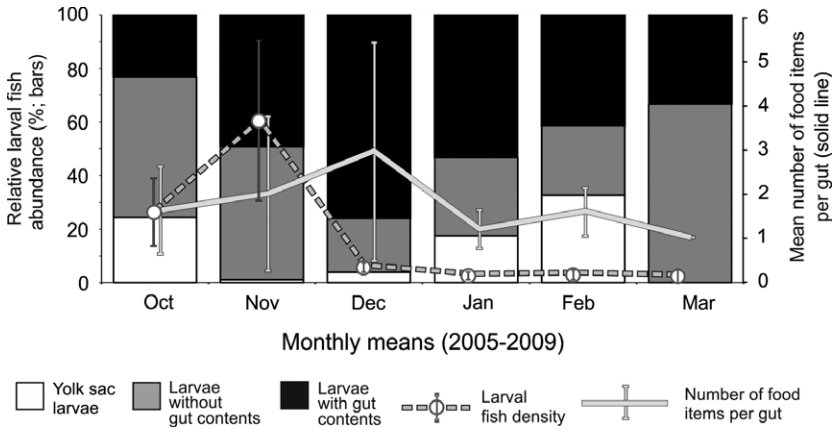

Fig. 4. Monthly averages of the relative abundance of total larval fish (dotted line), yolk-sac larvae, larvae with empty guts and larvae gut contents (white, grey and black bars, respectively) during 2005–2009. Solid line represents average number of items per stomach. October and November yielded significantly greater larval fish numbers than the rest of the sampling season (Kruskal–Wallis test, $P < 0.05$).

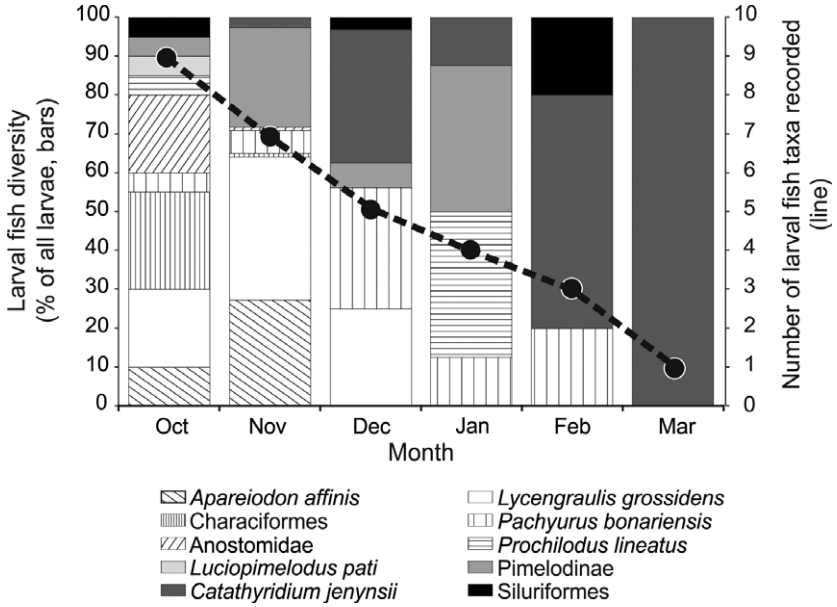

Fig. 5. Temporal changes (monthly means) in the taxonomic composition of feeding larval fish assemblages and total numbers of taxa recorded during 2005–2009, based on pooled data for the two coastal stations (SY and IT in Fig. 1) and the main channel (MC in Fig. 1).

probably due to the toxic effects of microcystin (Boltovskoy *et al.* 2013). Thus, in the Salto Grande the temporal overlap between the presence of larval fish and veligers is considerably lower than in other waterbodies that do not develop cyanobacterial blooms. In the Paraguay, Paraná and Uruguay rivers, veligers are present in high densities from October–November to March or April (Boltovskoy *et al.* 2015), thus totally overlapping the period when fish larvae are most abundant (de Resende 2003). In contrast, previous studies and our results show that in the lower section of Salto Grande, where summer cyanobacterial blooms are strongest, veligers were abundant for only 3 of the 6 months when larval fish were present (Fig. 3a,b). Monthly changes in the feeding preferences of fish larvae for veligers were particularly noticeable, with maxima in December, when larval fish feeding activity and the abundance of veliger predators are greatest. From January onwards, despite the sustained abundance of veliger predators in the ichthyoplankton, their feeding preference for mussel larvae decreases noticeably, in association with decreases in the availability of this food item (Fig. 7d). Abrupt changes in the feeding

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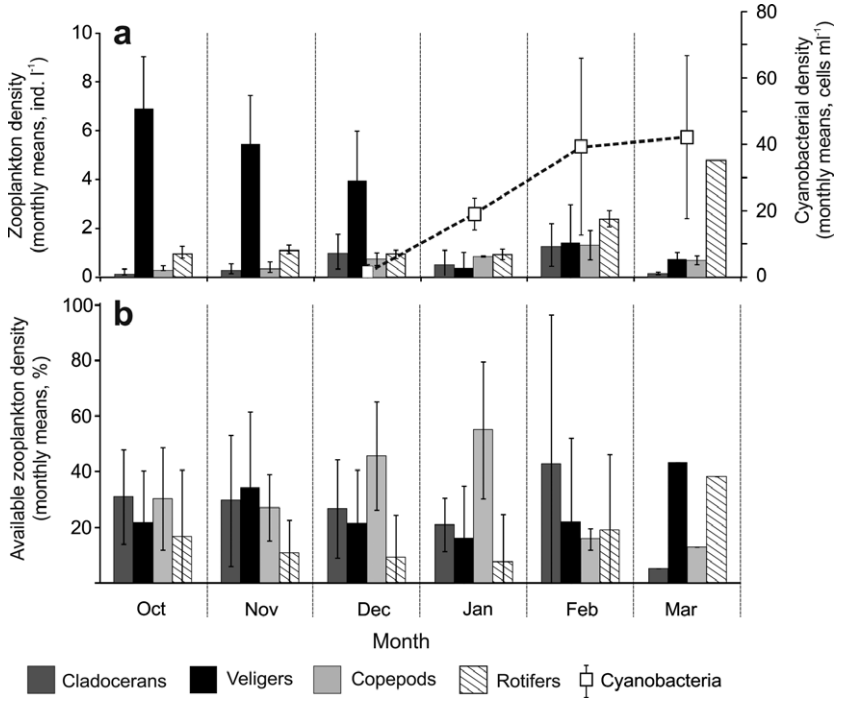

Fig. 6. Mean monthly values for zooplankton and cyanobacterial densities. (a) Absolute zooplankton abundance and cyanobacterial densities (data from Boltovskoy *et al.* 2013) based on all the samples for the sampling periods covered. Veliger densities were significantly greater in October–December than in January–March. (b) Zooplankton densities recorded in the zooplankton samples where the paired ichthyoplankton sample yielded fish larvae with gut contents. Error bars denote SD.

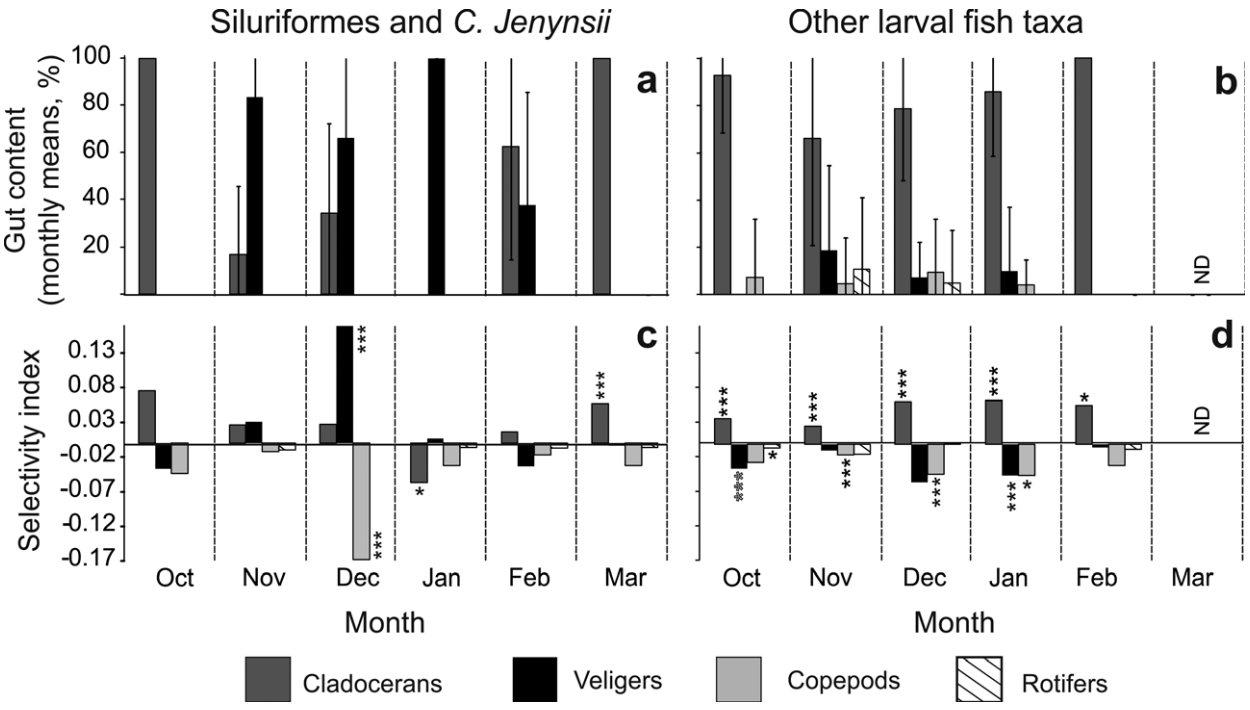

Fig. 7. Monthly means for the proportions of gut contents for larval fish that selectively consumed veligers (a) or cladocerans (b), and the corresponding selectivity indices (c, d). Left-hand panels include Siluriformes and *Catathyridium jenynsii;* right-hand panels include all other fish taxa (see Table 2). Asterisks denote significant differences between the proportions of the corresponding prey in the water column and in the gut content at $P < 0.05$ (*), $P < 0.01$ (**) or $P < 0.001$ (***) (Chi-square tests).

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Table 3. Comparative data of results of this work with previous studies in other environments of the Río de la Plata watershed. "Total zooplankton" includes veligers, cladocerans, copepods and rotifers (a), or veligers, cladocerans, copepods and insect larvae (b)

Environment/ River	Main channel, Middle Paraná River	Middle and Lower Paraná River	Lower Paraguay River	Middle Paraná River	Lower Uruguay River	Salto Grande reservoir	Salto Grande reservoir
Source of data	Rossi (2008)	Paolucci *et al.* (2007)	Paolucci *et al.* (2015)	Paolucci *et al.* (2015)	Paolucci (2002)	Paolucci (2002)	This work
Sampling period	Nov 1996–Mar 1997	Oct 2000–Mar 2001	Nov 2005	Nov 2005	Oct 2000–March 2001	Oct 2000–March 2001	Oct 2005–Mar 2009
Total number of samples	51	36	11	9	142	74	95
Total larvae retrieved	50 658	10 970	11 177	4085			577
Larval fish density (ind. m^{-3} ± SD)	7.1 ± 0.8	–	24.7 ± 19.7	8.4 ± 7.0	2.3 ± 3.2	4.7 ± 5.5	–
Mean number of larvae per sample	993.3 ± 508.2	304.7	1016.1 ± 680.5	453.9 ± 427.8	24.0 ± 32.0	50.5 ± 85.0	6.3 ± 14.2
Samples with fish larvae (%)	96.1	100.0	100.0	100.0	84.5	82.4	64.2
Total larvae with yolk sac (%)	20.4	43.0	61.0	59.5			9
Diet analysis							
Feeding fish larvae	819	1043	1275	806	–	–	523
Larvae with empty guts † (%)	379 (46.3)	800 (76.7)	448 (74.4)	443 (85.2)	–	–	278 (53)
Larvae with gut contents † (%)	440 (53.7)	243 (23.3)	154 (25.6)	77 (14.8)	–	–	245 (47)
Number of items per stomach	5.4 ± 6.5	4.5 ± 3.5	2.3 ± 1.9	3.3 ± 3.8	–	–	2.3 ± 3.2
FO of veligers (%)	59.7	56.8	14.2	68.4	–	–	20.0
Veliger density in the plankton (ind. L^{-1})	2.1 ± 0.4	–	0.8 ± 0.5	5.5 ± 2.3	–	–	3.1 ± 3.9
Veliger % of total zooplankton	53.7 ± 6.7a	–	32.0b	85.9b	–	–	49.2a

† Percentages refer to total feeding larvae.

selectivity in association with changes in the abundance of veligers were also reported for the Paraguay–Paraná watershed by Paolucci *et al.* (2015).

Temporal uncoupling of ichthyoplankton from veligers, resulting from the toxic effects of *Microcystis* spp. on *Limnoperna* veligers, seems to be at least partly responsible for the lower impact of the invasive bivalve on larval fish diets. This supports the notion that feeding selectivity is highly dependent on the availability of prey, which in turn determines the rate of predator–prey encounters (Graeb *et al.* 2004; Fulford *et al.* 2006; Paolucci *et al.* 2010a).

The Salto Grande reservoir has been characterized as a large river-like reservoir with multiple arms, where cyanobacterial blooms are strongest and most frequent along the littoral areas in the vicinity of the dam (O'Farrell *et al.* 2012). Thus, we contend that both effects, i.e. differences in the larval fish-specific composition and the toxic effects of *Microcystis* spp. on *Limnoperna* veligers, are responsible for the low importance of veligers in larval fish diets compared with other waterbodies of the same basin.

Previous studies provided evidence pointing at the positive trophic impact of the veligers of invasive bivalves on native larval fish (Paolucci *et al.* 2007, 2015; Nack *et al.* 2015), including experimental data showing that fish growth is enhanced in the presence of the new trophic resource (Paolucci *et al.* 2010b). Our results indicate that these trophic relationships are not always as simple and straightforward as previously envisioned. The combined effects of a substantially modified fish assemblage and the periodic toxic algal blooms result in a much more complex situation with most probably negative consequences. Toxic cyanobacterial blooms, which are enhanced by the invasive mussel (Boltovskoy *et al.* 2013), not only affect *Limnoperna*'s reproduction but also the reproduction, development, feeding and survival of the fishes (Pizzolon *et al.* 1999; Ojaveer *et al.* 2003; Palíková *et al.* 2007; Ghazali *et al.* 2009; Gómez

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2014). Thus, the positive effects of the availability of *Limnoperna* veligers as a trophic resource may be largely outweighed by those of its adults through their enhancement of cyanobacterial blooms.

These results underscore the complexity of the biotic relationships brought about by the introduction of new species, and particularly the ambiguities involved when attempting to label the impacts as negative or positive. In this respect, because of their fast dispersion and wide-ranging effects, freshwater invasive mussels, including *L. fortunei* and *Dreissena* spp. (Karatayev *et al.* 2015), offer unique chances of disentangling the intrinsic effects of the species itself from those of the species and its interactions with the environment invaded on the final outcome of the impacts of the invasion. Regional differences seem to be responsible for the fact that for *Dreissena polymorpha* and *D. rostriformis bugensis*, two of the most aggressive freshwater invaders worldwide (Nalepa & Schloesser 2013), enhancements of cyanobacterial blooms seem to be restricted to waterbodies with low P concentrations only (<25 μg total P L^{-1}; Sarnelle *et al.* 2005), whereas in South America *Limnoperna* boosts cyanobacterial growth at P concentrations above 100 μg total P L^{-1} (Cataldo *et al.* 2012). Despite the fact that *D. polymorpha* has been invading Western Europe since the 1700's, and North America since 1986 (Karatayev *et al.* 2007), as of 1997 only ten European and five North American larval fish species were recorded to consume *Dreissena* veligers (Molloy *et al.* 1997); as opposed to 18 recorded in South America as consumers of *Limnoperna* larvae, which first invaded the subcontinent around 1990. The results presented in this work underscore further the importance of environmental settings on the relationships between the invader and local species, showing that sharp differences characterize not only widely separated geographic areas but also different waterbodies within the same basin.

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