

Trophic Relationships of *Limnoperna fortunei* with Larval Fishes

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Abstract This chapter reviews investigations concerning the importance of veligers of the exotic bivalve *Limnoperna fortunei* in the diets of larval fish in the Río de la Plata basin. These studies have shown that of the 25 fish taxa studied, 18 consumed veligers of *L. fortunei*. These species included the most abundant members of Characiformes and Siluriformes. The relative frequency and biomass contribution of *L. fortunei* larvae differed strongly in pimelodid and *Prochilodus lineatus* larvae at different developmental stages and in different environments. Thus, as fish larvae grew, their diets shifted from veligers to other prey items. The fact that the earliest fish larvae are the most active consumers of veligers is particularly significant because these early larvae usually represent the most vulnerable life stage when mortality rates are the highest. In addition, field data and laboratory experiments indicate that small crustaceans have been largely replaced by *L. fortunei* veligers in diets of fish larvae, especially when veligers are abundant. Selectivity for feeding on veligers was recorded in the field and in laboratory experiments by manipulating prey density. Experiments also demonstrated that *P. lineatus* larvae grew to a significantly larger size with a high concentration of veligers in the diet. This new and abundant food resource appears to have a very important impact on the survival and growth of *P. lineatus* and probably other fish species as well.

Keywords *Limnoperna fortunei* · Golden mussel · Predation by fish · Ecological impact · Trophic interactions · Fish diet · Fish larvae · Veligers

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Introduction: Bivalve Invaders as Prey in Aquatic Ecosystems

One of the most important and extensively studied effects of introduced bivalves is their impact on trophic relationships and food web structures (Karatayev et al. 2007b; Bulté and Blouin-Demers 2008; García-Ortega et al. 2010). For example, several species of adult fish have incorporated the zebra mussel into their diets, but not always with beneficial results (French and Bur 1996; Molloy et al. 1997; García-Ortega et al. 2010). In South America, at least 50 fish species have been recorded to feed on adult *Limnoperna fortunei*, and this mussel has become an important food item for native fish of ecological and economic importance (see Chapter “Trophic Relationships of *Limnoperna fortunei* with Adult Fishes” in this volume; Boltovskoy and Correa 2015). Furthermore, the planktivorous larvae and juveniles of several fish species benefit from very high densities of the planktonic larval stages of *L. fortunei* (Paolucci et al. 2007).

Many planktivorous fish larvae in South American rivers are the product of reproductive migrations, in which mature adults migrate upstream to spawn, after which the larvae drift passively downstream until they reach a marginal wetland (Carolsfield et al. 2004). Even though these species migrate upstream for spawning, other aspects of these movements have species-specific traits, such as the extent and timing of migrations (Welcomme 1979; Fuentes and Espinach Ros 1998). This results in an ichthyoplankton characterized by a mix of different species and different developmental stages. In addition, larval feeding behaviors of these species are also different, depending on their developmental stage and environmental conditions (Rossi 2008). For example, larvae of the sábalo, *Prochilodus lineatus*, migrate from the main channel toward marginal lagoons while depending mostly on their yolk reserves for energy (Rossi 1992; Fuentes and Espinach Ros 1998; Paolucci 2002). Active feeding begins once they have reached marginal lagoons, which serve as nursery areas for several key fish species (Rossi 2008). In contrast, catfish larvae (Pimelodidae) and the larvae and juveniles of several ichthyophagous species start feeding in the channel shortly after hatching (Merigoux and Ponton 1998; Rossi 2001; Makrakis et al. 2008).

Importance of Veligers in Larval Fish Diets

Using samples collected in 1996–1997, Rossi (2008) studied the trophic behavior of larval fish in the main and secondary channels of the Middle Paraná River (Fig. 1a) and found that veligers of *L. fortunei* were consumed by ten fish taxa (Table 1). Of these fishes, pimelodid larvae were the heaviest consumers of this new prey item. On a larger scale study of the impact of these veligers, Paolucci et al. (2007) analyzed fish larvae in the Middle and Lower Paraná during 2000–2001 and in subsidiary marginal lagoons in 2004 (Fig. 1a, b). They reported that *L. fortunei*

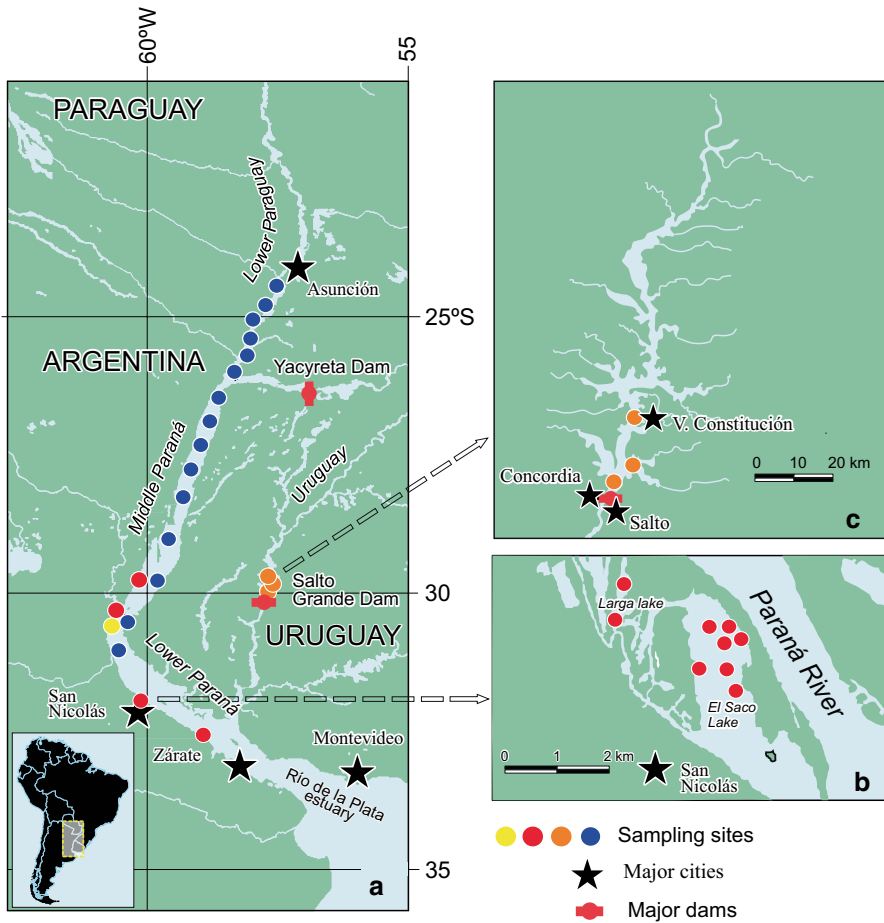


Fig. 1 Location of sampling sites for studies investigating larval fish predation on veligers of *Limnoperna fortunei*. Red circles: data from Paolucci et al. (2007). (a) Lower and Middle Paraná River. b Marginal environments); yellow circle: data from Rossi (2008); orange and blue circles: data from Paolucci (2010) (a Paraná and Paraguay rivers. c Salto Grande Reservoir)

veligers were actively consumed by 11 of 15 larval fish taxa surveyed (Table 1). At that time, *L. fortunei* was recorded in the guts of *P. lineatus*, *Iheringichthys labrosus*, *Luciopimelodus pati*, *Sorubim lima*, *Pimelodus* spp., and *Parapimelodus valenciennis*, as well as the larvae of other unidentified species of Anostomidae, Doradidae, Characiformes, and Pimelodidae (Fig. 2a–g). These first studies showed that veligers of *L. fortunei* were also present, although at low importance, in the gut contents of piscivorous species, such as *Pseudoplatystoma* sp. and *Rhaphiodon vulpinus*. In a subsequent analysis of the local ichthyoplankton, which included the Lower Paraguay River, Middle Paraná River, and the Salto Grande Reservoir (Fig. 1a, c), the list of consumers of veligers was extended to 18 out of a total of 25 analyzed taxa (Table 1; Paolucci 2010). In the Paraguay River and its marginal

Table 1 (continued)

Species/taxa	Total FO (%) [N]	Maximum FO (%)	Total biomass (µg)	Main channel, Middle Paraná River ^a	Main channel, Middle and Lower Paraná River ^b	Marginal lagoons, San Nicolás ^b	Paraná and Paraguay rivers ^c	Salto Grande Reservoir ^c
Sampling period				1996–1997	2000–2001	2004	2005	2005–2009
Fam. Cynodontidae								
<i>Rhapiodon vulpinus</i>	-	-	-	X				
Characiformes NI	25.0 [2]	20.0	5.46			X	X	x
Clupeiformes								
Fam. Engraulidae								
<i>Lycengraulis grossidens</i>	4.2 [3]	11.1	0.04					X
Pleuronectiformes								
Fam. Achiridae								
<i>Catathyridium jenyssii</i>	73.9 [17]	85.7	3.52				X	x
Perciformes								
Fam. Sciaenidae	5.2 [1]	11.1	0.05	x			x	X
Total				10	8	7	11	7

Maximum FO was calculated per environment and its corresponding environment is marked in capital bold font

N total number of guts containing veligers of *L. fortunei*, NI not identified

^a Data of veliger predators are from: Rossi 2008

^b Data of veliger predators are from: Paolucci et al. 2007

^c Data of veliger predators are from: Paolucci 2010

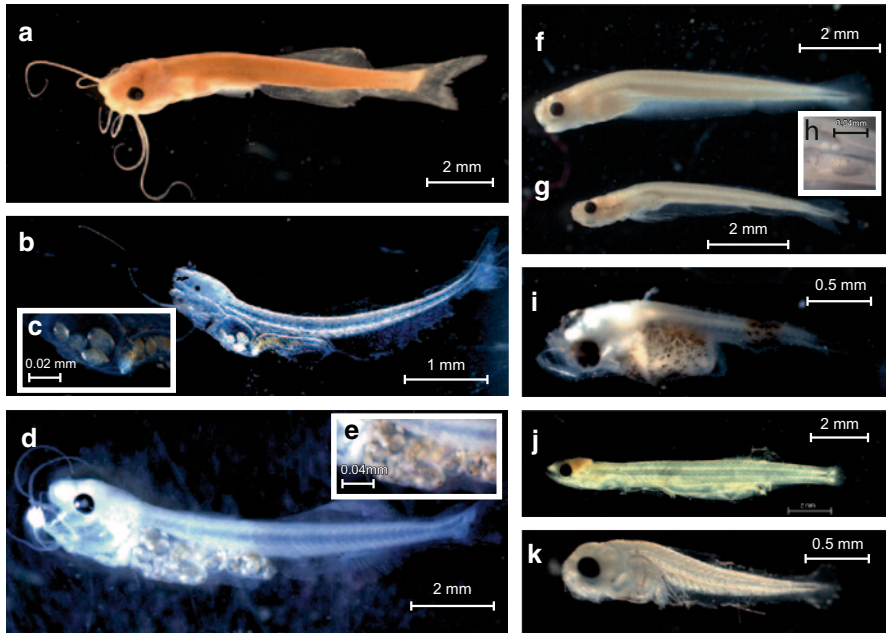


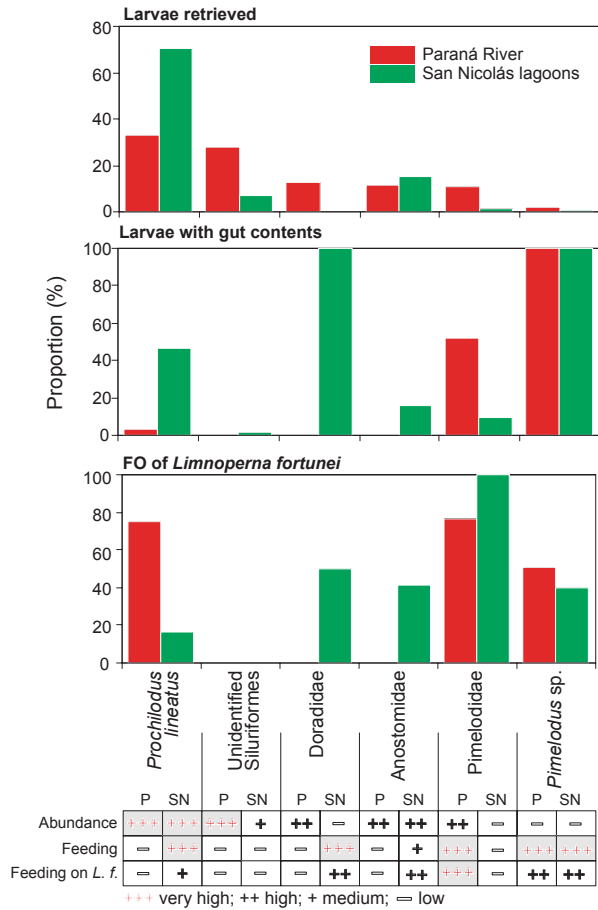
Fig. 2 Some of the larval fish species that feed on *Limnoperna fortunei* veligers. **a** Mesolarva of catfish, *Iheringichthys labrosus*. **(b, d)** Pimelodid protolarva. **(c, e, h)** Veligers of *L. fortunei* in gut contents. **f** *Prochilodus lineatus* protolarva. **g** Anostomid protolarva. **i** Flatfish, *Cathartidium jennynsii*. **j** Anchovy larva, *Lycengraulis grossidens*. **k** Sciaenid larva. (Modified from Paolucci 2010)

and lentic environments, several species of Clupeiformes, Pleuronectiformes, and Perciformes (Fig. 2i–k) were added to the list of predators. The temporal overlap between fish and mussel reproductive periods results in a stable food supply for the larval fishes and is a key factor in this relationship. In comparison, the zebra mussel, *D. polymorpha*, often has a shorter reproductive period (Karatayev et al. 2007a; see Chapter “Parallels and Contrasts between *Limnoperna fortunei* and Species of *Dreissena*” in this volume), and this may be one of the reasons that zebra mussel veligers are much less important in the diets of North American fish larvae (Banard et al. 2006).

Feeding on Veligers by Larval Fish in the Main Channel Versus Marginal Environments

Some larval fish start feeding in the main river channel, while others forage in marginal water-bodies of the alluvial plain, and data from both environments were compared by Paolucci et al. (2007). These authors found that in the main channel of the Paraná River, eight taxa had *L. fortunei* larvae in their guts. Among these, pimelodid larvae such as *I. labrosus*, *L. pati*, and *S. lima* were by far the most

Fig. 3 Taxonomic composition, proportions of larvae with gut contents, and frequency of occurrence (FO) of *Limnoperna fortunei* for the dominant fish taxa (those comprising >94% of all the larvae retrieved) in the Paraná River and San Nicolás lagoons. (Based on data from Paolucci et al. 2007)



active consumers of veligers (Fig. 3). Among the Characiformes in their study, only *P. lineatus* consumed *L. fortunei* in the main channel; however, veligers were the only identifiable food item recorded for all of these fish larvae. In the San Nicolás lagoons (a marginal environment connected to the river; Fig. 1a), seven out of ten taxa they investigated had *L. fortunei* in their guts. Approximately 20% of the Characiformes consumed veligers. For the Siluriformes, the proportion was similar (23%), but these fishes were comparatively scarce in these lagoons (ca. 10% of all larvae collected).

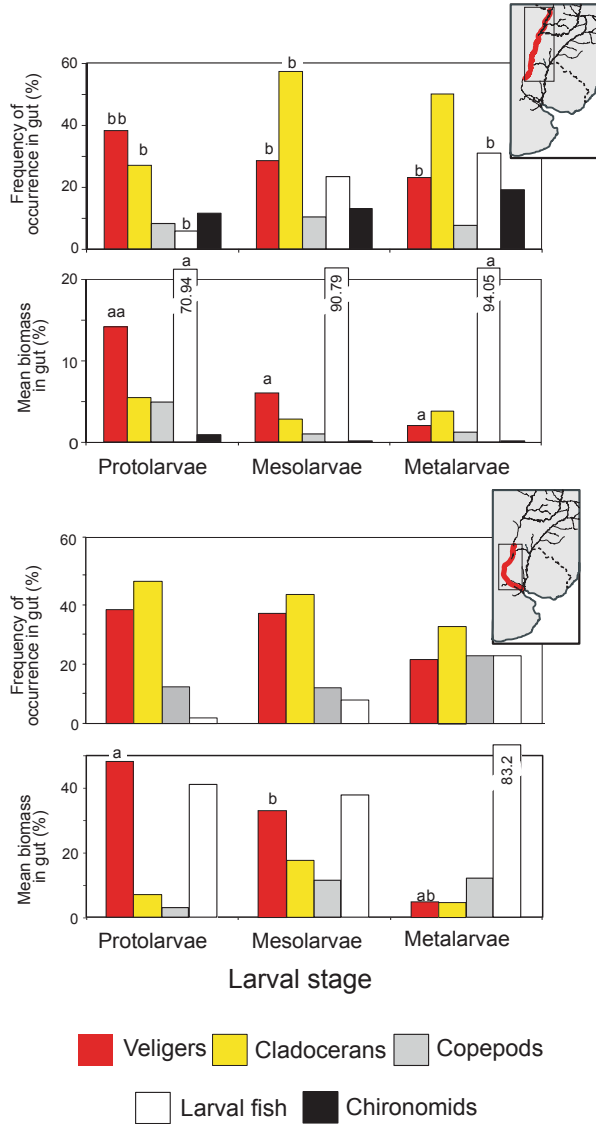
Differences in taxonomic compositions and feeding activities of larval fish assemblages between the main channel and marginal environments seem to be the main factors affecting the frequency of occurrence (FO) of *L. fortunei* in diets found by Paolucci et al. (2007; Fig. 3). The proportions of feeding larvae that had *L. fortunei* in their gut varied between 20% (San Nicolás lagoons) and 56% (Paraná River). In terms of biomass, however, the mean contributions of veligers in larval fish diets was smaller, ranging from 8% (Paraná) to 12% (San Nicolás) (mean weighted val-

ues), but contributions as high as 100% were recorded for some taxa in the Paraná River. Larvae of the sábalo, *P. lineatus*, which is the most abundant species in the Paraná-Uruguay watershed (Sverlij et al. 1993; Bonetto 1998), were dominant in both environments (Fig. 3). In the Paraná River, only 3% had gut contents, while in San Nicolás almost half of the specimens had food in their stomachs. On the other hand, for Siluriformes, proportions of nonempty guts in the Paraná were comparable to those in San Nicolás. Similar observations of differences between the main channel and secondary rivers have been made by Rossi (1992).

Ontogenetic Dietary Shift and Veliger Impact

It is well known that interactions between larval fish and their prey change over time (Lazzaro 1987; Merigoux and Ponton 1998), and field studies on the importance of *L. fortunei* veligers in the diets of larval fishes have also demonstrated ontogenetic changes (Paolucci et al. 2007; Rossi 2008; Paolucci 2010). In absolute terms, the FO and biomass of *L. fortunei* larvae in the guts of proto-, meso-, and metalarvae of mostly pimelodid species collected in the Lower and Middle Paraná and Paraguay rivers had more or less similar values (Paolucci et al. 2007; Paolucci 2010). However, as a percentage of total occurrence or biomass, size-related patterns in the diets of fish larvae were evident (Fig. 4). Protolarvae fed chiefly on *L. fortunei* veligers and cladocerans with fewer copepods and fish larvae (Fig. 4). Mesolarvae consumed veligers, cladocerans, and copepods in similar proportions, but exhibited increased frequencies of fish and insect 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 15 to 45% in protolarvae and mesolarvae, to only 3% in the metalarvae (Fig. 4). Thus, as larvae grew, their diet shifted from *L. fortunei* veligers to other larger prey items. Similar trends in the importance of veligers during the development of larval fish were observed by Rossi (2008) for pimelodid species such as *S. lima*, *Pimelodus* sp., and particularly *Pseudoplatystoma cf. corruscans*. These results clearly highlight the importance of *L. fortunei* veligers as prey during the earliest developmental stages of larval fishes. The fact that the earliest fish larvae are the most active consumers of veligers is particularly significant because they usually represent the most vulnerable life history stage where mortality rates are the highest (Elliott and Persson 1978).

Fig. 4 Average frequency of occurrence (FO) and total biomass (% contribution) of major prey items found in protolarvae, mesolarvae, and metalarvae, pooled data for the Paraguay River and Middle Paraná River (*upper panels*), and the Middle and Lower Paraná River and San Nicolás lagoons (*lower panels*). Letters denote significant differences between developmental stages at $p < 0.01$ (a) or $p < 0.05$ (b) (ANOVA, Duncan post-hoc test). (Based on data from Paolucci et al. 2007 and Paolucci 2010)



Selectivity for Veligers by Fish Larvae as a Function of Prey Density: Field Evidence

Preliminary analyses of the feeding preferences of native larval fishes, such as *P. lineatus* and anostomid larvae, in marginal environments (Fig. 5a), showed that the veligers of *L. fortunei* were selected positively over cladocerans and copepods (Paolucci et al. 2007). The importance of *L. fortunei* in the diets of larval fishes was up to seven times higher than that expected based on the relative abundance of veligers in the zooplankton. A subsequent study of selectivity and feeding behavior of larval fish collected in the main channel recorded higher impact and preference values for veligers of *L. fortunei* in the Paraná River than in the Paraguay River (Fig. 5b; Paolucci et al. 2015). Comparison of the larval fish diet between the Paraguay and Paraná rivers indicates that average veliger FO was ca. five times more common in fishes caught in the Paraná River (68.4% of which consumed *L. fortunei* vs. 14.2%; Fig. 6). In the Paraguay River, in contrast, cladocerans were usually favored over other prey, often accounting for significantly higher proportions of all items in the stomachs than in the water-column (Fig. 5b). Selectivity behaviors were not evenly distributed among taxa, but restricted to Characiformes, *C. jenynsii*, *I. labrosus*, and pimelodid larvae (Fig. 5b). In addition, selectivity toward veligers was positively correlated with the absolute abundance of veligers in the water column (Fig. 6); when more veligers were available, fish larvae relied on them more as prey. As seen in other studies (Deudero and Morales-Nin 2001; Graeb et al. 2004; Fulford et al. 2006), veliger density plays a central role in selectivity by the predators, mainly due to an increase in the rate of predator-prey encounters.

Effects of Developmental Stage and Veliger Density on Selectivity: Experimental Evidence

As in field studies for other fish species, comparisons of gut contents versus available food determined in laboratory experiments demonstrated that selectivity behavior was a function of prey density and the developmental stage of *P. lineatus* (Paolucci 2010; Paolucci et al. 2010a). For protolarvae, average proportions of veligers, small cladocerans, and nauplii were always higher in the gut contents than in the prey offered indicating selectivity for these items (positive values in Fig. 7) (small cladocerans and nauplii were the main prey of *P. lineatus* larvae before *L. fortunei* was present in South America; Rossi 1992). Mesolarvae preyed on veligers selectively only when these were very abundant in the experimental tanks (enriched veliger concentrations in Fig. 7); however, when veliger concentrations dropped, they were consumed less selectively, with gut contents yielding lower proportions of veligers. Mesolarvae were especially efficient at consuming small and medium-sized cladocerans, whose selectivity indices were almost invariably posi-

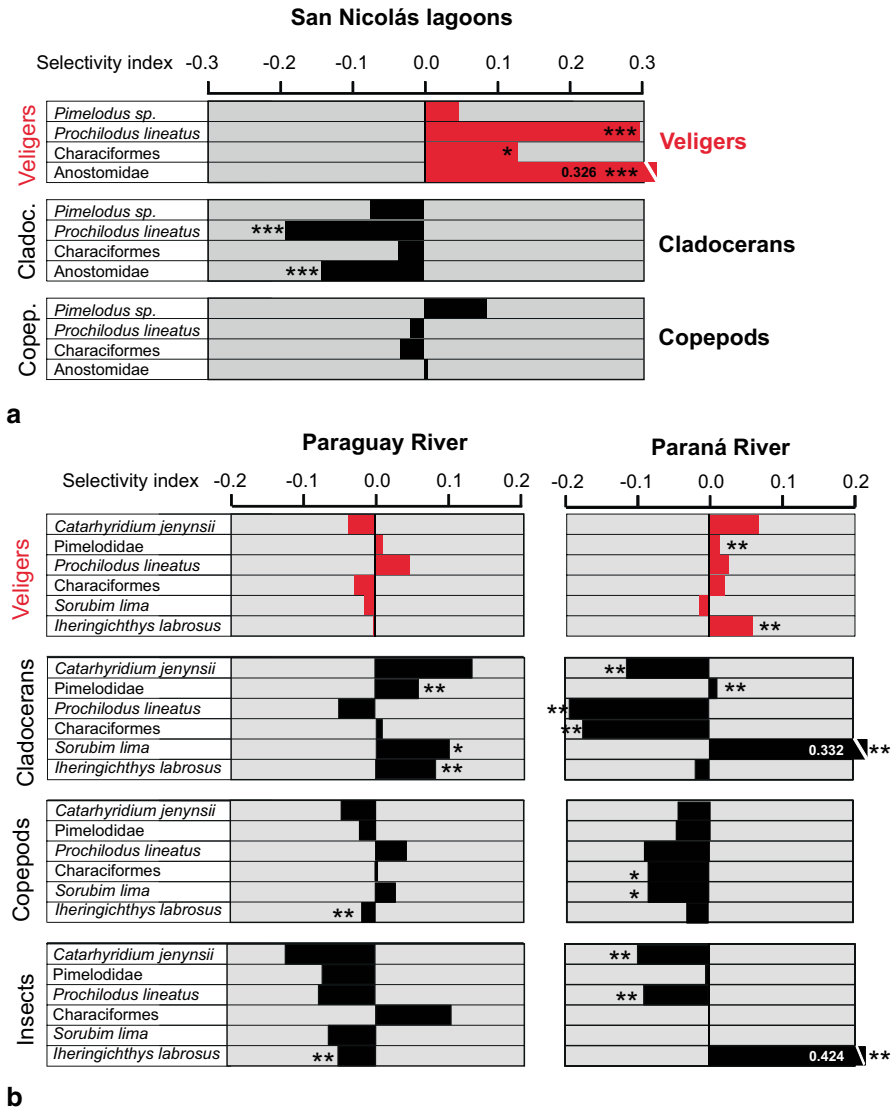
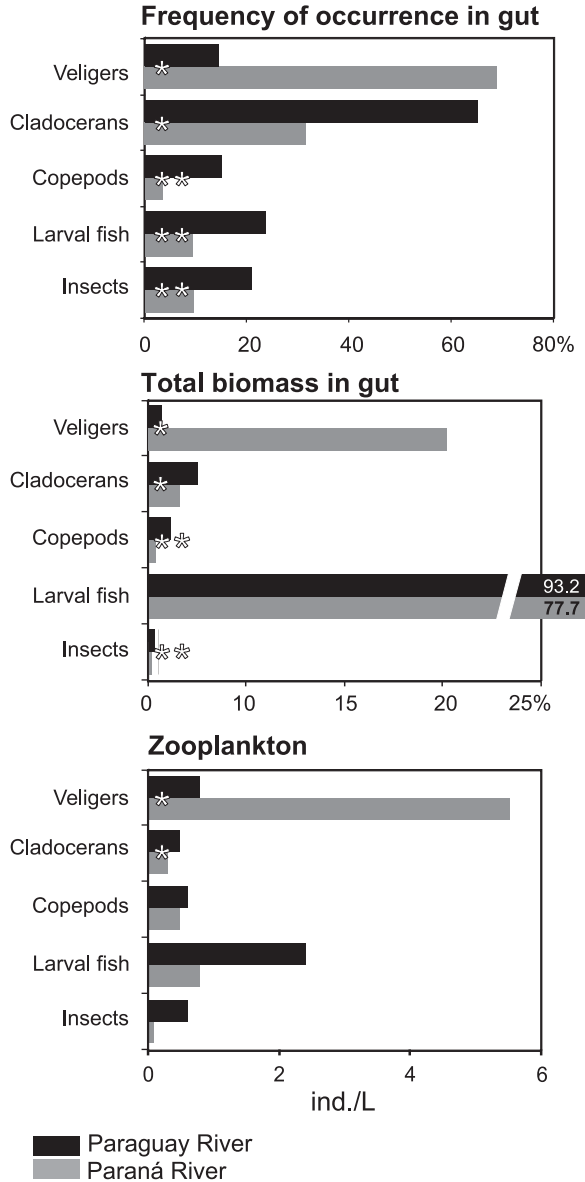


Fig. 5 Mean selectivity index for the prey items assessed for the most abundant fish species present in San Nicolás lagoons (a) and in the Paraguay and Paraná rivers (b). Asterisks denote significant differences between proportions of the corresponding prey in the water column and in the gut contents at $p < 0.05$ (*), $p < 0.01$ (**), or $p < 0.001$ (***) (Chi-square tests). (Based on data from Paolucci et al. 2007 and Paolucci et al. 2015)

tive and statistically significant (Fig. 7). In contrast with younger larvae, metalarvae never selected veligers, regardless of their concentration in the experimental tanks, and they clearly favored small and medium-sized cladocerans. For *P. lineatus*, as

Fig. 6 Contribution of the five main food items to the diet of fish larvae and zooplankton composition recorded in the Paraguay and Paraná Rivers. Statistically significant differences between the two rivers are denoted with *asterisks* (* $p < 0.05$; ** $p < 0.01$, Kruskal-Wallis test). (Modified from Paolucci et al. 2015)



well as for pimelodid larvae, the highest positive selectivity values were also associated with the highest proportions of veligers in the zooplankton.

Laboratory results and available field data for these fish species (Paolucci et al. 2007; Rossi 2008; Paolucci et al. 2010a) indicate that small crustaceans have been largely replaced by veligers, especially when veligers are abundant. This dietary switch, however, is restricted to the earliest larvae. As fishes grow larger and de-

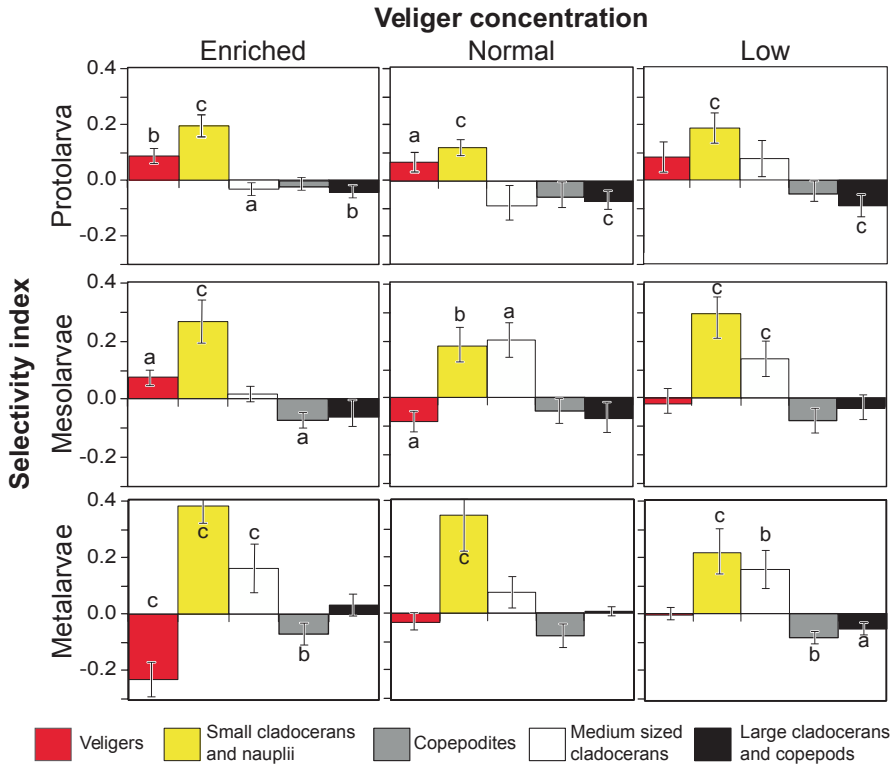


Fig. 7 Average selectivity index per prey item assessed for protolarvae ($n=15$), mesolarvae ($n=15$), and metalarvae ($n=15$) in three experimental settings (*enriched*, *normal*, and *low concentrations* of veligers). Error bars denote confidence intervals at $p < 0.05$. Letters denote significant differences between available prey and gut contents at $p < 0.05$ (a), $p < 0.01$ (b), or $p < 0.001$ (c) (Chi-square tests) (Modified from Paolucci et al. 2010a)

velop a larger mouth gape (Fig. 8a), the relative importance of large crustaceans increases. The replacement of crustaceans by veligers of *L. fortunei* in the diet of larval fishes is chiefly due to the fact that veligers are poor swimmers, with limited neuromuscular coordination and poor predator-avoidance behavior compared to crustacean zooplankton. Cladocerans, in turn, are slower and less agile than copepods. This gradient in predator-avoidance capabilities seems to be the main prey-selection factor during the earliest life stages of a fish. Indeed, for many fish species mollusc larvae have been reported to be preferred over crustaceans (Pepin and Penney 1997; Lehtiniemi et al. 2007), and cladocerans are generally preferred over copepods (Cooper and Goldman 1980; Vanderploeg et al. 1982; Clarke et al. 2004), sometimes regardless of prey size (Werner 1974). However, it is worth noting that several of these fish species also prey on the juvenile and adult stages of *L. fortunei* when they reach a larger developmental stage (see Chapter “Trophic Relationships of *Limnoperna fortunei* with Adult Fishes” in this volume).

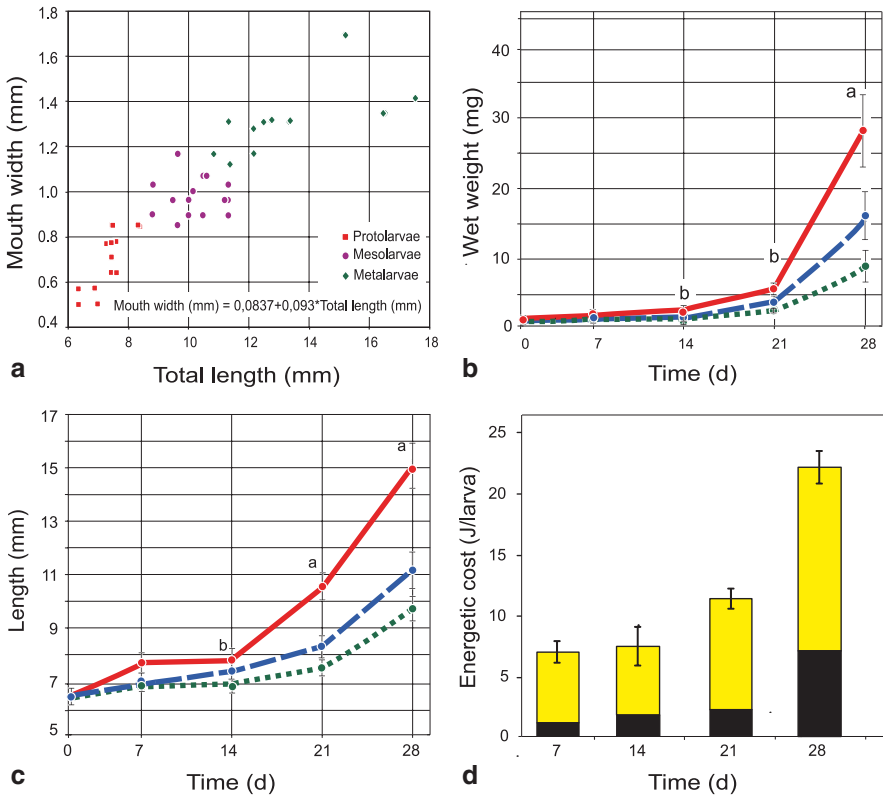


Fig. 8 **a** Correlation between total length and mouth width of the *Prochilodus lineatus* larvae used in the selectivity experiments ($R=0.917$; $p<0.01$; $n=45$; modified from Paolucci et al. 2010a). Growth as **b** wet weight (mg) and **c** total length (mm) of larval fish fed three different diets: veliger-enriched (solid red line), natural (dashed blue line), and low-veliger (dotted green line). Vertical bars denote 95% confidence intervals. Letters denote significant differences. (ANOVA, $p<0.01$) as **a** between all diets; or (**b**) between at least one pair of diets. **d** weekly energetic costs of growth (black bars) and standard metabolic rate (yellow bars) according to the mean weight of the larval fish used in respiration experiments. Error bars denote 95% confidence intervals of the combined energetic costs. (**b**, **c**, and **d** modified from Paolucci et al. 2010b)

Effects on Growth of Larval Fishes

Even in fish that are important predators of bivalves, some negative effects have been reported (French and Bur 1996; Nagelkerke and Sibbing 1996; Magoulick and Lewis 2002). These have been explained by the low caloric content of bivalve larvae compared to traditional food items, mainly due to the presence of shells that are not assimilated. However, growth experiments carried out using newly hatched *P. lineatus* larvae (with yolk-sac absorption completed) and different veliger concentrations showed positive rather than negative effects (Paolucci et al. 2010b). This experimental approach not only supported the idea that this new and abundant

resource is selectively preyed upon by this larval fish, but also demonstrates that veligers of *L. fortunei* can significantly enhance the growth of *P. lineatus* larvae. Different veliger concentrations had significant effects on growth, for both total length and wet weight, of *P. lineatus* larvae; those fed a veliger-enriched diet had the highest growth performance, followed by those fed natural and low-veliger diets (Fig. 8b, c).

Similar to that observed in other studies with larval fishes (Halver 2001; Tes-hima et al. 2004), the enhanced growth rates observed by Paolucci et al. (2010b) may depend on the biochemical composition and caloric content of the veligers, as well as the energy costs involved in prey capture. Chemical composition analyses showed high protein and lipid contents for veligers with lipid contents being higher than those of cladocerans and copepods. This combination of high protein and fat contents, like that found in veligers of *L. fortunei*, has been highlighted by several authors as important in the diet of larval fish (Sargent et al. 1999; Lazo 2000; Rønnestad et al. 2007). While protein is the most important body component and accounts for over 50% of the ash free dry weight (AFDW) in these organisms, lipids provide necessary energy during the fast-paced larval fish development period. Mostly as a consequence of high lipid content (17% of the AFDW), a significantly higher specific caloric content was found in veligers also (24.88 ± 1.81 kJ/g dry weight) followed by cladocerans and copepods (Paolucci et al. 2010b). In addition to high energy density, veligers had a higher dry biomass than crustacean prey of the same or greater total length, and consequently veligers had comparatively higher total energy content sufficient to support the costs of growth and standard metabolic rate (Fig. 8d).

The energy density of veligers of *L. fortunei* is slightly higher than that recorded for adults of the invasive bivalve *Dreissena polymorpha* and other bivalve larvae (between 17.3 and 22.7 kJ/g) (Blaber 1979). In addition to the biochemical composition, the reduced energetic costs associated with the capture of slower prey, such as veligers, in comparison with faster prey, such as cladocerans, and especially copepods, may also have had an effect on larval growth. The results of these physiological studies combined with observations made during experimental and field investigations imply that selective feeding on slow and easy-to-capture prey results in a lower energetic cost of feeding and can result in a positive energetic impact that could enhance growth rates of larval fishes (Lazzaro 1987; Lankford and Targett 1997).

Impacts at Population and Community Levels

All these results suggest that fish species whose larvae have been observed to feed on veligers of *L. fortunei* have greatly benefited from its presence, and the impact of this new resource on fish populations is most likely very important. It is noteworthy that fish species whose diets rely heavily on *L. fortunei* are among the most abundant and ecologically important in the Paraná-Paraguay river system (Sverlij et al.

1993; Espinach Ros and Fuentes 2001). For example, deposit-feeding adults of *P. lineatus* constitute the main food item of larger ichthyophagous species (Sverlij et al. 1993). Thus, feeding conditions for *P. lineatus* may strongly affect abundances of many other fish species. Consequently, the effects of these shifts in the feeding behavior of larval fishes are conceivably not restricted to the organisms directly involved in the interactions, but may have cascading effects both up and down trophic webs (MacIsaac et al. 1999; Yan et al. 2001; Clarke et al. 2004). Insofar as the new interactions modify established grazing pressures, they can strongly affect species composition and size structure of the zooplankton community, which in turn may change phytoplankton abundance and composition (Strecker and Arnott 2008). Indirect impacts on other fishes may also derive from these ecological rearrangements through the direct consumption of veligers (Paolucci et al. 2007), or from changes in the availability of other food items.

Larval Fish Predation as Biological Control

Whether or not grazing on veligers by larval fish is able to curtail the growth of mussel populations is a question of major interest. Sylvester et al. (2007) suggested that adult mussels will not be controlled by fish predation, but a similar estimate for veligers is more complicated. Several key elements remain unknown; in particular, the reproductive output of *L. fortunei* on a basin-wide scale is unclear. Assuming conservative densities of 1000 ind/m³ for veligers (Boltovskoy et al. 2009) and around 3 ind/m³ for fish larvae (Fuentes and Espinach Ros 1998), and an ingestion rate of 2 veligers/h (Paolucci et al. 2010a), one could speculate that on a steady-state basis *P. lineatus* consumes daily between 10 and 20% of the standing stock of veligers. This figure could probably be doubled to include other species of fish that consume veligers (Paolucci et al. 2007; Paolucci et al. 2010a). However, the reproductive period of *L. fortunei* (around September–April) is much longer than that of most fishes (between November–December and February–March (cf. Rossi et al. 2007), and this must decrease the long-term impact significantly. Thus, although these estimates are very rough, they agree with the conclusion of Sylvester et al. (2007) who concluded that predation impact on the geographical spread of *L. fortunei* is probably minor, and the potential for predation to control the spread of the bivalve seems limited.

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