

Trophic Relationships of *Limnoperna fortunei* with Adult Fishes

Daniel Cataldo

Abstract In South America, the inventory of species that feed on *Limnoperna fortunei* has increased steadily; in 2006, 18 fish species had been identified as predators of *L. fortunei*, whereas 7 years later, the list had grown to almost 50 species. In some areas, fishes that consume *L. fortunei* represent >50% of the species regularly present in commercial fisheries, including traditionally omnivorous, iliofagous, and ichthyophagous forms. Several economically important species have significantly changed their feeding habits since the mussel's introduction, shifting from a diet based on plants and detritus to one dominated by adult mussels. Consumption of golden mussels is not restricted to fishes provided with teeth that can crush and grind the shells; many toothless species swallow whole specimens or nibble on the exposed siphons and mantle edges of the bivalve. Golden mussels can account for up to 100% of the gut contents of some fish species, especially during the summer. Feeding of fishes on *L. fortunei* often involves the selective consumption of the smaller mussel size classes. Fish predation pressure on the mussel is likely high and it probably represents the most significant mechanism that modulates *L. fortunei* populations, but it is very unlikely to eradicate the mussel altogether. No comprehensive, large-scale studies are yet available on the effects of this new food supply on local fish stocks, but ancillary information suggests that these effects are likely very significant. Impacts are not restricted to species that consume the mollusc, but also affect species that benefit from this new food resource indirectly, including large ichthyophagous species feeding on molluscivorous forms, as well as on those that consume the organic matter-enriched sediments by the mussel's feces and pseudofeces.

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

D. Cataldo (✉)

Facultad de Ciencias Exactas y Naturales, Instituto de Ecología, Genética y Evolución de Buenos Aires (IEGEB), Universidad de Buenos Aires-CONICET, Ciudad Universitaria, 1428 Buenos Aires, Argentina
e-mail: daniel@ege.fcen.uba.ar

Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'-CONICET, Buenos Aires, Argentina

© Springer International Publishing Switzerland 2015
D. Boltovskoy (ed.), *Limnoperna fortunei*, Invading Nature - Springer Series in Invasion Ecology 10, DOI 10.1007/978-3-319-13494-9_13

Introduction

The fish fauna of the Río de la Plata basin comprises around 500 species (Bonetto 1986), including many large species with significant economic value. From the point of view of their mode of feeding, these species have historically been attributed to a few classical categories: omnivorous, iliophagous/detritivorous, planktophagous, and ichthyophagous, but the boundaries between these categories are diffuse and change with fish age, habitat, and time of the year, among others. These trophic shifts suggest that feeding preferences are flexible and often depend on the most profitable resource available.

Before the introduction of the Asian clam *Corbicula fluminea* (probably in the 1970s: Ituarte 1994), and the golden mussel *Limnoperna fortunei*, around 1990 (Pastorino et al. 1993), molluscs were generally a minor component of fish diets (Gneri and Angelescu 1951; Bonetto et al. 1963; Ringuelet et al. 1967; Alonso 1978; Oliva et al. 1981). The invasion of these bivalves, and particularly of *L. fortunei*, in the Río de la Plata watershed confirmed the behavioral and trophic adaptability of South American fishes: many species originally included in either of the trophic categories above are presently known to actively feed on these invasive bivalves, especially *L. fortunei*. The feeding modes used by different species to prey on *L. fortunei* are diverse, as most probably are the energetic benefits involved.

The inventory of species that feed on *L. fortunei* has increased steadily, in part due to new surveys, and in part because of the mussel's geographic expansion. In 2006, 18 fish species had been identified as predators of *L. fortunei* in South American inland waters (García and Montalto 2006), whereas 7 years later, the list had grown to almost 50 species (Table 1). In some areas, fishes that consume *L. fortunei* represent > 50% of the species regularly present in commercial fisheries.

This chapter reviews our current knowledge of the consumption of adult *L. fortunei* by fishes. It furnishes an overview of the species known to feed on the mussel, as well as an account of the techniques employed by species with dissimilar anatomical adaptations to feed on this prey. The potential impact of this resource on local fish assemblages is discussed. The chapter is restricted to information from Argentine and Brazilian waterbodies; no data on dietary changes have been reported from the other countries invaded by the mussel.

Omnivorous Species

Omnivorous fishes are characterized by their high trophic plasticity, consuming a variety of items and often favoring widely available resources. In the Río de la Plata watershed, one of the typical and abundant representatives of this group is *Leporinus obtusidens* (locally known as “boga,” in Argentina, and “piapara” or “piava,” in Brazil). Originally, the diet of this species chiefly included aquatic plants, seeds, and to a lesser extent smaller fishes and molluscs (Mastrarrigo 1950;

Table 1 Fish species known to consume *L. fortunei*. Geographic areas are *GW* Guaíba watershed (Patos and Mirim lagoons, São Gonçalo Channel), *LP* Lower Paraná River, *MP* Middle Paraná River, *RP* Rio de la Plata estuary, *UP* Upper Paraná River, *UP(I)* Upper Paraná, Itaipu Reservoir, *UR* Uruguay River. Bold species names denote fishes that consistently use *L. fortunei* in their diet in sizable numbers

Species	Area	References
<i>Asyanax aff. fasciatus</i>	GW	Lopes and Vieira (2012)
<i>Auchenipterus osteomystax</i>	UP(I)	Oliveira et al. (2010)
<i>Brochiloricaria chauliodon</i>	RP	García and Protogino (2005)
<i>Crenicichla punctata</i>	GW	Lopes and Vieira (2012)
<i>Cyphocharax voga</i>	GW	Lopes and Vieira (2012)
<i>Cyprinus carpio</i>	LP-RP	Cataldo et al. (2002)
<i>Geophagus brasiliensis</i>	GW	Lopes and Vieira (2012)
<i>Hoplias malabaricus</i>	UP(I)-GW	Lopes and Vieira (2012); Oliveira et al. (2010)
<i>Hyostomus cf. laplatae</i>	GW	Montalto et al. (1999)
<i>Hyostomus commersoni</i>	UP(I)-GW	Lopes and Vieira (2012); Oliveira et al. (2010)
<i>Hyostomus regani</i>	UP(I)	Oliveira et al. (2010)
<i>Hyostomus ternetzi</i>	UP(I)	Oliveira et al. (2010)
<i>Hyostomus uruguayensis</i>	LP	Boltovskoy and Cataldo (1999)
<i>Iheringichthys labrosus</i>	UP(I)-UR	Oliveira et al. (2010); Masdeu et al. (2011); Belz et al. (2012)
<i>Leporinus friderici</i>	UP(I)	Oliveira et al. (2010)
<i>Leporinus macrocephalus</i>	UP(I)	Oliveira et al. (2010)
<i>Leporinus obtusidens</i>	UP-MP-LP-RP	Montalto et al. (1999); Boltovskoy and Cataldo (1999)
<i>Loricaria Loricaria nudiventris</i>	LP-RP	Cataldo et al. (2002)
<i>Loricaria Loricaria vetula</i>	LP-RP	Cataldo et al. (2002)
<i>Loricariichthys anus</i>	GW	Lopes and Vieira (2012)
<i>Megalancistrus aculeatus</i>	UP	Belz et al. (2012)
<i>Megalancistrus parananus</i>	UP(I)	Oliveira et al. (2010)
<i>Meynisi lippincottianus</i>	UP(I)	Oliveira et al. (2010)
<i>Micropogonias furnieri</i>	GW-RP	López Armengol and Casciotta (1998); Lopes and Vieira (2012)

Table 1 (continued)

Species	Area	References
<i>Oxydoras kneri</i>	LP-RP	Cataldo et al. (2002)
<i>Paraloricaria cf. vetula</i>	LP-RP	Boltovskoy and Cataldo (1999); Garcia and Protogino (2005)
<i>Parachuhenipterus galeatus</i>	UP(I)	Oliveira et al. (2010)
<i>Piaractus mesopotamicus</i>	UP(I)	Lösch et al. (2009); Oliveira et al. (2010)
<i>Pimelodus albicans</i>	LP-MP-RP	Montalto et al. (1999); Boltovskoy and Cataldo (1999)
<i>Pimelodus maculatus</i>	UP-MP-LP-RP-GW	Montalto et al. (1999); Cataldo et al. (2002); Baptista and Zibetti (2006)
<i>Pimelodus pintado</i>	GW	Lopes and Vieira (2012); Vieira and Lopes (2013)
<i>Pimelodus</i> sp.	MP	Montalto et al. (1999)
<i>Pirinampus pirinampu</i>	UP(I)	Oliveira et al. (2010)
<i>Plagioscion squamosissimus</i>	UP(I)	Oliveira et al. (2010)
<i>Potamotrygon cf. brachurus</i>	MP	Montalto et al. (1999)
<i>Potamotrygon motoro</i>	UP(I)	Oliveira et al. (2010)
<i>Prochilodus lineatus</i>	UP(I)	Oliveira et al. (2010)
<i>Pterodorus granulatus</i>	UP-MP-LP-UR-RP-GW	Boltovskoy and Cataldo (1999); Montalto et al. (1999); Ferriz et al. (2000); Cataldo et al. (2002); Garcia and Protogino (2005); Cantanhêde et al. (2008); Vermulm and Giamas (2008); González-Bergonzoni et al. (2010); Oliveira et al. (2010); Belz et al. (2012)
<i>Pterygoplichthys anisitsi</i>	UP(I)	Oliveira et al. (2010)
<i>Rhamdia quelen</i>	UP(I)-GW	Lösch et al. (2009); Lopes and Vieira (2012)
<i>Rhinodoras dorbignyi</i>	MP-RP	Montalto et al. (1999) Garcia and Protogino (2005)
<i>Rineloricaria microlepidogaster</i>	GW	Lopes and Vieira (2012)
<i>Rineloricaria strigilata</i>	GW	Lopes and Vieira (2012)
<i>Satanoperca pappaterra</i>	UP(I)	Oliveira et al. (2010)
<i>Schizodon borellii</i>	UP(I)-MP	Montalto et al. (1999); Oliveira et al. (2010)
<i>Serrasalmus maculatus</i>	UP(I)	Oliveira et al. (2010)
<i>Serrasalmus marginatus</i>	UP(I)	Oliveira et al. (2010)

Ringuelet et al. 1967). However, after *L. fortunei* became available, *L. obtusidens* has largely switched its diet to mussels that now represent 64–100% of its gut contents (Montalto et al. 1999; Penchaszadeh et al. 2000; Cataldo et al. 2002). This species has strong teeth that allow it to bite, tear off, and grind mussel valves (Braga 1993). Other related species that have also been reported to consume *L. fortunei* are *Leporinus macrocephalus*, *Leporinus friderici*, and *Schizodon borellii* (Table 1).

Piaractus mesopotamicus is a large characid native to the Paraná-Paraguay river system that is widely cultured in Brazil, Argentina, and Paraguay. It has strong molar teeth adapted to crushing and fragmenting its food, which allows it to widely utilize *L. fortunei* in its diet. When raised in fishnet cages in lakes and reservoirs colonized by *L. fortunei*, the mussel can represent a major nuisance because it grows on the nets and clogs them rapidly. On the other hand, these mussels may represent a major source of food for the enclosed fishes that have been observed to feed on them exclusively (Lösch et al. 2009).

Another group of very abundant typically omnivorous fishes, known by the vernacular name of “armado” (Argentina) or “armal” (Brazil), have also benefited from the new food resource represented by *L. fortunei*. *Pterodoras granulosus*, one of the most widely distributed representatives of this group, is a euryphagous species which feeds on most widely available items (Panatieri and Del Barco 1981). After the invasion of *L. fortunei*, this species has changed its diet significantly, and mussels now represent up to 82–100% of the biomass of its gut contents. Up to 2830 shells of *L. fortunei* have been recorded in a single digestive tract of *P. granulosus* (Montalto et al. 1999; Cataldo et al. 2002; García and Protogino 2005). *P. granulosus* lacks strong dentition, and therefore shells are swallowed whole. Other related species, including *Rhinodoras dorbignyi* and *Oxidoras kneri*, have also been reported to consume golden mussels (Montalto et al. 1999; Cataldo et al. 2002).

Among the benthic, euryphagous species, catfishes (*Pimelodus maculatus*, *Pimelodus albicans*, *Pimelodus argenteus*) are the most abundant in the Río de la Plata watershed. Their small oral villiform teeth cannot crush mussel shells, which are thus ingested whole (Montalto et al. 1999; Cataldo et al. 2002). These species are important in riverine food webs, as they represent a major component of the diet of most large, ichthyophagous species.

The carp (*Cyprinus carpio*), introduced to Argentina around the turn of the nineteenth century (Baigún and Quirós 1985), is present in large numbers in most South American lentic and lotic waterbodies. This typically omnivorous fish feeds on insect larvae, crustaceans, plants, detrital material, etc. (Colautti 1997, 2001; Menni 2004), and since the introduction of *L. fortunei*, it has been recorded to feed on the mussel as well (Cataldo et al. 2002).

Illophagous Species

Illophagous species typically feed on organic matter-rich sediments, but they also consume small particulate periphytic material scraping the surface of objects covered by an organic film. Organic films on hard substrata often encompass mussels,

and these bivalves have become an occasionally important component of the diet of iliophagous fishes. Among the species that depict this feeding behavior, the members of the family Loricariidae are very important because of their abundance and diversity (*Hypostomus uruguayensis*, *Hypostomus laplatae*, *Hypostomus commersoni*, *Hypostomus regani*, *Hypostomus ternetzi*, *Paraloricaria vetula*, *Megalancistrus parananus*, *Pseudoheminodon laticeps*). The sucking, ventrally located mouths of these species are adapted to scraping the surface of leaves, rocks, branches, and other objects collecting adhering material, including small (usually <5 mm) *L. fortunei*. The mussel has often been observed to represent up to 100% of the diet of various Loricariidae (Montalto et al. 1999; Cataldo et al. 2002; García and Protopino 2005; Oliveira et al. 2010; Belz et al. 2012; Lopes and Vieira 2012).

Prochilodus lineatus (locally known as “sábalo” in Argentina, or “curimatá” in Brazil) deserves special attention. This medium-sized fish (adult individuals weight about 2–3 kg; Sverlij et al. 1993) represents >60% of the fish biomass in the Paraná-Uruguay river system (Bonetto 1998). Economically, the sábalo is the most important exploitable species in the Río de la Plata watershed. In Argentina, it accounts for ca. 90% of the freshwater fish exports (Iwaszkiw 2005; Iwaszkiw and Lacoste 2011), with landings varying around 15,000–30,000 t per year in the last decade (Food and Agriculture Organisation, FAO data). Surveys carried out in the middle and upper Paraná River, including the Itaipu Reservoir, show that adult golden mussels are seldom present in the gut of *P. lineatus* (Montalto et al. 1999; Lösch et al. 2009; Oliveira et al. 2010). On the other hand, specimens recovered in Salto Grande Reservoir (Uruguay River, Argentina-Uruguay), have been observed to contain large numbers of adult *L. fortunei* in their stomach contents (José Venzal, pers. comm.).

Observation of medium-sized sábalo specimens kept in captivity in fish tanks stocked with *L. fortunei* shows that fishes hover over the mussel clusters and bite off pieces of soft tissue protruding from the partly open valves. Although this species is provided with only small incisiform teeth, its protractile mouth allows it to efficiently grasp chunks of siphons or mantle edge, tearing them off the mussel. After a few days, only the empty valves of exposed mussels remain on the substrate, the soft tissue having been totally consumed by the fishes. Admittedly, no in situ observations have been made to provide proof that this feeding behavior takes place in the field, but there does not seem to be any reason to assume otherwise. Assessment of consumption of golden mussels by fishes is normally based on records of the mussels' shells, or pieces thereof, in the guts of the predators (Montalto et al. 1999; Penchaszadeh et al. 2000; Cataldo et al. 2002). The fact that *P. lineatus* can tear off the soft tissue leaving the valves intact suggests that the examination of stomach contents can significantly underestimate the importance of mussels as a trophic resource of the sábalo, as well as for any other fish species with a similar behavior.

In addition to direct consumption of mussels, iliophagous fishes, including *P. lineatus*, can benefit from the organic matter-enriched sediments derived from the “shunt” of suspended particulate organic matter to the bottom as mussel feces and pseudofeces (Sardiña et al. 2008; Cataldo et al. 2012; Boltovskoy and Correa 2015; see Chapter “Nutrient Recycling, Phytoplankton Grazing, and Associated Impacts of *Limnoperna fortunei*” in this volume).

Ichthyophagous Species

Ichthyophagous fishes comprise mostly large, actively swimming species provided with canine and villiform teeth used for piercing and holding the prey. These species do not normally consume mussels, but exceptions have been reported. *Hoplias malabaricus* (“tararira” in Argentina, “traíra” in Brazil) is a typical fish predator common in most South American freshwater bodies. In Brazil, where it represents an important fisheries resource, it has been reported to feed actively on small (ca. 1 cm) *L. fortunei*, which can account for up to 20% of its gut contents (Oliveira et al. 2010; Lopes and Vieira 2012). Even fishes of the family Serrasalmidae, which include several species of “palometa” and “piraña”, have been recorded with *L. fortunei* in their stomachs (Oliveira et al. 2010).

Marine Species

Dietary changes associated with the invasion of the golden mussel in South America are not restricted to freshwater fishes, but have also been recorded in marine species that regularly enter the freshwater zone of the Río de la Plata estuary. The whitemouth croaker (*Micropogonias furnieri*) is a marine demersal species widely distributed from the Gulf of Mexico (around 24°N) to the Gulf of San Matías (Argentina, 41°S), which supports important fisheries in Brazil, Uruguay, and Argentina (Sardiña and Lopez Cazorla 2005; Acha et al. 2008). During the spring and summer, the whitemouth croaker enters the estuary to spawn (Acha et al. 2008), at which time adults come in contact with *L. fortunei* beds. Small fish do not consume golden mussels, but most of those > 200 mm do. Mussel shells are crushed by the croaker’s strong molariform teeth (López Armengol and Casciotta 1998).

Predator–Prey Size Relationships

Several studies have shown that feeding of fishes on *L. fortunei* involves the selective consumption of the smaller size classes. For example, the size of mussels recorded in the gut contents of 12 fish species from São Gonçalo Channel (Brazil) (3–15 mm) was substantially lower than that of the local mussel populations (4–32 mm) (Lopes and Vieira 2012; Table 1; Fig. 1a). Similar results have been reported for *Pimelodus pintado* from Mirim Lake (Vieira and Lopes 2013; Fig. 1b), and *Rhamdia quelen* from Itaipu Reservoir (Brazil) (Lösch et al. 2009).

The strength of this relationship between the size of the predator and that of its prey, as well as the relative importance of mussels as a food item, is largely modulated by the feeding mode of the fishes. Two major groups can be identified: one comprised of fishes that cannot break the shell and therefore ingest whole organisms, and the other comprised of animals with dentition that allows them to bite off shell fragments and crush the valves before ingesting them.

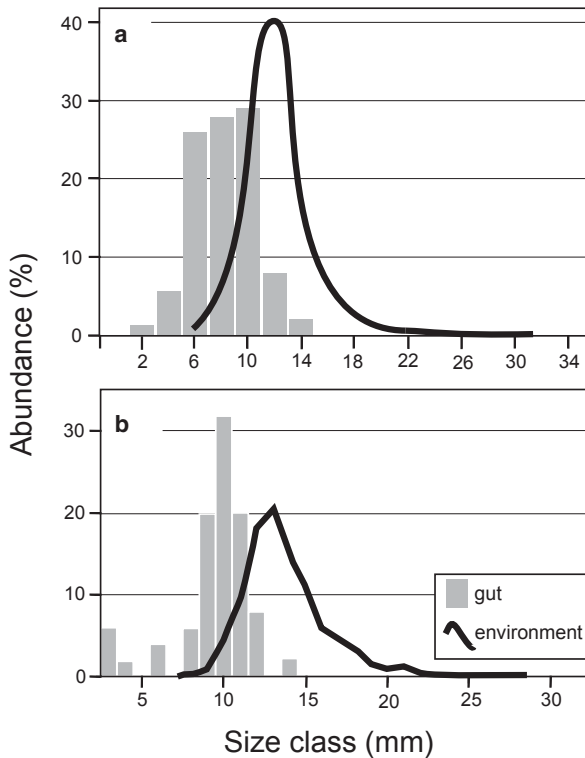


Fig. 1 Comparison of shell size distributions of *L. fortunei* collected in the environment (line) and retrieved from fish guts (bars). **a** Eight fish species (*Rineloricaria strigilata*, *Pimelodus pintado*, *Rhamdia* aff. *quelen*, *Hoplias malabaricus*, *Rineloricaria microleptodogaster*, *Astyanax fasciatus*, *Hypostomus commersoni*, and *Crenicichla punctata*) from the Patos-Mirim lagoon system (Brazil; from Lopes and Vieira 2012). **b** *Pimelodus pintado* from São Gonçalo Channel (Brazil). (From Vieira and Lopes 2013)

Most opportunistic species ingest whole shells, whereby the ability to tear off animals from the mussel bed and the size of the predator's mouth play a major role in the feeding process. Vieira and Lopes (2013) noticed that *P. pintado* below 10 cm in length do not consume *L. fortunei*, but as the fish grows in size the mussel becomes an increasingly more important food item. At 10–15 cm, ca. 5% of the fishes consume *L. fortunei*, whereas at 25–30 mm around 50% do (Fig. 2a). Additionally, the size of the mussels consumed changes little with fish size (Fig. 2b). Montalto et al. (1999), in their study in the Middle Paraná River encompassing nine fish species, also noticed a clear association between the size of the predator and that of the mussels consumed: small fishes selected *L. fortunei* below 6 mm in length, whereas larger species fed on mussels up to over 15 mm.

These results suggest that for fishes that ingest whole mussels, a major limitation is the size of their mouth. In contrast, fishes with teeth capable of crushing the shell

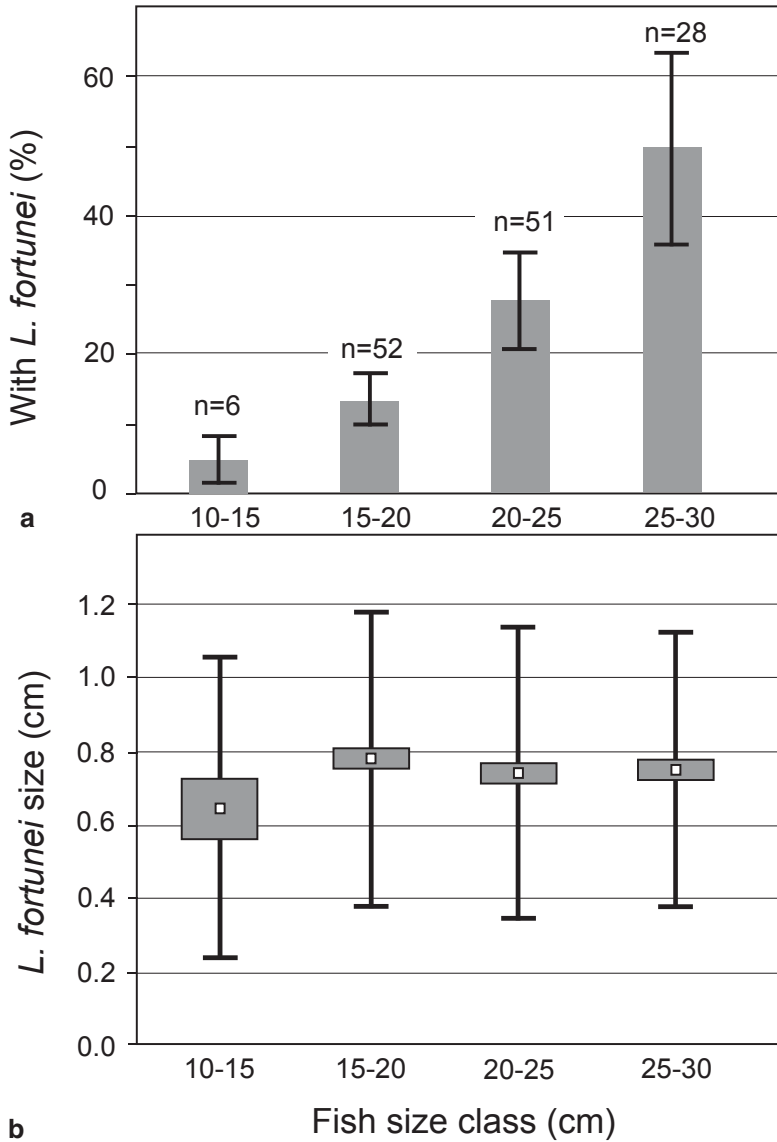


Fig. 2 **a** Proportions of *Pimelodus pintado* of different size with *L. fortunei* in their guts (mean and standard deviation; *n*: number of fishes). **b** Box plot of lengths of *L. fortunei* shells consumed by *P. pintado* of different size (median value, first and third quartiles, and range of values). Based on data from São Gonçalo Channel (Brazil) collected in spring 2005. (Modified from Vieira and Lopes 2013)

can benefit from a larger size-range of prey. Among the latter, a salient example is *L. obtusidens*. This species is a medium-sized fish (up to 80 cm in length), widely used for human consumption and production of fishmeal in the Río de la Plata

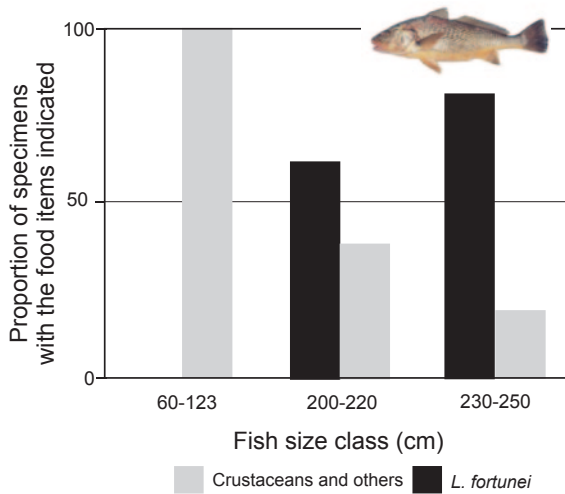


Fig. 3 Proportions of whitemouth croakers (*Micropogonias furnieri*) with *L. fortunei* and with other prey in their digestive tracts as a function of fish size. Data from the Río de la Plata estuary (Argentina) collected in Oct–Nov 1996; total number of fishes analyzed: 17. (From López Armengol and Casciotta 1998)

watershed countries. The range of sizes consumed by this species is very wide; specimens of *L. fortunei* below 6 mm are mostly found intact in stomach contents, whereas larger mussels are crushed. Despite this ability to break shells, mussels over 15 mm in length are chiefly consumed by large *L. obtusidens* (Montalto et al. 1999; Penchaszadeh et al. 2000). Lopes and Vieira (2012) suggested that enhanced predation of smaller mussels might be due to the fact that they tend to break free from the substrate and wander about more often than larger individuals (Uryu et al. 1996), thus spending more time away from a mussel agglomerate, where they are less vulnerable to predation. Direct evidence of this effect, however, is lacking.

Working on the whitemouth croaker, *Micropogonias furnieri*, López Armengol and Casciotta (1998) noticed that fishes below 123 mm in length fed chiefly on crustaceans, whereas in larger size classes the importance of crustaceans decreased and that of *L. fortunei* increased (Fig. 3).

It should be noticed that estimates of *L. fortunei* consumption by fishes that crush the shells is complicated and quite probably often biased, particularly with respect to the number and size of the mussels ingested. In a survey carried out in fish culture net cages deployed in Itaipu Reservoir (Upper Paraná River), all examined specimens of *P. mesopotamicus* (“pacú”) had their gut contents filled with *L. fortunei*, but they were destroyed to such a degree that neither the number of mussels nor their sizes could be determined (Lösch et al. 2009). Other fish species have posed the same problem for gut analyses, even when their stomachs are totally occupied by mussel remains (e.g., *L. obtusidens*; Cataldo et al. 2002). Observations made in captivity indicate that *L. obtusidens* does not always tear off whole mussels,

often biting off parts of the shell, while the remainder is left attached to the substratum. Large mussels often show bite scars on their periostracum (Penchaszadeh et al. 2000). In order to circumvent this problem to estimate the number of mussels consumed by fish species that destroy the shell, authors have resorted to using various proxies, such as the “beaks” (the umbral region of the shell) (Penchaszadeh et al. 2000), or the ligament (López Armengol and Casciotta 1998) as an indicator of mussel numbers. However, the feeding mode described above, whereby only the distal part of the shell is torn off and ingested by the fish (while the “beak” and the ligament are left behind) may introduce a significant bias in these methods.

Seasonal Trends in Mussel Consumption by Fishes

A salient aspect of *L. fortunei* as a food item is the fact that, unlike many other organisms with shorter life cycles (including most planktonic resources), its adults are available for consumption throughout the year. Unsurprisingly, time-series studies of its use by fishes indicate that *L. fortunei* is preyed upon almost uninterruptedly (Penchaszadeh et al. 2000). Nevertheless, regardless of the availability of mussel prey, fish’s feeding activity differs among seasons. In the summer, 80–100% of the specimens of *L. obtusidens* retrieved had fed on mussels, whereas during the winter (July–August), specimens with *L. fortunei* in their stomachs dropped to 0% (Fig. 4; Penchaszadeh et al. 2000). Ancillary observations on seasonal differences in the feeding of several fishes of the Río de la Plata estuary also suggest that feeding activity is lowest during the winter (Cataldo et al. 2002).

This seasonal trend, however, does not seem to hold elsewhere in the Río de la Plata watershed, where in addition to seasonal changes, interannual differences have been described. In a survey carried out in Mirim Lake (Brazil) in 2005 and 2008, Vieira and Lopes (2013) found no *L. fortunei* in the stomachs of *P. pintado* in the summer, autumn, and winter of 2005. The mussel was first recorded in the diet of this species in the spring of 2005 (September–November), when it was consumed by 22% of the 180 specimens surveyed. Three years later, in the spring of 2008, proportions of *P. pintado* with *L. fortunei* in their guts increased to 61%, and the mussel had become the most important item in the diet of this predator (Vieira and Lopes 2013). Since *L. fortunei* started invading Mirim Lake around 2005 (Langone 2005), this increase is likely associated with the spread of the mussel in the system.

In some cases, a delay in the use of this new prey by its potential consumers may conceivably be associated with the time required by predators to get used to the novel trophic resource. However, an increase in the use of *L. fortunei* by fish over time is more likely to stem from the growth of the predators’ populations in response to better feeding and survival conditions.

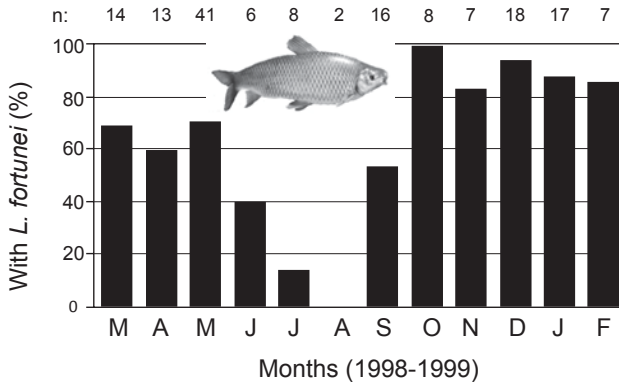


Fig. 4 Proportions of *Leporinus obtusidens* from the Río de la Plata estuary (Argentina) with *L. fortunei* prey in their digestive tract throughout an annual cycle. (Based on data from Penchaszadeh et al. 2000)

Degree of Digestion of the Bivalves

As reviewed above, consumption of *L. fortunei* is not limited to those fish species that are anatomically best adapted to obtain and ingest mussels, but also involves typically omnivorous, iliophagous, and ichthyophagous species. However, regardless of the importance of mussels in their diet, the ability to digest this prey may differ between species.

Fishes possessing strong teeth that can crush the shells gain full access to the soft tissues. In the stomach contents of *L. obtusidens* and *L. macrocephalus*, 80–100% of the mussels are finely fragmented and the soft tissue is partially or totally digested (Montalto et al. 1999; Cataldo et al. 2002; Oliveira et al. 2010). Crushed shells and digested soft tissue have also been recorded in several other species, including *P. mesopotamicus*, *M. furnieri*, *Astyanax fasciatum*, *Geophagus brasiliensis*, and *Crenicichla punctata* (López Armengol and Casciotta 1998; Lösch et al. 2009). Some other species, including several not armed with strong crushing or grinding teeth, have also been recorded with their stomachs full of broken and fragmented *L. fortunei* shells (e.g., *Megalancistrus parananus*, *Pimelodus maculatus*, *P. albicans*; Montalto et al. 1999; Oliveira et al. 2010).

For fishes that swallow whole shells, the degree to which mussels are effectively digested is probably slightly, but not significantly lower. Oliveira et al. (2010) noticed that ~80–90% of *L. fortunei* specimens recorded in the digestive tract of *P. granulosus* and *Serrasalmus marginatus* are intact. However, in *P. granulosus* from the Middle Paraná River whole *L. fortunei* shells had their valves open and their soft tissues partly digested (Montalto et al. 1999). Belz et al. (2012) investigated the feasibility of long distance transport of *L. fortunei* in the stomachs of fish. They analyzed the diet of five of the most likely candidates to disperse the mussel: *P. granulosus*, *Megalancistrus aculeatus*, *Satanoperca papaterra*, *Potamotrygon motoro*, and *Iheringichthys labrosus*. Live *L. fortunei* were only recorded in three specimens

of only one of the five species analyzed, *P. granulatus*. Of the 2198 individuals of *L. fortunei* present in the digestive tract of this species, 70 were found alive in the stomach, but only four were alive in the distal section of the intestine. These results suggest that crushing the shells upon ingestion may favor digestion, but breakage is not required for fishes to benefit from this trophic resource.

It has been suggested that the sharp edges of crushed *L. fortunei* shells may lacerate the anal area of their predators (e.g., *Rineloricaria microlepidogaster*; *R. strigilata*; Lopes and Vieira 2012). However, wounds could have been the result of the animals attempting to free themselves from the net. Ad hoc observations of many specimens in a wide range of species failed to reveal evidence of lacerations caused by ingested shell fragments (López Armengol and Casciotta 1998; Montalto et al. 1999; Penchaszadeh et al. 2000).

Effects of *L. fortunei* on Local Fish Populations

The number of fish species that feed on *L. fortunei* has increased steadily, largely because of the mussel's northward geographic expansion into areas with increasingly higher fish diversity. Predation pressure on the mussel is likely high and, together with consumption of veligers by larval fishes (see Chapter “Trophic Relationships of *Limnoperna fortunei* with Larval Fishes” in this volume), is probably the most significant mechanism that modulates *L. fortunei* populations, but it is very unlikely to eradicate the mussel altogether.

As useful as they are, the studies reviewed above are limited in scope and fall short of providing a comprehensive assessment of the effects of this new food supply on fish stocks. These effects are likely very significant. In the delta of the Lower Paraná River, predators (presumably mostly represented by fishes) consume ca. 6 kg of whole mussel mass per square meter, eliminating up to over 90% of the yearly production of *L. fortunei* (Sylvester et al. 2007). Nakano et al. (2010) estimated that predators eliminate ca. 97% of the mussels in Lake Ohshio, a Japanese reservoir, affecting not only biomass but also the size-structure of the populations. In the Itaipu Reservoir (Upper Paraná River), 24 of the 36 species (3752 specimens) surveyed in 2005–2006 were found to prey on *L. fortunei* (Oliveira et al. 2010).

Impacts are not restricted to species that consume the mollusc, but also affect species that benefit from this new food resource indirectly, such as the large and economically most valuable ichthyophagous species that feed on other fishes (e.g., *Pseudoplatystoma fasciatum*, *Pseudoplatystoma corruscans*, *Salminus maxillosus*, *H. malabaricus*, *Paulicea luetkeni*, *Luciopimelodus pati*). Furthermore, *L. fortunei* transfers large amounts of organic matter from the water column to the sediments through filtration and the formation of feces and pseudofeces (Sardiña et al. 2008; Cataldo et al. 2012), which boosts invertebrate densities (Sylvester et al. 2007; Sardiña et al. 2008, 2011; see Chapter “Relationships of *Limnoperna fortunei* with Benthic Animals” in this volume). This is important for deposit-feeding fish species, some of which, like *P. lineatus*, are very abundant, represent important fishing

resources, and are the main food items of most ichthyophagous species (Bonetto 1998). Adult *L. fortunei* represent not only an additional food item but also one energetically more profitable than the plant- and detritus-based foods which characterized the diet of these fish species before the introduction (Ferriz et al. 2000).

The impact of these trophic shifts on local fish stocks is probably high, but has not yet been quantified. Argentine freshwater fish landings increased three-fold after the introduction of *L. fortunei* (Boltovskoy et al. 2006), which may suggest better recruitment and survival conditions, but interpretation of this trend is complicated by several factors, including changes in fishing regulations, fishing pressure, fish export trends, and profitability of the industry during the time span involved. In addition, exploitation of freshwater fish resources in the countries colonized by the mussel is largely artisanal and statistical information is scarce, fragmentary, and most probably very incomplete (Iwaszkiw 2001, 2005).

Dreissena polymorpha, the zebra mussel, has been shown to increase the abundance of littoral fish species (through enrichment of coastal bottom areas with organic matter), and decrease the abundance of pelagic fishes (due to depletion of zooplankton forage species through grazing) (Strayer et al. 2004). This trend, however, subsequently changed and open-water species returned to preinvasion levels (Strayer et al. 2014). The effects of *L. fortunei* on South American fish stocks are probably different because filter-feeding fishes are less abundant (the most abundant species in these large floodplain rivers are iliophagous and detritivorous; Bonetto 1998) and particulate organic carbon (POC) loads are very high. The mean concentration of POC in the Paraná River (about 3.5 mg/L: Depetris 1976; Depetris and Paolini 1991; Depetris and Pasquini 2007) is much higher than in most of the waterbodies invaded by *Dreissena* species (typically around 0.15–1 mg/L in the Great Lakes; Fanslow et al. 1995; Barbiero and Tuchman 2004; Johengen et al. 2008), which suggests that filtering organisms are not food-limited in most South American waterbodies invaded by *L. fortunei* (Sylvester et al. 2005).

Indigenous filter-feeding benthic animals in the Paraná watershed are scarce, and therefore most of the POC is flushed out into the ocean through the Río de la Plata estuary. *L. fortunei*, the first and only abundant macrobenthic filter-feeder, is intercepting an important proportion of this particulate organic matter and retaining it in the system for use by a wide array of animals (Boltovskoy et al. 2006; Boltovskoy and Correa 2015), which most probably represents an important energetic subsidy for the entire system.

While *L. fortunei* as a new food resource has likely had positive effects on fish populations, trophic relationships are but one of many possible interactions between fishes and the mussel. In Japan, trematode parasites introduced with the golden mussel (as an intermediate host) have been found to inhibit gamete production in some fish species (Tanaka et al. 2004; see Chapter “Parasites of *Limnoperna fortunei*” in this volume). Indirect interactions are numerous and can operate through various ecosystem compartments. For example, cyanobacterial blooms promoted by the mussel (Cataldo et al. 2012) can trigger massive fish kills. Clarification of the water-column can facilitate visual predation of zooplankton by fish. Enhancement of macrophyte growth (Boltovskoy et al. 2009) can provide shelter for adult

and larval fishes, etc. Thus, it is conceivable that the positive effects of *L. fortunei* as food may be offset by its negative impacts through any of these, or other as yet unknown mechanisms.

References

- Acha ME, Mianzan H, Guerrero R, Carreto J, Giberto D, Montoya N, Carignan M (2008) An overview of physical and ecological processes in the Rio de la Plata Estuary. *Cont Shelf Res* 28:1579–1588
- Alonso C (1978) Estudio del contenido gástrico de *Pimelodus clarias maculatus* (Lacepede 1803) (Pices, Pimelodidae). *Iheringia (Série Zoologia)* 51:45–61
- Baigún CM, Quirós R (1985) Introducción de peces exóticos en la República Argentina. INIDEP (Instituto Nacional de Investigación y Desarrollo Pesquero, Argentina), Departamento de Aguas Continentales, Informe Técnico. INIDEP (Instituto Nacional de Investigación y Desarrollo Pesquero, Argentina), Departamento de Aguas Continentales, Informe Técnico, pp 1–90
- Baptista CT, Zibetti V (2006) Mexilhão dourado (*Limnoperna fortunei*) como recurso alimentar de peixes do arroio Pelotas, Pelotas, RS: resultados preliminares. XV Congresso de Iniciação Científica, VIII Encontro de Pós-Graduação, Universidade Federal de Pelotas (Brazil)
- Barbiero RP, Tuchman ML (2004) The deep chlorophyll maximum in Lake Superior. *J Gt Lakes Res* 30(Supplement 1):256–268
- Belz CE, Darrigran GA, Netto OSM, Boeger WA, Ribeiro PJ (2012) Analysis of four dispersion vectors in inland waters: the case of the invading bivalves in South America. *J Shellfish Res* 31:777–784
- Boltovskoy D, Cataldo D (1999) Population dynamics of *Limnoperna fortunei*, an invasive fouling mollusc, in the lower Paraná River (Argentina). *Biofouling* 14:255–263
- Boltovskoy D, Correa N (2015) Ecosystem impacts of the invasive bivalve *Limnoperna fortunei* (golden mussel) in South America. *Hydrobiologia* 746:81–95
- Boltovskoy D, Correa N, Cataldo D, Sylvester F (2006) Dispersion and ecological impact of the invasive freshwater bivalve *Limnoperna fortunei* in the Río de la Plata watershed and beyond. *Biol Invasions* 8:947–963
- Boltovskoy D, Karatayev A, Burlakova L, Cataldo D, Karatayev V, Sylvester F, Mariñelarena A (2009) Significant ecosystem-wide effects of the swiftly spreading invasive freshwater bivalve *Limnoperna fortunei*. *Hydrobiologia* 636:271–284
- Bonetto AA (1986) Fish of the Paraná system. In: Davies BR, Walker KF (eds) *The ecology of river systems*. Dr. W. Junk Publishers, Dordrecht, pp 573–588
- Bonetto AA (1998) Panorama sinóptico sobre la ictiofauna, la pesca y la piscicultura en los ríos de la cuenca del Plata con especial referencia al Paraná. *Rev Ictiol* 6:3–15
- Bonetto AA, Pignalberi C, Cordiviola E (1963) Ecología alimentaria del “amarillo” y “moncholo” *Pimelodus clarias* (Bloch) y *Pimelodus albicans* (Valenciennes) (Pisces, Pimelodidae). *Physis* 24:87–94
- Braga L (1993) Los Anostomidae (Pisces, Characiformes) de Argentina. *Fauna de Agua Dulce de la República Argentina* 40:1–61
- Cantanhêde G, Hahn NS, Gubiani ÉA, Fugli R (2008) Invasive molluscs in the diet of *Pterodoras granulosus* (Valenciennes, 1821) (Pisces, Doradidae) in the Upper Paraná River floodplain, Brazil. *Ecol Freshw Fish* 17:47–53
- Cataldo D, Boltovskoy D, Marini V, Correa N (2002) Limitantes de la expansión de *Limnoperna fortunei* en la Cuenca del Plata: la predación por peces. Terceras Jornadas para la Conservación de la Fauna Íctica del Río Uruguay, Paysandú (Uruguay)

- Cataldo D, Vinocur A, O'Farrell I, Paolucci E, Leites V, Boltovskoy D (2012) The introduced bivalve *Limnoperna fortunei* boosts *Microcystis* growth in Salto Grande Reservoir (Argentina): evidence from mesocosm experiments. *Hydrobiologia* 680:25–38
- Colautti DC (1997) Ecología de la carpa *Cyprinus carpio* en la cuenca del río Salado, provincia de Buenos Aires. PhD Thesis, Universidad Nacional de La Plata (Argentina), pp 1–260
- Colautti DC (2001) La carpa y el pejerrey, ¿enemigos? In: Grosman F (ed) Fundamentos biológicos, económicos y sociales para una correcta gestión del recurso pejerrey. Editorial Astyanax, Azul (Argentina), pp 85–94
- Depetris PJ (1976) Hydrochemistry of the Paraná River. *Limnol Oceanogr* 21:736–739
- Depetris PJ, Paolini JE (1991) Biogeochemical aspects of South American rivers: the Paraná and the Orinoco. In: Degens ET, Kempe S, Richey JE (eds) Biogeochemistry of major world rivers. Wiley, Chichester, pp 105–125
- Depetris PJ, Pasquini AI (2007) The geochemistry of the Paraná River: an overview. In: Iriondo MH, Paggi JC, Parma MJ (eds) The middle Paraná River. *Limnology of a subtropical wetland*. Springer, Berlin, pp 143–174
- Fanslow DL, Nalepa TF, Lang GA (1995) Filtration rates of the zebra mussel (*Dreissena polymorpha*) on natural seston from Saginaw Bay, Lake Huron. *J Gt Lakes Res* 21:489–500
- Ferriz RA, Villar CA, Colautti D, Bonetto C (2000) Alimentación de *Pterodoras granulosus* (Valenciennes) (Pisces, Doradidae) en la baja Cuenca del Plata. *Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”* 2:151–156
- García M, Montalto L (2006) Los peces depredadores de *Limnoperna fortunei* en los ambientes colonizados. In: Darrigran GA, Damborenea C (eds) Bio-invasión del mejillón dorado en el continente americano. Editorial Universitaria de La Plata, La Plata, pp 113–129
- García ML, Protogino LC (2005) Invasive freshwater molluscs are consumed by native fishes in South America. *J Appl Ichthyol* 21:34–38
- Gneri FS, Angelescu V (1951) La nutrición de los peces iliófagos en relación con el metabolismo general del ambiente acuático. *Rev Insti Investig Cienc Nat* (anexo al Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”) 2:1–44
- González-Bergonzoni I, Teixeira-de Mello F, Vidal N, D'Anatro A, Masdeu M (2010) Reappearance and diet of juvenile armado catfish (*Pterodoras granulosus*) in Lower Uruguay River, (Río Negro, Uruguay). *Bol Soc Zool Urug* 19:42–46
- Ituarte CF (1994) *Corbicula* and *Neocorbicula* (Bivalvia: Corbiculidae) in the Paraná, Uruguay and Río de la Plata basins. *Naut* 107:129–135
- Iwaszkiw JM (2001) Pesqueras continentales del tramo argentino de la Cuenca del Plata. Consejo Federal de Inversiones. Consejo Federal de Inversiones, Buenos Aires (Argentina), pp 1–279
- Iwaszkiw JM (2005) Estadísticas de exportaciones pesqueras de la Cuenca del Plata, Argentina 1994–2005. IV Taller Internacional sobre enfoques regionales para el desarrollo y gestión de embalses en la Cuenca del Plata, Salto Grande, Argentina-Uruguay
- Iwaszkiw JM, Lacoste FF (2011) La pesca artesanal en la Cuenca del Plata (Argentina) y sus implicancias en la conservación de la biodiversidad. *Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”*. Nueva Serie 13:21–25
- Johengen TH, Biddanda BA, Cotner JB (2008) Stimulation of Lake Michigan plankton metabolism by sediment resuspension and river runoff. *J Gt Lakes Res* 34:213–227
- Langone JA (2005) Notas sobre el mejillón dorado *Limnoperna fortunei* (Dunker, 1857) (Bivalvia, Mytilidae) en Uruguay. *Publicacion Extra del Museo Nacional De Historia Natural y Antropologia* (Montevideo, Uruguay) 1:1–18
- Lopes M, Vieira J (2012) Predadores potenciais para o controle do mexilhão-dourado. In: Mansur MCD, Santos CP, Pereira D, Padula Paz IC, Leite Zurita ML, Raya Rodriguez MT, Vilar Nehrke M, Aydos Bergonci PE (eds) Moluscos límnicos invasores no Brasil. *Biologia, prevenção, controle*. Redes Editora, Porto Alegre, pp 357–363
- López Armengol MF, Casciotta JR (1998) First record of the predation of the introduced freshwater bivalve *Limnoperna fortunei* (Mytilidae) by the native fish *Micropogonias furnieri* (Sciaenidae). *Iberus* 16:105–108

- Lösch JA, Boscolo WG, Feiden A, Kleber Lorenz E, Bittencourt F (2009) Presença de mexilhão dourado no trato gastrointestinal de três espécies nativas de peixes cultivadas em tanques rede no reservatório de Itaipu. Anais do I Seminário Internacional de Ciência, Tecnologia e Ambiente, Cascavel (Brazil)
- Masdeu M, Teixeira-de Mello F, Loureiro M, Arim M (2011) Feeding habits and morphometry of *Iheringichthys labrosus* (Lütken, 1874) in the Uruguay River (Uruguay). Neotrop Ichthyol 9:657–664
- Mastrarrigo V (1950) La Boga. Contribución a su conocimiento biológico. Almanaque del Ministerio de Agricultura y Ganadería (Argentina) 25:417–426
- Menni RC (2004) Peces y ambientes en la Argentina continental. Monografía del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” 5:1–316
- Montalto L, Oliveros OB, Ezcurra De Drago I, Demonte LD (1999) Peces del Río Parana medio predadores de una especie invasora: *Limnoperna fortunei* (Bivalvia, Mytilidae). Rev Fac Bioquid Cienc Biol (Universidad Nacional del Litoral) 3:85–101
- Nakano D, Kobayashi T, Sakaguchi I (2010) Predation and depth effects on abundance and size distribution of an invasive bivalve, the golden mussel *Limnoperna fortunei*, in a dam reservoir. Limnology 11:259–266
- Oliva A, Ubeda CA, Vignes IE, Uriondo A (1981) Contribución al conocimiento de la ecología alimentaria del bagre amarillo (*Pimelodus maculatus* Lacepede 1803) del Río de La Plata (Pisces, Pimelodidae). Comunicaciones del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”. Ecología 1:31–50
- Oliveira CR, Fugi R, Brancalhão KP (2010) Fish as potential controllers of invasive mollusks in a neotropical reservoir. Nat Conserv 8:140–144
- Panati AE, Del Barco D (1981) Peces de la provincia de Santa Fe. 9. Peces omnívoros preferentemente de fondo, de verano. Armado gallego (*Pterodoras granulosus*). CYTA, Ministerio de Agricultura y Ganadería de Santa Fé. Argentina 25:21–23
- Pastorino G, Darrigran GA, Martín SM, Lunaschi L (1993) *Limnoperna fortunei* (Dunker, 1857) (Mytilidae), nuevo bivalvo invasor en aguas del Río de la Plata. Neotropica 39:101–102
- Penchaszadeh PE, Darrigran GA, Angulo C, Averbuj A, Brögger M, Dogliotti A, Pirez N (2000) Predation of the invasive freshwater mussel *Limnoperna fortunei* (Dunker, 1857) (Mytilidae) by the fish *Leporinus obtusidens* Valenciennes, 1846 (Anostomidae) in the Río de la Plata, Argentina. J Shellfish Res 19:229–231
- Ringuelet RA, Aramburu RH, Alonso de Aramburu A (1967) Los peces argentinos de agua dulce. Comisión de Investigación Científica, Gobernación de la Provincia de Buenos Aires, La Plata (Argentina), pp 1–602
- Sardiña P, Lopez Cazorla AC (2005) Trophic ecology of the whitemouth croaker, *Micropogonias furnieri* (Pisces: Sciaenidae), in south-western Atlantic waters. J Marin Bio Assoc U K 85:405–413
- Sardiña P, Cataldo D, Boltovskoy D (2008) The effects of the invasive mussel, *Limnoperna fortunei*, on associated fauna in South American freshwaters: importance of physical structure and food supply. Fundam Appl Limnol/Archiv Hydrobiol 173:135–144
- Sardiña P, Chaves E, Marchese M (2011) Benthic community responses to invasion by the golden mussel, *Limnoperna fortunei* Dunker: biotic homogenization vs environmental driving forces. J N Am Benthol Soc 30:1009–1023
- Strayer DL, Hattala KA, Kahnle AW (2004) Effects of an invasive bivalve (*Dreissena polymorpha*) on fish in the Hudson River estuary. Can J Fish Aquat Sci 61:924–941
- Strayer DL, Hattala KA, Kahnle AW, Adams RD (2014) Has the Hudson River fish community recovered from the zebra mussel invasion along with its forage base? Can J Fish Aquat Sci. 71:1146–1157
- Sverlij SB, Espinach Ros A, Orti G (1993) Sinopsis de los datos biológicos y pesqueros del sábalo *Prochilodus lineatus* (Valenciennes, 1847). Food and Agriculture Organization, Rome (Italy), pp 1–64

- Sylvester F, Dorado J, Boltovskoy D, Juárez A, Cataldo D (2005) Filtration rates of the invasive pest bivalve *Limnoperna fortunei* as a function of size and temperature. *Hydrobiologia* 534:71–80
- Sylvester F, Boltovskoy D, Cataldo D (2007) Fast response of freshwater consumers to a new trophic resource: predation on the recently introduced Asian bivalve *Limnoperna fortunei* in the lower Parana River, South America. *Austral Ecol* 32:403–415
- Tanaka H, Deno T, Kondo T (2004) Effect of gasterostome trematode infection on growth and reproduction in *Limnoperna fortunei* (Bivalvia: Mytilidae). *Memoirs of Osaka Kyoiku University, Series III, Nat Sci Appl Sci* 53:1–7
- Uryu K, Iwasaki K, Hinoue M (1996) Laboratory experiments on behaviour and movement of a freshwater mussel, *Limnoperna fortunei* (Dunker). *J Molluscan Stud* 62:327–341
- Vermulm JH, Giamas MTD (2008) Ocorrência do mexilhão dourado *Limnoperna fortunei* (Dunker, 1857), (Mollusca; Bivalvia; Mytilidae), no trato digestivo do “Armal” *Pterodoras granulosus* (Valenciennes, 1821) (Siluriformes; Doradidae), do Rio Paraná, São Paulo, Brasil. *Boletim do Instituto de Pesca de São Paulo* 34:175–179
- Vieira JP, Lopes MN (2013) Size-selective predation of the catfish *Pimelodus pintado* (Siluriformes: Pimelodidae) on the golden mussel *Limnoperna fortunei* (Bivalvia: Mytilidae). *Zoologia* 30:43–48