Relationships of *Limnoperna fortunei* with Benthic Animals

Francisco Sylvester and Paula Sardiña

Abstract Similar to other invasive bivalves, *Limnoperna fortunei* has a variety of effects on other benthic animals. These effects have been studied in the Paraná-Paraguay-Uruguay river system, Río de la Plata estuary, and in the reservoir Embalse Río Tercero since the invasion of South America by the bivalve. The bulk of information accumulated indicates that *L. fortunei* has predominantly positive effects on meiofaunal groups. Increases in the abundance, biomass, and richness of many groups are attributed to substrate enrichment from the bivalve's feces and pseudofeces as well as refugia provision amid the valves. Nonetheless, negative impacts on some groups (gastropods) and the homogenization of benthic fauna following colonization by the mussel have also been reported. Large-sized invertebrates can also be detrimentally affected by this mussel's biofouling, as severe cases of epifaunal growth have been reported for native crabs and mussels, including the invasive clam *Corbicula fluminea*. However, consequences to affected individuals and impacts at the population level have not yet been assessed. A variety of animals, including fish, crabs, turtles, waterfowl, and some mammals, may benefit from predation on this new abundant prey item, although the consequences to predator populations remain unstudied. Despite marked similarities with *Dreissena polymorpha,* there are a number of differences regarding the effects of the two bivalves arising from differences in their biology and ambient dissimilarities between their respective environments. The extrapolation of results obtained for *Dreissena* species, abundant in the *L. fortunei* literature, can be misleading due to these differences.

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Introduction

The golden mussel establishes a variety of interactions with other animals after invasion. Over the last 15 years, coincidental with the widespread colonization of Japanese and South American aquatic ecosystems by *Limnoperna fortunei,* a wealth of scientific knowledge has built up describing these interactions. A substantial part of this knowledge has been produced in the area of the Río de la Plata basin, while the rest of the available information comes from other basins in South America. In Japan, investigations have centered on its population dynamics and particularly on biofouling control measures, while research on its relationships with native fauna has lagged behind. Conclusions on the effects of *L. fortunei* are, therefore, necessarily biased towards the characteristics of South American environments, typically dominated by large floodplain rivers with high organic-mater contents and sediment load, hosting a diverse community of fishes and low abundance of native filter-feeders (Boltovskoy and Correa 2015). While some of the effects will most probably differ in other environmental settings and continents (see Chapter "Ecology and Environmental Impact of *Limnoperna fortunei*: Introduction" in this volume), the literature reviewed here comes from three countries—Argentina, Uruguay, and Brazil, comprising most of the bivalve's invasive range outside Asia.

This chapter reviews the consequences of *L. fortunei* invasions for other animals, chiefly meiofaunal, benthic invertebrates (relationships with the zooplankton and with fishes are dealt with in other chapters of this volume). These interactions are comparatively well studied and give rise to a large number of effects that are transmitted to other compartments of aquatic ecosystems. The information available on epizoic macrofouling by *L. fortunei* and its consumption by nonfish animals is also reviewed. We examine similarities and differences with the zebra mussel, the better-studied, northern-hemisphere counterpart of *L. fortunei*. However, care has been taken to discriminate between knowledge based on actual observations and assumptions derived from the extrapolation of information reported for the zebra mussel. In view of the information compiled, future research steps are suggested.

Effects on Accompanying Benthic Invertebrates

Types of Studies

Several studies have assessed the effects of *L. fortunei* on benthic invertebrate communities. Studies dealing with the facilitation and, to a lesser extent, inhibition of fauna living on or amid valves of *L. fortunei* can be broadly classified in two types:

(1) Studies based on the comparison of natural or preexisting artificial underwater substrata colonized by mussels with substrata barren of them and (2) studies based on the evaluation of artificial hard substrata deliberately deployed for colonization by mussels and other invertebrates. Most surveys belong to the first type (Mansur et al. 2008; Fagondes de Freitas and Kapusta 2010; Karatayev et al. 2010; Sardiña et al. 2011; Burlakova et al. 2012; Kapusta and Fagondes de Freitas 2012; Spaccesi and Rodrigues Capitulo 2012). Only one study has attempted to compare benthic communities before and after invasion by *L. fortunei* (Darrigran et al. 1998), but its results are limited by the fact that pre-*L. fortunei* data were derived from a variety of sources, time periods, and areas whose direct comparability with post-*L. fortunei* information is uncertain.

In the second type of study, artificial hard substrata deployed for colonization were used by Sylvester et al. (2007) and Sardiña et al. (2008). Comparisons in surveys using artificial substrata are more straightforward because they contrast invertebrate communities on areas with and without *L. fortunei* established on the same type of substrate and right next to each other. In contrast, natural substrata normally involve comparison of communities on *L. fortunei* beds (hard substrata) with nearby soft-bottom communities on silt or sand. Another advantage is that for artificial substrata precise knowledge of the age of the community is available, which allows for analyses of time-related changes. A limitation of this method resides in the extrapolation of results to natural conditions, as assemblages developed on artificial substrata over limited periods may differ from natural ones, or correspond only to early successional stages. Sampling of mature assemblages evolved on natural substrata over long periods can yield more realistic information on the long-term impacts of the mussel.

Population and Community Effects

Available studies indicate that *L. fortunei* has a strong effect on benthic invertebrate communities. An exhaustive revision of the literature yielded at least 200 species reported to be directly affected by the presence of *L. fortunei* in invaded freshwater ecosystems across South America (Table 1). These organisms belong to a wide range of taxonomic groups including Mollusca (at least 51 taxa), Annelida (42), Insecta (38), Crustacea (32), Rotifera (7), Turbellaria (4), Collembola (3), Bryozoa (3), Chelicerata (2), Tardigrada (2), Nematoda, Hydrozoa, Kamptozoa, and Porifera (for the latter four no further taxonomic information was provided; Table 1). It should be noted that the number of taxa for which an effect has been quantitatively assessed and statistically established is considerably lower (see below). Despite this limitation, the bulk of evidence at hand very clearly indicates that *L. fortunei* is a significant ecosystem component having a marked influence on benthic invertebrate communities.

Although negative impacts on invertebrate populations have been reported, positive effects predominate in the literature likely reflecting their prevalence also in nature. A comparison of invertebrate communities associated to artificial substrata

Table 1 Summary of conclusions reporting effects of *L. fortunei* on benthic invertebrates

Phylum/subphylum	Class/order	Functional feeding group	Prevailing effect	Total records	Taxa most affected	Trait affected	Source
Cnidaria	Hydrozoa	P	+	2 (+)	Hydridae	A	9,10
Platyhelminthes	Turbellaria	P	+	6 (5+, 1±)		A B	7,9,10,11,18,21
Rotifera	Rotifera	CG P	+	7 (+)		A B	20,21
Nematoda	Nematoda	CG P	+	5 (4+, 1−)		A B	7,17,18,20,21
Tardigrada	Tardigrada	MP	+	3 (+)		A B	17,20,21
Mollusca	Bivalvia	CF	−	14 (12−, 2+)	*Corbicula fluminea,* Anodontites, Diplodon	A R	10,11,13,14
	Gastropoda	CG (Planorbidae), S	+/−	30 (17+, 12−, 1±)	Positive mainly Cochliopidae Negative mainly Planorbidae and Chilinidae	A B	5,7,9,10,11,13,14,18,20,21
Annelida	Aphanoneura	CF	+	1 (+)	Aelosoma	A	7
	Hirudinea	P	+	20 (16+, 3−, 1±)	Helobdela	A B R	7,9,10,11,17,20,21
	Oligochaeta	CG	+	39 (32+, 6−, 1±)	Naididae and Tubificidae	A B R	1,7,9,10,11,16,17,18,20,21
	Polychaeta	CG	+	2 (+)		A	9,10
Crustacea	Amphipoda	CG	+	7 (5+, 1−, 1±)	Hyalella	A B R	7,9,10,14,18,20
	Cladocera	CF CG S (Alona, Bosmina)	+	9 (6+, 3−)	Chyrodirae (Alona, Camptocercus), Bosminidae, Moinidae	A B	15,17,20,21
	Copepoda	CF	+	11 (+)	Cyclopoida and Harpacticoida	A B	17,18,20,21
	Decapoda	CG	+/−	4 (2+, 2−)	Aegla	A	6,11,12,21
	Isopoda	CG Sh	+	4 (3+, 1−)		A B R	7,17,18
	Ostracoda	CF	+	4 (3+, 1−)	Cyprididae	A B	17,18,20,21

Table 1 (continued)

Phylum/ subphylum	Class/order	Functional feeding group	Prevailing effect	Total records	Taxa most affected	Trait affected	Source
	Tanaidacea	CG	+	3 (+)	Sinelobus	A B R	7,18,20
Chelicerata	Arachnida	P (Hydrachnidiae), S Sh (Orbitidae)	+	4 (4+, 1±)	Hydrachnidiae and Orbatidae	A B	9,10,17,20,21
Entognatha	Collembola	CG	+	4 (3+, 1−)		A	9,10,20
Insecta	Coleoptera	S (larvae), Sh (adult)	+	2 (+)	Elmidae	A	9,10
	Diptera (Chironomidae)	CF CG (Chironominae), P (Tanypodinae)	+/−	16 (9+, 5 −, 2±)	Positive mainly Chironominae and Tanypodinae Negative mainly Chironominae	A B	7,9,10,11,18,20,21
	Diptera (others)	CG P S Sh	+	12 (8 +, 3 −, 1 ±)	Ceratopogonidae, Psychodidae, Tabanidae, Tipulidae	A	9,10,11,20
	Ephemeroptera	CG S Sh	+	11 (9+, 2−)		A	2,9,10,11,20,21
	Odonata	P	+	2 (+)	Coenagrionidae	A	9,10
	Trichoptera	CF CG P S Sh	+	9 (7+, 1−, 1±)		A B	2,9,10,11,18

Functional feeding group: *CF* collector-filterer, *CG* collector-gatherer, *MP* macrophyte piercer, *P* predator, *S* scraper, *Sh* shredder. Prevailing effect: + positive, − negative, ± neutral. Total records: number of publications reporting interaction events between *L. fortunei* and the specified taxon. Trait affected: *A* abundance, *B* biomass, *R* taxonomic richness. Sources: *1* Armendáriz et al. (2011), *2* Brugnoli et al. (2005), *3* Burlakova et al. (2012), *4* Carvalho Torgan et al. (2009), *5* César et al. (2012), *6* Darrigran (2002), *7* Darrigran et al. (1998), *8* Darrigran et al. (2000), *9* Fagondes de Freitas and Kapusta (2010), *10* Kapusta and Fagondes de Freitas (2012), *11* Karatayev et al. (2010), *12* Lopes et al. (2009), *13* Mansur et al. (2003), *14* Mansur et al. (2008), *15* Marçal and Callil (2008), *16* Ramseyer and Marchese (2009), *17* Sardiña et al. (2008), *18* Sardiña et al. (2011), *19* Scarabino (2004), *20* Spaccesi and Rodrigues Capitulo (2012), *21* Sylvester et al. (2007), *22* Uhde et al. (2012)

covered by *L. fortunei* and substrata barren of the mussel conducted by Sylvester et al. (2007) showed that the establishment of *L. fortunei* beds increases benthic invertebrate abundance and biomass. Temporal profiles of invertebrate occupation over colonized and barren substrata were sharply different with barren areas saturating earlier (Fig. 1). A positive correlation between mussel and accompanying invertebrate biomass (Fig. 1) suggests that mussel beds increase the carrying capacity of benthic habitats.

The establishment of *L. fortunei* also enhances invertebrate richness. A survey conducted in the Jacuí River (southeastern Brazil) observed a considerably higher taxonomic richness (23 vs. 15 families) associated with *L. fortunei* colonies than with barren sediments (Kapusta and Fagondes de Freitas 2012). Similar results were obtained by Karatayev et al. (2010) in a reservoir in central Argentina, where significantly more invertebrate species were found in samples from *L. fortunei* druses (clumps or aggregations of mussels around either a stone or other hard object, held together by byssal threads), than in samples from the surrounding sediment. 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 (Boltovskoy and Correa 2015). 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.

Local increases in species richness, however, do not necessarily translate into a higher overall diversity (as measured by numbers of species and their proportions). Armendáriz et al. (2011) found that the presence of *L. fortunei* increased oligochaete richness but not evenness. The study by Karatayev et al. (2010) found that while species' richness increased in *L. fortunei* druses, similarity between samples with *L. fortunei* was significantly higher than that between sediment samples, suggesting a reduction of β-diversity This result agrees with that of Sardiña et al. (2011), who concluded that the spread of *L. fortunei* can promote faunal homogenization across benthic communities even though overall invertebrate abundance and biomass are enhanced. The bottoms of South American rivers are dominated by soft muddy and sandy sediments offering limited habitat opportunities for epifaunal groups. These studies suggest that while *L. fortunei* valves create islands of complex hard substrata that facilitate benthic invertebrate communities, these islands are more similar between themselves than were the original communities (Fig. 2). Thus, while *L. fortunei* promotes benthic invertebrate communities locally, a likely concomitant effect is the homogenization of bottom faunas across habitats. A potentially important caveat to these results is the fact that druses and mussel beds host significantly higher diversities and abundances, which may yield inventories less biased by omissions of the rare species, and thus artificially enhance bed-to-bed or druse-to-druse similarities when compared with similarities between bare sediment samples.

An important factor regulating the magnitude of facilitation and inhibition by *L. fortunei* is the amount of hard substrate available for colonization by the mussel. Partially due to the lack of information on this trait, most assessments of *L. fortunei* densities are anecdotal and normally restricted to local density maxima (Darrigran 2002; Boltovskoy et al. 2006; but see Boltovskoy et al. 2009). The dominance of

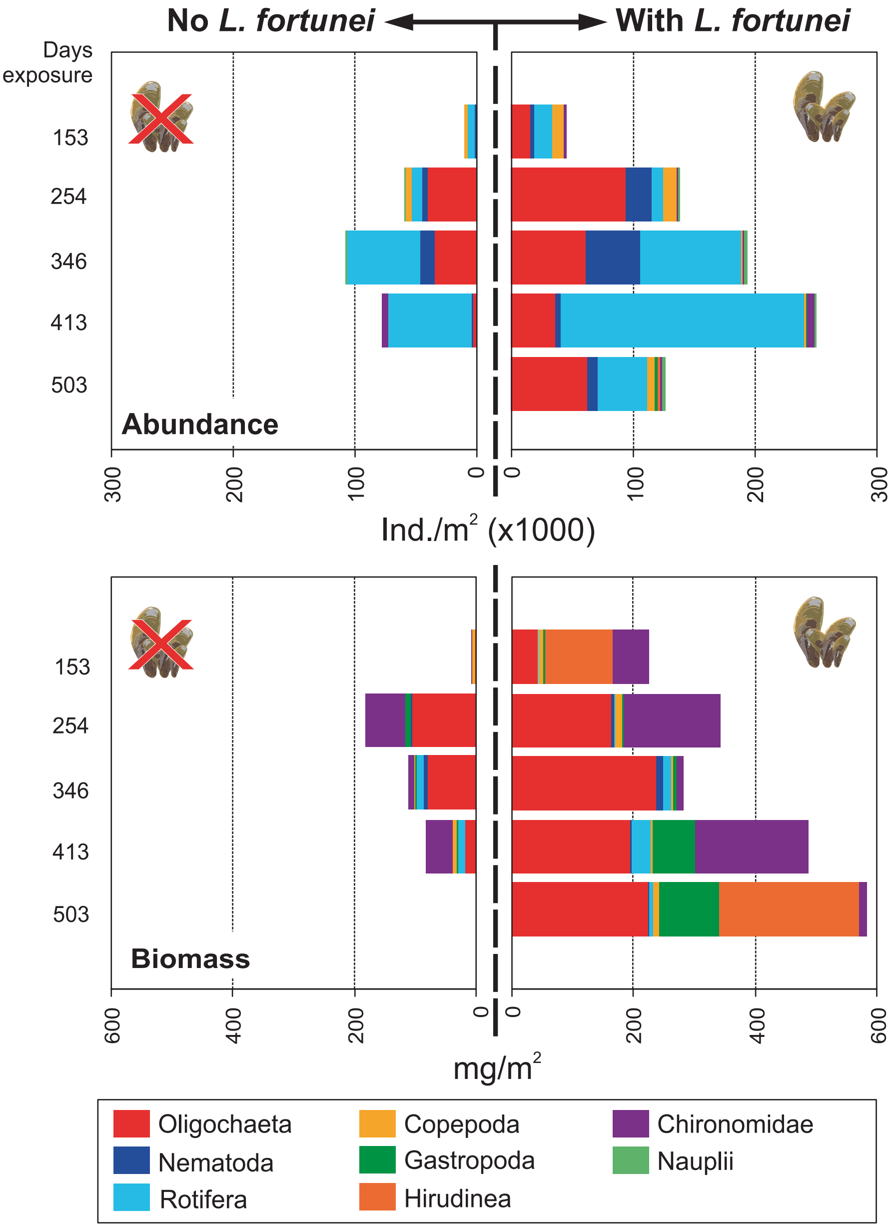

Fig. 1 Abundance and biomass of the dominant invertebrate groups in areas with and without *Limnoperna fortunei* mussels throughout a 503-day study period. Experimental substrata were deployed in the Lower Paraná River delta, South America, on 6 Nov. 2002 and successively retrieved on five occasions 153–503 days after the deployment. The accumulated overgrowth was calculated, and invertebrates were evaluated separately for substrate areas covered by *L. fortunei* and those barren of the mussel. The positive correlation between mussel and associated invertebrate biomass suggests that mussel beds increase the carrying capacity of benthic habitats. (Based on data from Sylvester et al. 2007)

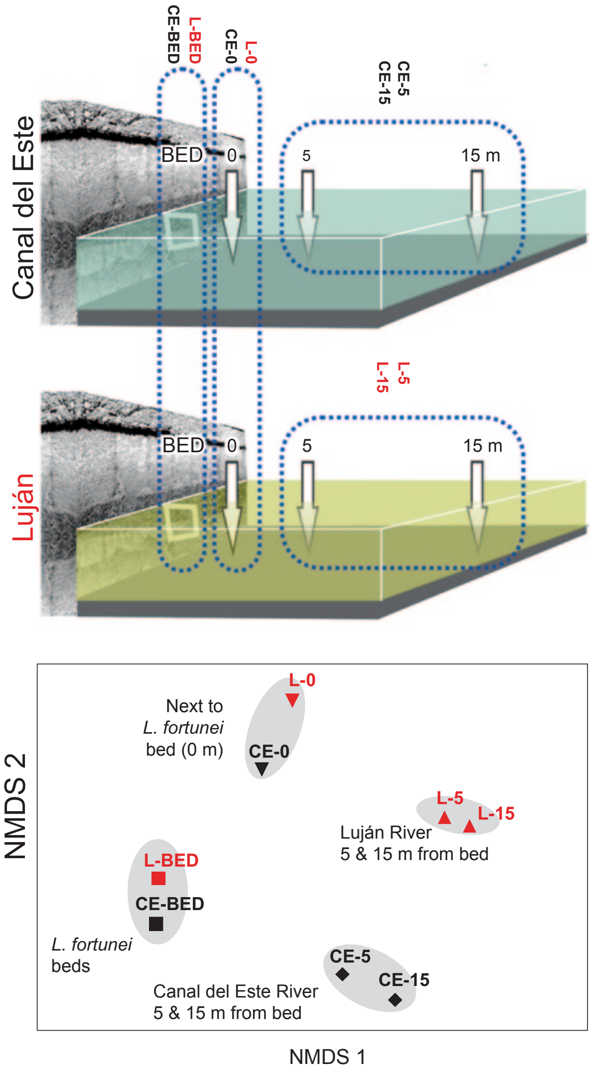

Fig. 2 Experimental setting (*upper panel*) and nonmetric multidimensional scaling (*NMDS*) analysis (*lower panel*) of a study evaluating the interaction between *Limnoperna fortunei* and benthic invertebrate communities at different spatial scales and under different environmental conditions: highly polluted Luján River (*L*) versus the less polluted Canal del Este River (*CE*; Lower Paraná River delta, South America). At each river, benthic samples were obtained from mussel beds (*L-BED* and *CE-BED*), and from sediments next to the mussel beds (0 m; *L-0* and *CE-0*), 5 m downstream (*L-5* and *CE-5*), and 15 m downstream (*L-15* and *CE-15*) from the mussel beds. Sampling location in the mussel beds is represented by the white sampling frame on the revetment. Invertebrate communities did not differ significantly between rivers in *L. fortunei* beds and at sites immediately downstream (0 m), but differed strongly at sites 5 and 15 m downstream from the mussel beds; *dotted frames* (*upper panel*) and *shaded areas* (*NMDS* analysis, *lower panel*) denote similar sample pairs. (Based on data from Sardiña et al. 2011)

silt and sandy bottoms unsuitable for the establishment of *L. fortunei* colonies likely curbs the species' ecological impacts over large areas in South America.

Facilitation of invertebrate communities by *L. fortunei* also occurs in the silt-bottom-habitats around mussel beds, thus extending the influence of *L. fortunei* beyond the range of colonizable substrata (Sardiña et al. 2011). This effect is presumably due to the downstream dispersal of feces and pseudofeces that settle out on the bottom.

Effects on benthic invertebrate communities also cascade along food webs into other compartments of aquatic ecosystems. For example, Sardiña et al. (2011) observed significantly higher abundance and biomass of predatory isopods and turbellarians in mussel beds than elsewhere, which they associated with an increase in prey availability. Benthivorous fish, birds, and mammals may also benefit from these increases. Thus, the spread of positive interactions to neighboring habitats and along food webs can counterbalance the facilitating effects of *L. fortunei* on invertebrates.

Data at hand are still too scarce and too fragmentary to judge whether the changes observed to date are definitive, or will invertebrate diversities and abundances change in the future, as noticed for the zebra mussel. Long-term invertebrate declines due to competition for food (Lozano et al. 2001) are unlikely in South American waterbodies rich in particulate organic carbon (POC) (Sylvester et al. 2005; see Chapter "Ecology and Environmental Impact of *Limnoperna fortunei*: Introduction" in this volume). On the other hand, consumption of *L. fortunei* by predators has likely increased due to a rise in fish populations resulting from the introduction of a new abundant food item, and their acclimation to the new prey after over two decades of coexistence (Boltovskoy et al. 2006; see Chapter "Trophic Relationships of *Limnoperna fortunei* with Adult Fishes" in this volume). Higher predation pressure might reduce *L. fortunei* abundances to a lower level compared to early invasion values. If *L. fortunei* populations decline after initially peaking, ecological effects might wane (see Chapter "*Limnoperna fortunei* Colonies: Structure, Distribution and Dynamics" in this volume; Haynes et al. 1999). However, these effects may wax globally as *L. fortunei* keeps invading new watersheds.

Taxonomic and Functional Patterns

It is not easy to find general trends in the response of different taxonomic groups to the presence of *L. fortunei,* but some overall patterns may be extracted. In general, deposit-feeders, collector-gatherers, and scrapers appear to benefit from the presence of *L. fortunei*. Some predators are also positively impacted, while some small-sized groups (e.g., small scrapers) can be negatively impacted (Sardiña et al. 2011; Burlakova et al. 2012). Although evidence is mixed, hirudineans appear to be more positively than negatively impacted. The same applies to oligochaetes. All reports for water mites and sessile taxa, such as hydroids, suggest positive effects, although these groups are still largely understudied and conclusions are preliminary. Most reports for mobile meiofaunal crustaceans (including amphipods, cladocerans, copepods, isopods, and tanaidaceans) and aquatic insects (including water beetles, mayflies, dragonflies, caddisflies, and springtails) indicate positive effects. Both positive and negative effects on dipterans can be found in the literature (Table 1). Negative impacts have been observed for a number of groups, among which bivalves and gastropods have been the most frequently cited (Darrigran et al. 1998; Darrigran et al. 2000; Mansur et al. 2003; Scarabino 2004). However, negative responses have only been reliably demonstrated for a few species. These include some gastropod molluscs (*Heleobia parchappei, Biomphalaria* sp., *Potamolithus* sp., and some *Planorbidae*), chironomids (*Cryptochironomus* sp., *Harnischia* sp., and *Procladius* sp.), the oligochaete *Branchiura sowerbyi,* the ostracod *Cyprideis hartmanni,* and a ceratopogonid midge, *Culicoides* sp. (Sylvester et al. 2007; Sardiña et al. 2008, 2011; Karatayev et al. 2010; Table 1).

Although the general trends of the effects of *L. fortunei* on benthic invertebrates are reasonably clear, literature on the subject is not without disagreements. A vivid example is provided by gastropods, whose densities were reported to have decreased after the colonization by *L. fortunei* (Darrigran et al. 1998), whereas other field (Karatayev et al. 2010; Sardiña et al. 2011) and experimental data (Sylvester et al. 2007) suggest otherwise. Similarly, the diversity and abundance of Oligochaeta were found to be significantly higher in *L. fortunei* beds as compared with nearby substrate without the mussel (Darrigran et al. 1998; Sylvester et al. 2007; Sardiña et al. 2008), but the opposite trend was recorded when studying *L. fortunei* druses in comparison with nearby soft sediments (Karatayev et al. 2010). Stable mussel beds on natural and artificial hard substrata accumulate large amounts of silt between the mussels (Sardiña et al. 2008), whereas druses are highly mobile and less efficient in retaining the particulate material derived from the golden mussel's feces and pseudofeces. Thus, the comparative scarcity of Oligochaeta—typically soft bottom, burrowing organisms—in druses is probably associated with the fact that loose, soft sediments are scarce in these aggregates.

While some of the disagreements encountered in the literature may be attributable to species–specific effects or differences in regional or seasonal settings (Radziejewska et al. 2009; Karatayev et al. 2010; Sardiña et al. 2011), it is also conceivable that the lower precision of abundance estimates associated with the less abundant taxa and methodological, sampling-related disparities play an important role. For example, of the ten taxa found in higher numbers in the sediments than in *L. fortunei* druses by Karatayev et al. (2010), five were recorded in only one or two out of ten samples. In the comparison of pre- and post-*L. fortunei* conditions by Darrigran et al. (1998), only gastropods, hirudineans, and isopods were included in the pre-*L. fortunei* dataset, while other organisms, such as oligochaetes, flatworms, nematodes, crustaceans, and chironomids, were considered only in post-*L. fortunei* samples. Hirudineans were found to be less abundant in *L. fortunei* beds than on bare hard substrate (Sardiña et al. 2008); yet another study found some leeches (*Gloiobdella michaelseni* and *Helobdella stagnalis*) to be dominant in golden mussel-associated communities when analyzed at the species level (Karatayev et al. 2010)

Mechanisms for Positive Effects

Positive effects on invertebrate fauna are commonly attributed to the enhancement of food supply, provision of substrate, and refugia in the new habitat created among the valves (Fig. 3 and 4). The increase in food for benthic organisms chiefly occurs through biodeposition of organic-matter-rich feces and pseudofeces. *L. fortunei* is a bottom filter-feeding organism that essentially removes matter and energy from the water column and transfers it to the benthos in the form of feces, pseudofeces, and its own body mass, a function generally referred to as benthic-pelagic coupling (Karatayev et al. 2007). The combination of high filtration rates and elevated densities can make this process very effective in some areas. After colonization by *L. fortunei,* in the Río de la Plata basin a large amount of particulate organic matter that was previously flushed into the ocean became redirected to the benthos (Sylvester et al. 2005). The deposition of organic matter over the riverbed is linked to an increase in biomass of heterotrophs. Among the mussels' valves, a food-rich environment is generated that is profited by several organisms in the guilds of the deposit feeders and scrappers (Sardiña et al. 2011; Fig. 4).

Besides this biotic effect, there is also a physical effect. The sole presence of mussel valves transforms a flat surface into a rough, three-dimensional structure which offers a larger surface area for sessile organisms, as well as refuge from predators and the physical stress of wave and current action (Fig. 3 and 4). In studies conducted in several Argentine waterbodies, the local abundances of at least three gastropod species, *Heleobia piscium, Gundlachia moricandi,* and *Stenophysa marmorata,* were found to have increased substantially due to the protection supplied by the mussels' valves (Darrigran et al. 1998; Karatayev et al. 2010). Even

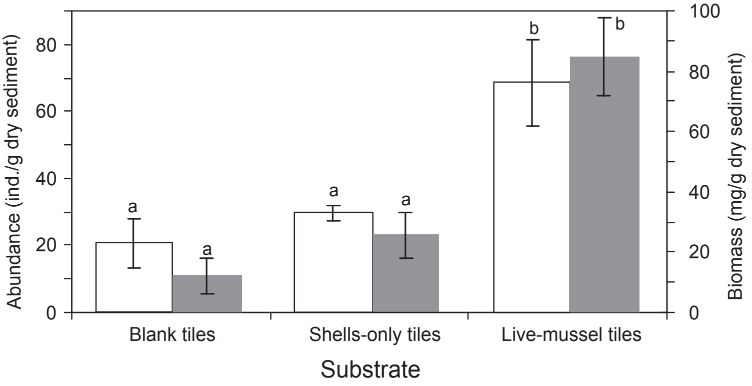

Fig. 3 Mean abundance and biomass (± SD) of invertebrates settled on artificial colonization tiles in three treatments: blank tiles (barren of *Limnoperna fortunei*), shells-only tiles (empty shells of *L. fortunei* glued together and to the upper and lateral surfaces of the tiles), and live-mussel tiles (living *L. fortunei* settled on the tiles). Different letters indicate significant differences among treatments. (Based on data from Sardiña et al. 2008)

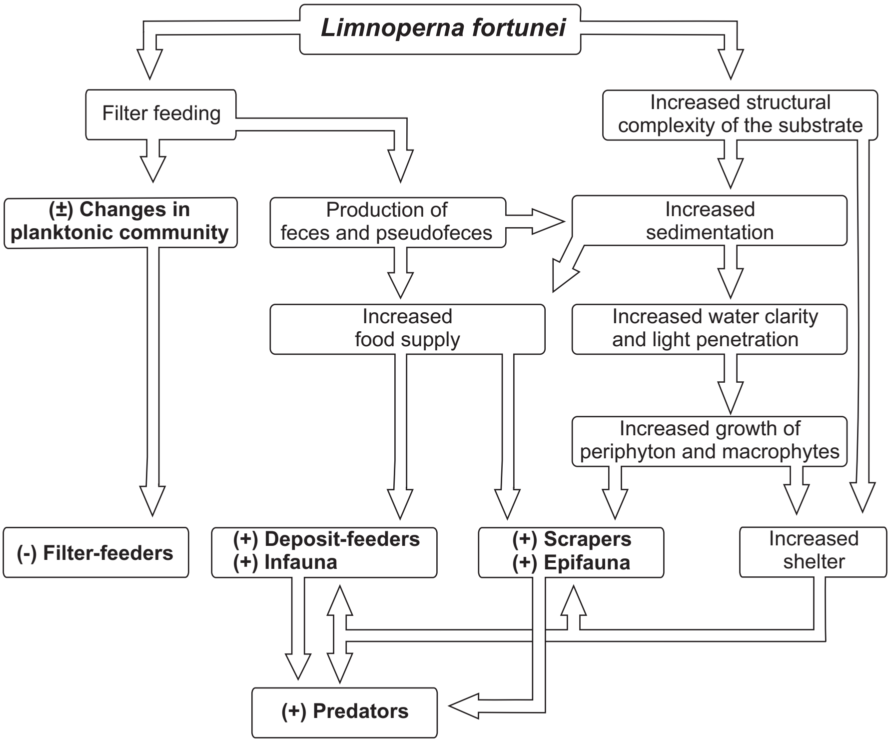

Fig. 4 Mechanisms for positive (+) and negative (−) effects of *Limnoperna fortunei* on benthic invertebrate functional feeding groups

some bivalves (*Sphaerium* sp.), a group commonly considered to be negatively impacted by *L. fortunei* (see below), have been found at higher abundances within *L. fortunei* beds (Karatayev et al. 2010). Sphaerid bivalves are tiny and mobile, and they might be able to find refuge from predators within mussel beds. While chiefly filter-feeders, sphaerids are also capable of deposit feeding and it is conceivable that some species find a suitable habitat among the valves of *L. fortunei* due to both abundant food and protection.

It is difficult to establish through descriptive studies whether physical or biotic factors play a greater role in the promotion of bottom invertebrates. Moreover, the two effects are not independent, as valve complexity also increases sedimentation of organic particles through the buffering of current and wave action (Sylvester et al. 2007; Sardiña et al. 2008; Fig. 4). In an attempt to distinguish between the two, Sardiña et al. (2008) deployed bare hard substrates (tiles), tiles with empty mussel shells glued to them, and tiles colonized by live mussels. Upon retrieval, they found that both live mussels and empty shells had promoted significantly higher invertebrate densities than blank tiles. While empty shells actually promoted higher sedimentation rates (in the absence of the cleansing currents generated by the mussels' siphons), live mussels supported a greater invertebrate biomass due to a richer organic matter content of their deposits (Fig. 3). The authors concluded that invertebrate communities in the Paraná River are enhanced by the presence of *L. fortunei* beds, and this is due more to the biotic effect of sediment enrichment than to increased substrate complexity.

Mechanisms for Negative Effects

Mechanisms proposed for population declines observed in South American aquatic habitats following the invasion of *L. fortunei* include substrate eutrophication (chironomids), biomagnification of contaminants (ostracods and nematodes), oxygen depletion (oligochaetes), and competition (gastropods) (Sylvester et al. 2007; Karatayev et al. 2010; Sardiña et al. 2011). Plankton depletion, direct predation of eggs and gameta, and competition for space have also been proposed as potential mechanisms underlying adverse effects on invertebrates (Scarabino 2004; Mansur et al. 2008). However, in most if not all cases, the mechanisms underlying negative effects were untested but assumed based on the extrapolation from the literature on North American *Dreissena* spp. invasions.

Available evidence suggests that both positive and negative effects of *L. fortunei* are habitat dependent. For example, oxygen depletion may be associated with *L. fortunei* beds as a result of the decomposition of feces and pseudofeces (Karatayev et al. 2010). While this effect is possible in deep, poorly mixed zones of lakes and ponds, it is unlikely in well-mixed rivers. Similarly, in sediments of stagnant habitats, burrowing species may be more exposed to anoxia than epifaunal species. As discussed below, indirect effects on benthic communities may also be strongly influenced by other environmental factors and ecosystem characteristics, such as the load of POC and the fauna species complement (see Chapter “Parallels and contrasts between *Limnoperna fortunei* and species of *Dreissena*” in this volume). The effects of *L. fortunei* on invertebrate fauna are also species dependent, as physiological tolerances may increase or decrease vulnerability to these effects.

Effects on Other Benthic Animals

Macrofouling

The most conspicuous and frequently cited negative impact by *L. fortunei* is epifaunal macrofouling, particularly on bivalves and gastropods. An extreme case illustrative of such impact was the observation of a crab, *Aegla platensis,* weighing barely one tenth the weight of the colony of *L. fortunei* attached to its back (Lopes et al. 2009). Specimens of the gastropod *Pomacea canaliculata,* and many bivalve species (such as *Anodontites trapesialis, A. trapezeus, Diplodon deceptus, D. koseritzi,* and *Leila blainvilliana*) have also been found fouled in aquatic habitats in

Argentina and Brazil (Darrigran et al. 2000; Mansur et al. 2003; Mansur et al. 2008; Karatayev et al. 2010). *L. fortunei* can also form colonies on top of other invasive bivalves such as the Asian clam *Corbicula fluminea* (Darrigran et al. 2000; Mansur et al. 2003). Shu and Wu (2005) reported that 35 % of the bivalves (*Arconaia lanceolata, Larnprotula leai, Larnprotula caveata,* and *Larnprotula rochechouarti*) of Lake Poyang (China) are fouled by *L. fortunei*. An interesting case is the macrofouling of *Trichodactylus borellianus*. This native South American crab can be subjected to severe macrofouling by *L. fortunei,* but mature specimens have the ability to feed on the mussel (Rojas Molina and Williner 2013). The net effect of this interaction remains a question. Unfortunately, the same uncertainties discussed above for benthic meiofauna apply to much of the information on macrofaunal fouling by *L. fortunei*. While some of the cases reported are very dramatic, they constitute isolated observations and their effects on the population level remain unclear.

Predation by Benthic Animals

The colonization of South American waterbodies by *L. fortunei* has not only offered shelter and food resources to benthic animals, but the mussel itself has become an attractive food item for a variety of resident groups. Besides fishes, which are well known to prey on larval and adult forms (see Chapters "Trophic Relationships of *Limnoperna fortunei* with Larval Fishes" and "Trophic Relationships of *Limnoperna fortunei* with Adult Fishes" in this volume), several invertebrates and vertebrates can prey on settled *L. fortunei* mussels. For example, in laboratory trials the native crabs *Zilchiopsis collastinensis* and *T. borellianus* have been observed to consume several sizes of mussels (Torres et al. 2012; Carvalho et al. 2013). While *L. fortunei* was not a preferred prey item for *T. borellianus,* its consumption by crabs ranging ~4–11 cm indicates that the mussel might constitute a new, potentially important, alternative prey item in times of shortage of other food (Carvalho et al. 2013).

Turtles also benefit from the new prey. The Brazilian slider, *Trachemys dorbigni,* feeds on *L. fortunei* mussels attached to dock pilings and other structures (Bujes et al. 2007). Even though a study by Hahn et al. (2014) did not find *L. fortunei* in the stomachs of 73 individuals of this species along the shores of São Gonçalo Canal and Mirim Lake in 2002–2003, this result should not be taken as indicative of a lack of consumption capabilities because this area was not colonized by the mussel until 2005 (Burns et al. 2006; Capítoli et al. 2008; Colling et al. 2012). The presence of shell debris in Brazilian slider feces confirms consumption of *L. fortunei* by this turtle (Bujes et al. 2007).

Other animals have been suggested as potential predators of golden mussels, including the crab-eating raccoon *Procyon cancrivorus,* the giant otter *Pteronura brasiliensis,* and the neotropical river otter *Lontra longicaudis*. Waterfowl such as coots, cormorants, grebes, gulls, ducks, and swans are also likely to consume this new food resource, although this assumption is largely based on the extrapolation of observations made on waterfowl feeding on zebra mussels in North America (Sylvester et al. 2007). It has been suggested that small invertebrates (crustaceans such as predatory isopods, decapods, and copepods, as well as other small invertebrates including leeches, gastropods, and insect larvae) may consume early settled stages of *L. fortunei* causing strong impacts on its populations (Sylvester et al. 2007; Nakano et al. 2010), although this type of predation has never been verified nor quantified.

Similarities and Differences with *Dreissena* spp.

The effects of *L. fortunei* on associated fauna are remarkably similar to those of *Dreissena* species, in particular *D. polymorpha*. Both are strong ecosystem engineers that increase the structural complexity of the substrate and provide shelter and food for other benthic invertebrates. Although negative impacts have been described for some species and habitats, both mussels have predominantly positive influences on their accompanying fauna. The ultimate impact of these changes has been associated with increased benthic invertebrate density, biomass, and taxonomic richness, and with decreased community diversity (Ward and Ricciardi 2007; Karatayev et al. 2010; Sardiña et al. 2011). Like *Dreissena* spp., *L. fortunei* positively affects predators and scrapers, particularly leeches (*Hirudinea*), flatworms (*Turbellaria*), and mayflies (*Ephemeroptera*), and negatively affects other bivalves (Ward and Ricciardi 2007). Also similar to *Dreissena* spp., *L. fortunei* exerts a mixture of positive and negative effects on gastropods. Unlike the zebra mussel, however, which has been linked to declines of large-bodied snails, particularly in the family Pleuroceridae (Ward and Ricciardi 2007), the golden mussel has been associated with a decline of small-bodied snails such as *Potamolithus* sp. and Planorbids (Sylvester et al. 2007; Sardiña et al. 2011). Competitive exclusion by larger snails within *L. fortunei* beds, and size-limiting interstitial spaces created amongst *D. polymorpha* shells have been proposed as the possible ecological venues in each case (Ricciardi et al. 1997; Sardiña et al. 2011).

Probably the most important difference between *L. fortunei* and *Dreissena* spp. derives from the fact that *Dreissena* spp. (in particular *Dreissena rostriformis bugensis*) are able to colonize soft sediments, while *L. fortunei* is rarely found on soft substrata (see Chapter "Parallels and Contrasts Between *Limnoperna fortunei* and Species of *Dreissena*" in this volume). Moreover, the strength and direction of the interactions between *Dreissena* spp. and other macroinvertebrates is correlated with sediment particle size. For example, infaunal (burrowing) organisms such as nematodes are positively effected in the presence of dreissenid mussels on hard substrata but negatively so on fine sediments (Ward and Ricciardi 2007). In contrast, the golden mussel favors nematodes in almost every case (Table 1). Similarly, strong positive interactions prevail between *L. fortunei* and epifaunal organisms such as gammarid amphipods and isopod crustaceans, whereas the positive effects of *Dreissena* spp. on these groups decline with decreasing particle size (Ward and Ricciardi 2007).

Another noteworthy difference between *L. fortunei* and *Dreissena* spp. relates to their effects on collector-gatherer organisms. The presence of *L. fortunei* is almost invariably associated with enhanced densities and biomass of deposit-feeders, mainly oligochaetes (82 % of the interactions reported are positive; Table 1). Conversely, a meta-analysis of 47 study sites conducted by Ward and Ricciardi (2007) found that the overall effect of *Dreissena* spp. on these organisms was neutral. It should be borne in mind, however, that this represents an average trend, and site-specific records for strong positive interactions abound in the literature on *Dreissena* spp. (Botts et al. 1996; Ricciardi et al. 1997; Bially and MacIsaac 2000).

Other differences between these mussels may arise from ambient differences between the ranges invaded by each species. There is, for instance, a sharp difference between the faunal composition of South American and North American waterbodies. While the North American lakes hosting a large proportion of *Dreissena* spp. populations are dominated by pelagic fish, most of the South American populations of *L. fortunei* occur in rivers hosting a wealth of benthivorous/detritivorous fish species that can benefit from substrate enrichment by the mussel. As a result, the benthic-pelagic coupling enhanced by the mussel is likely more significant in South American rivers colonized by *L. fortunei* than in the invasive range of the dreissenids (but see Karatayev et al. 2007). Another important environmental difference between both continents is the POC load of lotic habitats. In North American rivers, depletion by *Dreissena* spp. of the relatively scant bioseston can indirectly depress macroinvertebrates in sites away from mussel beds (Strayer and Smith 2001). In contrast, bioseston is probably not limiting in South American POC-rich rivers and this depression is less likely.

One can envision that marked differences such as long-term declines of mussel populations due to competition for food, as those documented for *Dreissena* invasions (Lozano et al. 2001; Ratti and Barton 2003) are unlikely in South America (Boltovskoy and Correa 2015). There still is, however, a need for long-term studies on the effects of *L. fortunei* on benthic communities in order to judge whether the changes described above are transient or permanent. In general, and despite rapid progress made in the last few years, particularly since the invasion of South America, scientific knowledge on *L. fortunei* runs far behind that of *Dreissena* spp.

Future Research Lines and Concluding Remarks

While notable progress has been made in the study of the relationships between *L. fortunei* and other animals, there is still a long way to go before we can understand the nature and magnitude of these relationships, and the ecosystem changes brought about by this invasion. Our major gaps in scientific information include the following:

Effects on Microfauna and Smaller Organisms Most of the studies on fauna associated with *L. fortunei* are restricted to meiofauna and macroinvertebrates, whereas studies on smaller organisms are almost completely lacking. Carvalho Torgan et al.

(2009) have documented at least 18 diatom species living on the valves of *L. fortunei*. It is likely that small animals are also affected and the onset of *L. fortunei* is having profound yet unexplored effects on benthic microfaunal and microbial communities.

Indirect and Long-Term Effects While most studies have looked into local, direct effects, ecosystem responses may vary at broader time and spatial scales as a consequence of indirect and feedback effects. For example, increases in water clarity and benthophagous fishes promoted by invasive mussels can subsequently impact benthic invertebrate populations (Ward and Ricciardi 2007; Fig. 4). These impacts may differ between mussel beds and distant habitats (Strayer and Smith 2001).

Synergistic and Antagonistic Effects In addition to golden mussels, in South American water bodies, there are other native and nonnative ecosystem engineers, such as rushes. The invasive macrophyte *Hydrilla verticillata* has been reported to host more *L. fortunei* on its surface than other (native) macrophytes (Michelan et al. 2014). The comparison of faunal facilitation by *L. fortunei* and other ecosystem engineers, as well as potential synergistic effects between them, remain largely unexplored.

Interactions Between Faunal Facilitation and Pollution Contrasts between abundances of *L. fortunei*-associated invertebrates at polluted and comparatively clean sites indicated that facilitation is the highest at low levels of environmental pollution in the Paraná River delta (Sardiña et al. 2011). While based on only two sites, this result suggests that some of the benefits produced to the benthos by *L. fortunei,* and from there to other compartments of the food web, may be offset by environmental pollution. This interaction and the potential rerouting and bio-magnification of contaminants through bottom food webs by *L. fortunei* are important research priorities because introduction gateways and some of the most densely invaded areas are estuaries and ports heavily impacted by human activities.

These information gaps are mere examples of potential future research. Actual blanks in the available information span a wide range of topics, many of which are key for understanding changes brought about by the invasion of *L. fortunei.*

We would like to conclude this chapter summarizing some of the problems that, in our view, have significantly slowed down the buildup of knowledge in this field of study. In the first place, extrapolation of conclusions from the much better studied zebra and quagga mussels is widespread in the literature on *L. fortunei,* particularly in the area of its impacts on native organisms. Some of the effects on other animals attributed to *L. fortunei* and most of the mechanisms underlying these effects have been drawn from literature on *D. polymorpha*; yet we have seen that species-specific and environment-specific differences may result in very different outcomes. While reviews highlighting likely impacts and native taxonomic groups potentially at risk that are based on the observations of *Dreissena* spp. were important during the early invasional stages of *L. fortunei* (e.g., Scarabino 2004; Brugnoli et al. 2005), current research needs to move forward with firsthand experimental work. The repetition time and again of untested conclusions can be both misleading and discouraging of research over matters for which we have developed a false perception of understanding.

In the second place, the dissemination of anecdotal, uninformative and nonquantitative information has become a problem in the literature on interactions between *L. fortunei* and benthic invertebrates. Circumstantial reports of macrofouling by the mussel or its incorporation in the diet of native species have shed little light on its effects on native ecosystems. These interactions need to be quantified at the individual and population levels.

In the third place, quantitative assessments need adequate statistical support. Out of about 280 cases reviewed in the literature, less than 45 (15 %) based their conclusions on statistical evidence or overwhelming differences (an order of magnitude or higher).

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