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Limnoperna fortunei (golden mussel) in
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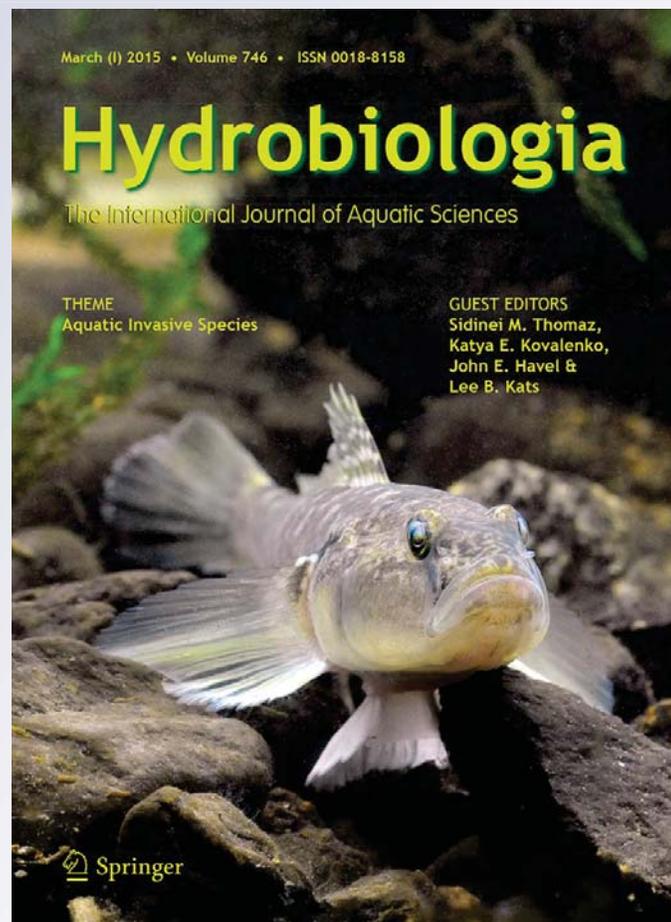
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Ecosystem impacts of the invasive bivalve *Limnoperna fortunei* (golden mussel) in South America

Demetrio Boltovskoy · Nancy Correa

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Abstract We summarize current knowledge on the effects of the invasive Asian bivalve *Limnoperna fortunei* (introduced in South America around 1990) on local biota. *Limnoperna* modifies nutrient concentrations and decreases concentrations of particulate organic matter in the water column (including phytoplankton and zooplankton), thus enhancing light penetration and stimulating growth of periphyton and macrophytes. Selective grazing and modification of the N:P ratio are responsible for strong enhancements of toxic cyanobacterial blooms. *Limnoperna* beds significantly enhance the numbers, biomass, and diversity of practically all accompanying invertebrates. The mussel's planktonic larvae represent an important food item for the larvae of 18 fish species, while juveniles and adults are consumed by at least 50

fish species. *Limnoperna* is the first and only abundant benthic filter-feeding animal in South American continental waters. The fact that it intercepts and retains in the freshwater lotic domain particulate organic matter that would otherwise be swept into the sea must represent an important energetic subsidy, but the ecosystem-wide consequences of this trophic shift have not yet been addressed. Comparison with the impacts of the zebra mussel in Europe and North America suggests important differences.

Keywords Invasive bivalves · South America · *Limnoperna fortunei* · Environmental impact

Introduction

Biological invasions by non-indigenous species have brought about profound changes affecting both the use of natural resources by man and relationships between ecosystem components. Freshwater systems, in particular lakes and reservoirs, have been identified as especially vulnerable to invasive species, among which mollusks and crustaceans are most significant (Karatayev et al., 2009). *Dreissena polymorpha* (Pallas, 1771), the zebra mussel, provides an excellent example of a highly successful freshwater invader: it has been expanding westwards from its native Caspian and Black seas since the 1700s, entered North America in the 1980s, and is still spreading both in Europe and

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in North America (Karatayev et al., 2006). As its range grew, reports of its impacts on man-made structures and on the biota multiplied (Karatayev et al., 2002; Kelly et al., 2010).

Another significant invader is *Limnoperna fortunei* (Dunker, 1857), the golden mussel. *Limnoperna fortunei* is a freshwater, byssate mytilid native to continental south east Asia. In the mid-1960s, this mussel was unintentionally introduced in Hong Kong (Morton, 1975), in the early 1980s in Korea (Kojima, 1982), in the late 1980s in Taiwan (Tan et al., 1987), and around 1990 in South America (Pastorino et al., 1993) and Japan (Kimura, 1994). In South America, due to its ability to travel attached to ship's hulls, *L. fortunei* spread swiftly upstream the Paraná-Paraguay waterway at a rate of up to 250 km year⁻¹ (Darrigran, 2002; Boltovskoy et al., 2006). Along non-navigable rivers, upstream colonization was significantly slower (about 20 km year⁻¹; Boltovskoy et al., 2006), yet also relentless. At present, *L. fortunei* inhabits a region from the Pantanal (Brazil, 18°S, 56.7°W) and the northernmost tributaries of the Paraná river (ca. 20°S), to the Río de la Plata estuary (34.8°S, 57.3°W), covering five countries (Argentina, Bolivia, Brazil, Paraguay, and Uruguay). Extensive mussel beds with reported densities of up to over 200,000 ind. m⁻² (Sylvester et al., 2007a; Spaccesi & Rodrigues Capitulo, 2012) are a dominant feature of the benthic fauna in the entire Río de la Plata watershed. In the plankton, *L. fortunei* larvae can outnumber cladocerans and copepods by orders of magnitude for up to 9–10 months of the year (Boltovskoy et al., 2006; Paolucci et al., 2007; Boltovskoy et al., 2009b).

Shortly after invasion, *L. fortunei* became a major nuisance for industrial installations that use raw lake or river water for cooling purposes. Clogging of water intake sieves and filters, pipes, heat exchangers, and condensers became a common difficulty, particularly for power plants (hydroelectric, thermal, and nuclear), requiring additional control and maintenance procedures (Perepelizin & Boltovskoy, 2014). Although economic assessments of the problems involved are scarce and isolated, it is clear that the mussel has had a significant negative impact on industrial activities.

Impacts on the biota, on the other hand, are much more intricate and complex. While some ecosystem effects parallel the changes observed for the zebra and quagga mussels in Europe and North America (reviewed in Karatayev et al., 2007), other effects

differ due to species-specific dissimilarities and/or to dissimilar ecological settings.

This work reviews current knowledge of the effects of *L. fortunei* on ecosystem properties in a number of South American lakes and rivers. These impacts are summarized in Table 1 and discussed in the sections below. Because several excellent reviews on the effects of invasive filtering mussels on European and North American aquatic systems have been published in the last years (e.g., Karatayev et al., 1997; Strayer et al., 1999; Karatayev et al., 2002; Kelly et al., 2010; Van der Velde et al., 2010), this work focuses specifically on those of *L. fortunei* in South America, highlighting some major gaps in our current knowledge. Information on *Dreissena* species is used for comparative purposes, particularly when stressing differences with the effects described for the golden mussel.

Effects of *L. fortunei* on nutrient concentrations

Short-term (6–24 h) experiments on the effects of *L. fortunei* on the water column show that the mussels significantly reduce turbidity, the amount of suspended organic matter, and increase the concentrations of dissolved ammonia, nitrates, and phosphates (Kawase, 2011; Cataldo et al., 2012a). Longer mesocosm incubations yield similar results for the first 24 h, but subsequently the response varies. By the end of the 35 days experiment performed by Cataldo et al. (2012a), nitrate concentrations increased slightly (as compared with the controls) (Fig. 1A), whereas ammonia and phosphates rose conspicuously (Fig. 1B, C). These results are similar to ecosystem effects of *Dreissena* (Karatayev et al., 2002).

Although short- and medium-term experiments yield useful insights into the influence of invasive mussels on nutrients and the biota, from the ecological point of view, the most important issue is how these impacts affect aquatic ecosystems in the long term (years to decades). For *L. fortunei*, the only long-term survey available is the one carried out in Embalse de Río Tercero reservoir (central Argentina, 32.2°S, 64.5°W), which was colonized by *L. fortunei* around 1998 (Boltovskoy et al., 2009a). In the time elapsed (1996–2008), ammonia in the water increased ca. 400%, total N increased 300%, and phosphates doubled (Fig. 2). Most significantly, the N:P ratio dropped from 16.3 (before *L. fortunei*) to 8.9 (after *L. fortunei*).

Table 1 Effects of *L. fortunei* or *L. fortunei*-related processes on the freshwater systems invaded. Potential impacts for which direct evidences are still insufficient are denoted with a question mark and bold

| Trait, component or process associated with the presence of <i>L. fortunei</i> | Direct effect | Indirect effect or consequence | Final effect | References |
|--|---|--|--|---|
| Grazing of POM & phytoplankton by <i>L. fortunei</i> larvae and adults | Increased water transparency | Deeper light penetration | Deeper light penetration | Boltovskoy et al. (2009a), Kawase (2011) |
| | | Enhanced light availability for macrophytes | More macrophytes | Boltovskoy et al. (2009a) |
| | | More macrophyte growth | More waterfowl | Boltovskoy et al. (2009a) |
| Grazing of phytoplankton by <i>L. fortunei</i> larvae and adults | Less nutrient consumption by phytoplankton | Enhanced nutrient availability for macrophytes | More macrophytes | Boltovskoy et al. (2009a) |
| | | Enhanced nutrient availability for periphyton | More periphyton | Cataldo et al. (2012b) |
| Nutrient recycling | Lower N:P ratio | More Cyanobacteria | More cyanobacterial blooms | Cataldo et al. (2012b), Boltovskoy et al. (2013) |
| Selective grazing of solitary Cyanobacteria | More colonial cyanobacterial cells | Higher survival of colonial Cyanobacteria | More cyanobacterial blooms | Cataldo et al. (2012b) |
| Chemical cues | Colony formation in Cyanobacteria | Higher survival of colonial Cyanobacteria | More cyanobacterial blooms | Cataldo et al. (2012b) |
| Cyanobacterial blooms (in lentic waterbodies) | Mortality of <i>L. fortunei</i> larvae | Less <i>L. fortunei</i> adults? | Sparser <i>L. fortunei</i> beds? | Gazulha (2010), Boltovskoy et al. (2013) |
| | Mortality of fishes and benthic organisms | Less fishes and benthic organisms? | Less nekton and benthos biomass and diversity? | Pizzolón et al. (1999) |
| Grazing of zooplankton | Less zooplankton? | Less food for zooplanktivorous organisms? | Less zooplanktivorous organisms? | Rojas Molina et al. (2010), Fachini (2011), Rojas Molina et al. (2011, 2012) |
| Selective grazing of zooplankton | Higher impact on smaller zooplankton | Lower survival of small zooplankton? | Modification of zooplanktonic proportions? Less Rotifera? | Rojas Molina et al. (2010), Fachini (2011), Rojas Molina et al. (2011, 2012) |
| Production of feces and pseudofeces | Increased proportion of organic matter in sediments | More food for benthic invertebrates | Higher abundance and diversity of benthic invertebrates | Darrigran et al. (1998), Sylvester et al. (2007b), Sardiña et al. (2008), Karatayev et al. (2010), Sardiña et al. (2011), Burlakova et al. (2012) |

Table 1 continued

| Trait, component or process associated with the presence of <i>L. fortunei</i> | Direct effect | Indirect effect or consequence | Final effect | References |
|--|--|--|---|--|
| <i>L. fortunei</i> beds | Increased shelter for invertebrate fauna | Higher invertebrate survival | Higher abundance and diversity of benthic invertebrates | Darrigran et al. (1998), Sylvester et al. (2007b), Sardiña et al. (2008), Karatayev et al. (2010), Sardiña et al. (2011), Burlakova et al. (2012) |
| | Consumption by adult fishes | More food for adult fishes | More fishes | López Armengol and Casciotta (1998), Boltovskoy and Cataldo (1999), Ferriz et al. (2000), García and Protogino (2005), Boltovskoy et al. (2006), Cantanhêde et al. (2008), Lösch et al. (2009), Montalto et al. (1999), González-Bergonzoni et al. (2010), Oliveira et al. (2010a), Masdeu et al. (2011), Belz et al. (2012), Lopes and Vieira (2012), Vieira and Lopes (2013) |
| | Consumption by waterfowl? | More food for waterfowl? | More waterfowl? | Boltovskoy et al. (2009a) |
| | Consumption of juveniles and adults by benthic invertebrates (e.g., leeches, gastropods, crustaceans, insect larvae) | More food for some benthic invertebrates | Higher abundance and diversity of benthic invertebrates? | Darrigran et al. (1998), Sylvester et al. (2007b), Sardiña et al. (2008), Karatayev et al. (2010), Sardiña et al. (2011), Burlakova et al. (2012) |
| <i>L. fortunei</i> veligers in the water column | Consumption by larval fishes | Higher larval fish survival | More fishes | Paolucci et al. (2007, 2010a, 2010b) |
| Overgrowth of various organisms (sponges, crustaceans, gastropods, bivalves) | Impair locomotion, prevent valve opening/closure, smother siphons, prevent normal growth? | Lower survival of some invertebrates? | Lower abundance and diversity of some invertebrates? | Darrigran (2002), Mansur et al. (2003), Scarabino (2004), Lopes et al. (2009), Karatayev et al. (2010), Rojas Molina and Williner (2013) |
| Intermediate host for fish parasites | Presence of new fish diseases | Lower survival of some fish species? | Less fishes? | Ogawa et al. (2004), Baba and Urabe (2011b) |

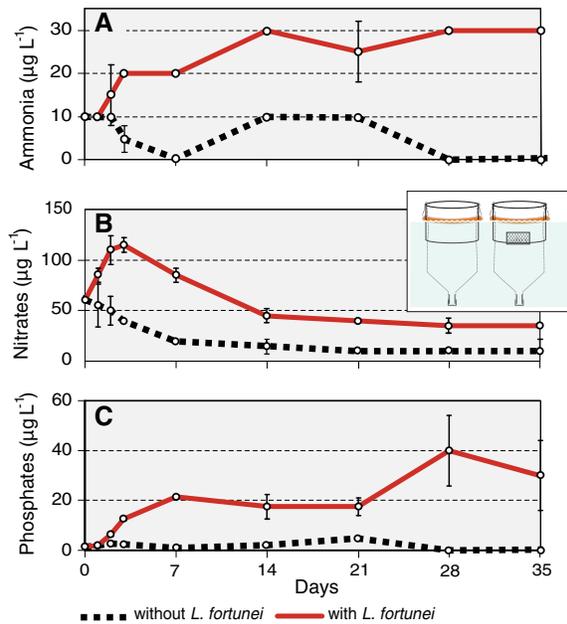


Fig. 1 Changes in the concentrations of nutrients in 400 l mesocosms (inset figure) deployed for 35 days in Salto Grande reservoir without mussels, and stocked with 300 adult specimens of *L. fortunei* (two replicates per treatment). In all cases, after 35 days, differences between concentrations were significant (ammonia, $P < 0.001$; nitrates, $P = 0.031$; phosphates, $P = 0.011$; Tukey tests) (from Cataldo et al., 2012b)

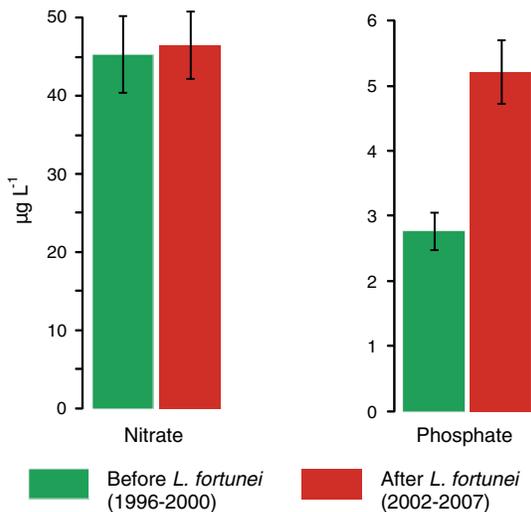


Fig. 2 Mean concentrations of nitrates and phosphates in Embalse de Río Tercero reservoir in 1996–2000 (before the waterbody was influenced by the presence of *L. fortunei*, which invaded in 1998; 29 datapoints), and in 2002–2007 (with high *L. fortunei* population densities; 33 datapoints). Based on data from Boltovskoy et al. (2009a)

Effects of *L. fortunei* on phytoplankton and toxic cyanobacterial blooms

Reported grazing rates of *L. fortunei* vary from 0.2 to 725 ml ind.⁻¹ h⁻¹, or 0.1 to 29.5 ml mg⁻¹ dry tissue (DT) h⁻¹ (Rückert et al., 2004; Sylvester et al., 2005; Pestana et al., 2009; Gazulha, 2010; Fachini, 2011; Cataldo et al., 2012a, b; Gazulha et al., 2012b; Frau et al., 2013). “Normal” filtration rates for 15–25 mm golden mussels range around 100 ml ind.⁻¹ h⁻¹, or ca. 2–4 ml mg⁻¹ DT h⁻¹. This is roughly comparable with data reported for other freshwater mussels (Sylvester et al., 2005; Karatayev et al., 1997), which indicates that strong impacts on the water column are due to high mussel densities and active water mixing, rather than to exceptional individual filtration rates. Indeed, none of the indigenous (mainly Unionidae) or introduced (*Corbicula fluminea*) South American bivalve species attain densities similar to those observed in *L. fortunei* beds, which on suitable substrates are typically around 5,000 ind. m⁻², and can occasionally exceed 200,000 ind. m⁻² (Sylvester et al., 2007a; Spaccesi & Rodrigues Capitulo, 2012).

In addition to alteration of the light environment, the two major components of the impact of bivalve filter-feeding on phytoplankton are (1) consumption of algal cells and (2) modifications in nutrient supply (Table 1). Short-term laboratory and mesocosm trials with *L. fortunei* indicate swift depletion of the experimental containers (Cataldo et al., 2012a). However, longer term studies suggest that after the initial decline, algal numbers recover partially, most probably stimulated by the increasing availability of nutrients (Cataldo et al., 2012b). Nevertheless, waterbodies that have been colonized by the mussel for years have less suspended particulate matter in the water column, including phytoplankton, than before the invasion. Ten years after having been colonized by *L. fortunei*, waters of Embalse de Río Tercero reservoir lost about 30–40% of their seston load, represented chiefly by algae, ca. 50% of their planktonic primary production, and became 30% clearer (Boltovskoy et al., 2009a). A similar trend was suggested for some marginal lagoons and tributaries associated with the Middle Paraná river (ca. 31.7°S, 60.6°W) (Devercelli & Peruchet, 2008; Rojas Molina & José De Paggi, 2008).

Many surveys highlight that grazing selectivity may involve a preference for smaller particle sizes

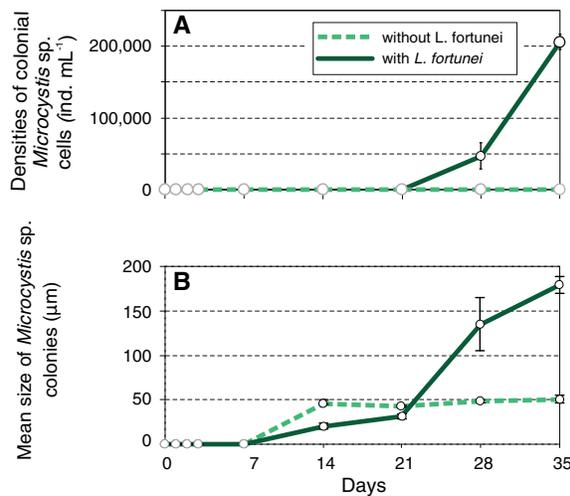


Fig. 3 Changes in the abundance of colonial cells of *Microcystis* spp. **A**, and in the size of these colonies **B** throughout 35-days experimental period in 400 L mesocosms with and without *L. fortunei* (two replicates per treatment) (from Cataldo et al., 2012b)

(<100 µm), phytoplankton over zooplankton, Euglenophyta over other algae, and single-celled phytoplankton over colonies and filamentous species (Rückert et al., 2004; Rojas Molina et al., 2010; Fachini, 2011; Cataldo et al., 2012b; Gazulha et al., 2012a; Frau et al., 2013).

Results on grazing on cyanobacteria, in particular *Microcystis*, are contradictory. Several surveys concluded that both toxic and non-toxic strains of *Microcystis* are actively consumed by the mussels (Rückert et al., 2004; Gazulha et al., 2012a). Others, however, found that microcystin LR hinders filtration significantly (Boltovskoy et al., 2009b; Fachini, 2011). Interestingly, a similar controversy is also found in studies on the effects of *Microcystis* on *D. polymorpha* (Dionisio Pires et al., 2005; Juhel et al., 2006). At any rate, regardless of its capabilities of consuming *Microcystis*, the golden mussel has very pronounced effects on the population dynamics of this cyanobacteria, strongly boosting its densities (Cataldo et al., 2012b) (Fig. 3A). Significantly, this growth is accompanied by an increase in the ratio of colonial to solitary *Microcystis*, and in the size of the colonies (Fig. 3B). There are several factors that account for this effect: (1) changes in nutrient availability and proportions, in particular the N:P ratio; (2) size-selective grazing, whereby small, solitary cells are eliminated, while colonies survive; (3) promotion of colony formation

through the production of chemical signals that trigger aggregation of solitary cells in order to avoid grazing; and (4) microcystin toxicity, deterring grazing as *Microcystis* biomass builds up (Cataldo et al., 2012b).

Promotion of *Microcystis* growth was also observed in North American waterbodies invaded by *D. polymorpha*, but only at low to moderate *P* concentrations (<25 µg total P l⁻¹; Sarnelle et al., 2005), whereas at high *P* values no enhancements are observed. As opposed to this pattern, in South America, *L. fortunei* boosts cyanobacterial numbers at very high total *P* levels (between 50 and ~100 µg total P l⁻¹ in the reservoir where these experiments were carried out; Cataldo et al., 2012b; O' Farrell et al., 2012).

A remarkable consequence of toxic cyanobacterial growth (at least partly promoted by *L. fortunei*'s activity) is that the blooms suppress the bivalves reproduction. This effect was suggested by several laboratory and field studies (Boltovskoy et al., 2009b; Gazulha et al., 2012b), and confirmed by the analysis of nine years of observational data in Salto Grande reservoir (Argentina/Uruguay, 31°S, 57.8°W) (Boltovskoy et al., 2013). Experimental results indicate that 10–20 µg l⁻¹ of microcystin LR kills up to 100% of the larvae in 48 h (Boltovskoy et al., 2013). The fact that larval numbers return to “normal” levels when blooms decline indicates that adult mussels survive through these adverse periods (Boltovskoy et al., 2009b, 2013).

Effects of *L. fortunei* on periphyton and aquatic macrophytes

As shown by studies of the zebra mussel and other sessile filter-feeding organisms, nutrient regeneration, clarification of the water column, and elimination of nutrient-consuming phytoplankton favor the growth of periphyton and aquatic macrophytes (Karatayev et al., 1997).

Research to date suggests that *L. fortunei* has similar effects. Its impact on the periphyton has been confirmed and quantified, showing significant increases in the presence of mussels (Cataldo et al., 2012a). Enhancements of aquatic macrophytes have also been observed: in Embalse de Río Tercero reservoir, *Elodea callitrichoides* became much more abundant after the waterbody was invaded by the mussel, but these changes have not been quantified (Boltovskoy et al., 2009a).

Effects of *L. fortunei* on zooplankton

Relationships between *L. fortunei* and zooplankton can involve multiple interactions (Table 1), including (but not restricted to): (1) feeding of adult mussels on planktonic animals, (2) mussel grazing on phytoplankton and other organic particles, thus competing with the zooplankton for food, (3) mussel larvae serving as a food resource for predatory zooplankton, and (4) mussel larvae serving as a food resource for predatory and filter-feeding animals in general (planktonic, nektonic, or benthic), thus reducing predation pressure on other zooplankton. Of these, only grazing of adult *L. fortunei* on zooplankton and predation of larval fish on mussel veligers have been addressed so far. Indirect relationships are conceivably numerous, but we only have vague hints of their potential impact on zooplanktonic communities.

In a survey of the diet of *L. fortunei* based on stomach contents, Rojas Molina et al. (2010) recorded 81 species of algae, 46 Rotifera, 17 Cladocera, and 4 Copepoda, ranging from 4 μm to >1 mm in size. Animal food was present in 96% of the stomachs analyzed, with the rotifers *Keratella* and *Lecane* as dominant components. Large food items (chiefly cladocerans and copepodids) were scarce in numbers, but in terms of biomass they accounted for 67% of the food ingested (Fig. 4). Several animal species were strongly and positively selected, especially Rotifera (also noticed by Fachini, 2011) and small Cladocera (Fig. 4). Positive selection was associated primarily with size, and also with neuromuscular coordination and escape responses (Rojas Molina et al., 2011, 2012).

Ecosystem-wide impacts of predation by *L. fortunei* on zooplankton have also been reported, suggesting that rotifers dropped in abundance after the invasion, whereas cladocerans and copepods were unaffected (Rojas Molina and José de Paggi, 2008). A similar effect was also reported for the zebra mussel (MacIsaac et al., 1995).

Effects of *L. fortunei* on benthic invertebrates

Analyses of the influence of *L. fortunei* on benthic organisms have been based on two approaches: (1) comparison of natural assemblages occurring in *L. fortunei* beds (attached to immobile substrate) or

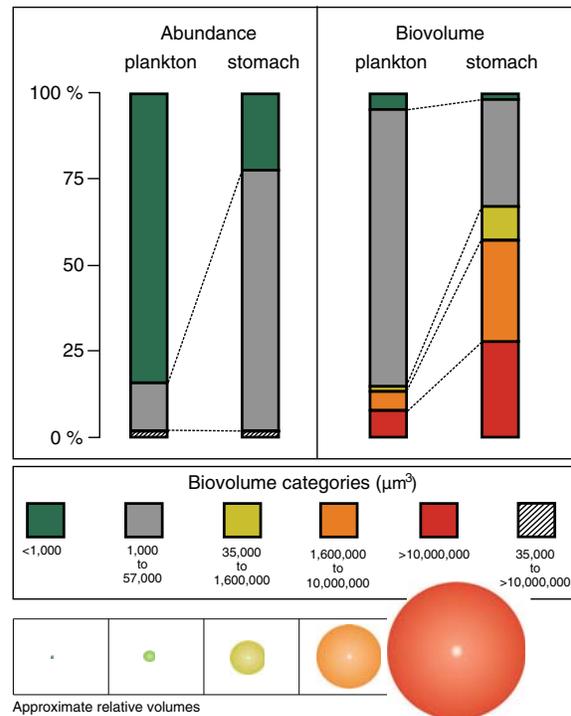


Fig. 4 Feeding selectivity of *L. fortunei* as shown by changes in the proportions of various planktonic organisms in the water column and in the mussels stomachs. Size categories (μm^3) include the following organisms, $<1,000$: Cyanobacteria, Chlorococcales, most Volvocales, most Bacillariophyceae Centrales, Chrysophyceae, and Cryptophyceae; $1,000$ to $57,000$: some Chlorococcales, filamentous Chlorophyceae, most Zygnematales, most Bacillariophyceae Pennales, Euglenophyta, and Dinophyceae; $35,000$ – $1,600,000$: Protozoa, Rotifera, Nematoda and *L. fortunei* larvae; $1,600,000$ – $10,000,000$: Chydoridae, Bosminidae, *Ceriodaphnia cornuta*, nauplii larvae and Ostracoda; $>10,000,000$: Copepoda and other Cladocera (Sididae, Moinidae, Daphnidae, Macrothricidae, Chydoridae). Plankton data are based on 14 plankton samples (seven for phytoplankton, and seven for zooplankton, from seven different sites); stomach contents data are based on 140 *L. fortunei* specimens around 17 mm in length, 20 from each of seven sites. Modified from Rojas Molina et al., (2010)

druses (clusters of mussels around a pebble or another mobile object) with those obtained nearby, in areas barren of mussels (Darrigran et al., 1998; Marçal & Callil, 2008; Karatayev et al., 2010; Sardiña et al., 2011; Burlakova et al., 2012), and (2) experimental studies with artificial substrates contrasting the abundance and composition of invertebrates recorded in areas with and without mussels (Sylvester et al., 2007b; Sardiña et al., 2008). In general, all studies concluded that in the presence of *L. fortunei*, benthic

diversity, abundance, and biomass increase significantly.

Using artificial substrates, Sylvester et al. (2007b) found that areas covered by *L. fortunei* host 43–100% more invertebrate biomass (excluding *L. fortunei*) than areas lacking the mussel. This study concluded that facilitation is due to changes in the physical structure of the substrate, as well as to the biological activity of the bivalves. In an attempt to separate these two effects, Sardiña et al., (2008) deployed artificial substrates with either a layer of living mussels, a layer of intact empty shells mimicking living mussels, or blank, bare tiles. After 64 days, biomass, abundance, and diversity were the highest on tiles with live mussels, followed by tiles with empty shells (Fig. 5). These differences have been attributed to the ability of mussel beds to retain sediments, and to the higher contents of organic matter in sediments associated with live mussels.

These studies suggest that most benthic invertebrates are facilitated by *L. fortunei*, and these species do not benefit equally. The direction and intensity of this influence are probably associated with several traits, in particular feeding mode. Epifaunal scrapers, deposit feeders, and their predators benefit the most, whereas some burrowing animals may thrive better in bare, especially fine, sediments (Ward & Ricciardi, 2007; Karatayev et al., 2010; Sardiña et al., 2011; Burlakova et al., 2012). It should be stressed, however, that the lack of a positive effect does not imply a negative influence. While the organisms that are presently facilitated by *L. fortunei* probably were restricted in occurrence before the invasion because they are unable to occupy soft sediments (Sardiña

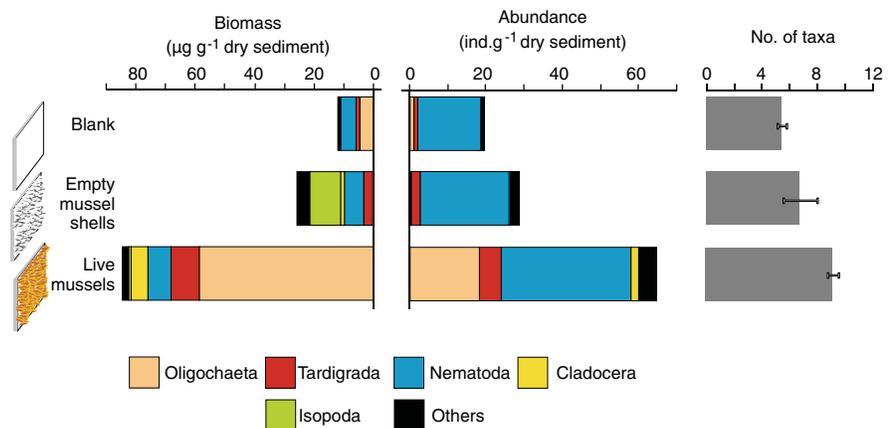
et al., 2011), the ones that do not benefit from mussel beds and druses may well be indifferent to the presence of the mussel.

Several studies suggested that freshwater invasive mussels homogenize the composition of benthic communities (Sardiña et al., 2011). Across waterbodies, similarities between communities associated with *L. fortunei* are significantly higher than the similarities between bare sediment samples (Karatayev et al., 2010; Sardiña et al., 2011; Burlakova et al., 2012). This effect is likely a result of the fact that *L. fortunei* beds represent isolated and highly populated islands of hard, biologically modified substrate in a sea of sparsely populated mud, rather than a consequence of their invasive nature. As noticed by Burlakova et al., (2012), mussel aggregates create habitat for species that would otherwise be infrequent in the environment, providing them with shelter and food.

L. fortunei as food for other organisms

For *L. fortunei*, potential predators have been identified in a number of groups, including leeches, gastropods, crustaceans, insect larvae, fishes, aquatic turtles, water birds, and aquatic mammals (crab-eating raccoons, river otters) (Sylvester et al., 2007a). Experimental results indicate that predators in the lower delta of the Paraná river (probably mostly fishes) eliminate up to 90% of the bivalve's biomass, or 6 kg of whole live mussels m⁻² year⁻¹ (Sylvester et al. 2007a). Nakano et al. (2010) estimated that predators eliminate 96–97% of the mussels in Lake Ohshio (Japan). This trophic subsidy is likely very

Fig. 5 Biomass, abundance, and diversity of invertebrates on artificial substrates (concrete tiles) without mussels (blank), with empty mussel shells, and with live mussels after deployment for 64 days in the lower delta of the Paraná river (three replicates per treatment). "Others" include Hydracarina, Ostracoda, Copepoda, and Gammaridea. Based on data from Sardiña et al. (2008)



important for local fauna, but as reviewed below, direct evidence of consumption is currently limited to larval and adult fishes, two crustaceans, and some ancillary observations on a few bird species.

Consumption of *L. fortunei* veligers by larval fishes

Densities of golden mussel larvae in the plankton can be very high, often outnumbering crustacean zooplankton (Boltovskoy et al., 2006; Paolucci et al., 2007; Boltovskoy et al., 2009b). These veligers have become an important food resource for local fish larvae.

Of 25 larval fish taxa surveyed in the rivers Paraná, Paraguay, and Uruguay, 18 have been found to feed on veligers (Paolucci, 2010). Proportions of feeding (i.e., post yolk-sac) fish larvae with *L. fortunei* veligers in their guts vary from 20 to 70% (Paolucci et al., 2007), and those for which veligers are the dominant component of the diet (in terms of biomass) make up 15–71% of the fish larvae examined (Paolucci et al., 2007). Mussel larvae are a particularly significant component of the diet of the youngest larval fish stages, presumably because veligers are an easy target because of their low mobility and poor escape responses. Around 30–35% of the protolarvae consume veligers; in mesolarvae, the share of veligers is smaller, dropping again in the latest developmental stage—the metalarvae (3%) (Paolucci et al., 2007).

Comparison of plankton samples and fish gut contents indicates that *L. fortunei* is preferred over copepods and cladocerans (Paolucci et al., 2007, 2010a, b), unless mussel larvae are scarce in the plankton, in which case cladocerans are favored (Paolucci, 2010). Veligers are not only readily available and widely consumed, but they also represent an energetically more profitable food resource yielding significantly higher growth rates than crustaceans (Paolucci et al., 2010b). Higher growth rates stem from the higher energy contents of veligers, and from the lower energy costs of capturing slow-moving prey (Paolucci et al., 2010b).

Significantly, veligers became the preferred food item for the larvae of some of the most abundant and ecologically important fish species, like several Pimelodidae and *Prochilodus lineatus*. The biomass of *P. lineatus* represents over 60% of the overall fish biomass in the Paraná-Uruguay system (Bonetto,

1998), and is the main prey of several large, ichthyophagous fishes. The fact that veligers are particularly important as a food resource for the earliest larval fish stages, for which mortality rates are highest, has likely forced important shifts in the dynamics of the species involved (Boltovskoy et al., 2006), as well as in those of other organisms that form part of their trophic webs.

Consumption of juveniles and adults of *L. fortunei*

The inventory of fish 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. García and Montalto (2006) identified 18 fish species as predators of *L. fortunei* in South American inland waters; seven years later, the list had increased to almost 50 species. In some areas, fishes that consume *L. fortunei* represent >50% of the species regularly present in commercial fisheries (Oliveira et al., 2010a).

The importance of mussels in the diet varies geographically, seasonally (Oliveira et al., 2010a), and with fish age (López Armengol & Casciotta, 1998). Fishes that have been consistently reported to rely heavily on *L. fortunei* for food include approximately a dozen species, with some of them feeding on the mussel almost exclusively (Ferriz et al., 2000; Penchaszadeh et al., 2000; Cataldo et al., 2002). If animal food was not underrepresented in fish gut analyses prior to introduction of the golden mussel (due to the scarcity of hard remains), plants and detritus were the main food items of these species (Ferriz et al., 2000). Presently, *L. fortunei* represents an additional food item that is widely available and energetically more profitable (Ferriz et al., 2000).

The effects of this new food supply on fish populations have not been assessed, but are likely significant. Impacts are probably not only restricted to species that consume the mollusk directly, but also species that may benefit from this new food resource indirectly, including many of the large ichthyophagous species that feed on other fishes. Furthermore, *L. fortunei* transfers large amounts of organic matter from the pelagic to the benthic domains through filtration and the formation of feces and pseudofeces (Sardiña et al., 2008; Cataldo et al., 2012b), which boosts invertebrate densities (Sylvester et al., 2007b; Sardiña et al., 2008, 2011; see above). This is probably important for deposit feeding detritivorous fish

species, which represent the bulk of the local fish fauna (Bonetto, 1998).

Argentine freshwater fish landings increased three-fold after invasion of *L. fortunei* (Boltovskoy et al., 2006), which may suggest better recruitment and survival conditions. However, interpretation of this trend has several confounding variables, including changes in fishing regulations, fishing pressure, and fish export trends.

In North America, *Dreissena* has been shown to increase the abundance of littoral species by enriching coastal bottom areas with organic matter but decrease the abundance of pelagic fishes due to depletion of zooplankton forage species through grazing (Strayer et al., 2004). The effects of *L. fortunei* on South American fish stocks are probably different because filter-feeding fishes are scarce and POC loads are very high (see “Concluding remarks” section).

In addition to fishes, two crab species (*Zilchiopsis collastinensis* and *Trichodactylus borellianus*) and one turtle have been observed to feed on *L. fortunei* (Bujes et al., 2007; Torres et al., 2012; Carvalho et al., 2013), but data on the importance of this item in their diet are still scarce.

In Embalse de Río Tercero reservoir, coot and grebe (*Fulica leucoptera*, *F. armillata*, *Podilymbus podiceps*) densities increased noticeably after introduction of the golden mussel, presumably in response to the areal growth of the beds of aquatic macrophytes on which the birds feed. Furthermore, both coots and grebes have been observed to dive and emerge with clusters of *L. fortunei* in their beaks (M. Hechem, pers. comm.), which suggests that they also feed on the mussel, as do other coot species on *Dreissena* in North America (Molloy et al., 1997).

Miscellaneous interactions of *L. fortunei* with other organisms

In addition to the impacts reviewed above, several other interactions between *L. fortunei* and native organisms have been reported, but most are restricted to anecdotal records.

Overgrowth of various benthic organisms, including sponges, crustaceans, gastropods, and other bivalves, has been observed repeatedly (Darrigran, 2002; Mansur et al., 2003; Lopes et al., 2009; Karatayev et al., 2010; Rojas Molina & Williner,

2013), and it has been suggested that the impact on some of them, in particular unionids, may be significant (Mansur et al., 2003; Scarabino, 2004). However, these conclusions are based on extrapolation of the known effects of the zebra mussel in Europe and North America (e.g., Schloesser et al., 1996), rather than on *ad hoc* local studies.

Mansur et al. (2003) reported that decrease in reed (*Scirpus californicus*) populations in some areas of southern Brazil may be associated with the settlement of *L. fortunei* on their roots resulting in the “suffocation” of the plants, but this conclusion is debatable (Boltovskoy et al., 2006).

In Japan, introduction of *L. fortunei* has been associated with the appearance of new fish parasites (trematodes) whose life cycle includes the mussel as an intermediate host (Ogawa et al., 2004; Baba & Urabe, 2011a). No such reports from South America are known yet.

Concluding remarks

Studies on the golden mussel have traditionally used *Dreissena polymorpha* as a model, which resulted in useful guidelines for defining potential interactions and fruitful research topics. However, similarities between these two species have often proved misleading when extrapolating to *L. fortunei* the effects of the zebra mussel on the systems invaded (Boltovskoy et al., 2006; Cataldo et al., 2012b; Boltovskoy et al., 2013). The mechanisms by which *L. fortunei* modifies living conditions for other organisms are largely the same as those described for *Dreissena* species (Karatayev et al., 1997; Ward & Ricciardi, 2007; Kelly et al., 2010; Burlakova et al., 2012), but the final results of these interactions are not necessarily alike. Intrinsic dissimilarities between the two species and environmental differences are responsible for significant differences in the impacts involved. Among the former, reproductive period, dissolved oxygen and calcium requirements, thermal regime, and resistance to pollution are probably of major importance. Environmental differences, in turn, involve clearer and colder waterbodies in Europe and North America than the warmer and more turbid South American rivers (Karatayev et al., 2007, 2010).

The Paraguay-Paraná-Uruguay floodplain river system invaded by *L. fortunei* in South America has marked

differences with the colder, clearer and more oligotrophic North American waterbodies colonized by *Dreissena*. Notably, the mean concentration of POC in the Paraná river (about 3.5 mg l^{-1} , 20–40% of it labile and available for biologic consumption: Depetris, 1976; Depetris & Pasquini, 2007) is much higher than in many of the waterbodies invaded by *Dreissena* (typically around $0.15\text{--}1 \text{ mg l}^{-1}$ in the Great Lakes; Fanslow et al., 1995; Barbiero & Tuchman, 2004; Johengen et al., 2008), which suggests that filtering organisms are less food limited (Sylvester et al., 2005). Furthermore, because indigenous filter-feeding benthic animals in the Paraná watershed are scarce, most of this organic matter 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. The ecosystem-wide effects of this new scenario are obviously a function of mussel densities throughout large areas, a situation which may seem unlikely in these floodplain rivers dominated by soft, unconsolidated sediments. However, indirect evidence suggests that the Paraná system does host large *L. fortunei* populations: veliger densities in the Paraná river and its outlet, the Río de la Plata estuary (mean annual values around $6,000\text{--}7,000 \text{ larvae m}^{-3}$; Boltovskoy et al., 2009b), are higher than those recorded in Embalse de Río Tercero (ca. $4,000 \text{ larvae m}^{-3}$), where average adult mussel densities are almost $1,000 \text{ ind. m}^{-2}$ (or $0.6 \text{ kg of whole mussel mass m}^{-2}$) (Boltovskoy et al., 2009a). This comparison suggests that densities of reproducing adults are high in the rivers, reinforcing the notion that large scale impacts are possible.

Complications for interpreting the effects of *L. fortunei* on the ecosystem are even more critical when attempting to label the impacts as negative or positive. A basic precautionary principle and the long list of examples where introduced species have been shown to have devastating effects on the biota (Simberloff, 2003) clearly support the need to make all efforts possible to keep biological invasions at bay, or to eradicate them if feasible. However, once a non-native species have been introduced and its eradication is out of the question (as is the case of *L. fortunei*), analyses of its interactions with the local biota should be based on evidence, rather than on extrapolations from other invasives and geographic areas. Much of the literature on the golden mussel has been oriented at forcibly

demonstrating the environmental harm caused by this invader, thus biasing if not the results, the interpretation of the evidence obtained (Bujes et al., 2007; Defeo et al., 2013). Data available indicate that many of the interactions between *L. fortunei* and local organisms result in negative outcomes (e.g., enhancement of cyanobacterial blooms, grazing on some phyto- and zooplankton, introduction of new fish parasites), whereas others are probably positive (e.g., food for larval and adult fishes, enhancement of benthic abundance and diversity).

As far as we know, in South America, *L. fortunei*'s range is still limited to one major watershed (Río de la Plata) and several minor basins (Mar Chiquita, Patos-Mirim, Guaíba, Tramandaí). Infestation of the next large watershed—the Amazon, has not been reported so far, but is most probably inevitable. The Amazon is navigable to ocean liners of virtually any tonnage, including ships with ballast water from infested ports along the Paraná-Uruguay-Río de la Plata waterways and the Guaíba basin, where compliance with international water ballast regulations is rather loosely enforced (Boltovskoy et al., 2011). This suggests that sooner or later *L. fortunei* will invade the Amazon and, eventually, other South and North American freshwater bodies (Ricciardi, 1998; Boltovskoy et al., 2006; Karatayev et al., 2006; Oliveira et al., 2010b). This spread will increase the need for objective, regional studies, untainted by a priori judgments on the environmental harm or benefit of the golden mussel.

So far we have only explored a few effects of this invader on local scales, but on the ecosystem scale our understanding of interactions of *L. fortunei* with the environment is still very limited. The following impacts would be particularly interesting questions for future research: biomagnification and transfer of contaminants (Villar et al., 1997), thermal shifts due to changes in water transparency (Yu & Culver, 2000), the homogenization of faunal composition across environments (Sardiña et al., 2011), facilitation of other invasive species (Ricciardi, 2001), changes in macrophyte growth, modifications in benthic oxygenation, overgrowth of other organisms, and trophic relationships with waterfowl and aquatic vertebrates other than fishes.

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