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[REVIEW]

Ecosystem Engineering Impact of *Limnoperna fortunei* in South America

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***Limnoperna fortunei,* or golden mussel, *has* invaded aquatic ecosystems in the Americas following it introduction from Southeast Asia. It is not only an aggressive invasive species, it is also a very effective ecosystem engineer, altering both ecosystem structure and function, and causes great ecological and economic impacts. This paper describes its impact as an ecosystem engineer (on benthic communities and the water column). A review of the existing scientific literature is presented, and the impact and the mechanisms by which the golden mussel modifies, maintains, and creates new environmental conditions in the invaded South American inland freshwater environments are analyzed. Understanding the ecosystem engineering roles of *L. fortunei* is important for its management and/or control in the invaded areas, and in cases of future invasions.**

Key words: golden mussel, Neotropical region, ecosystem engineering

INTRODUCTION

The effects of global change and trade globalization on the biosphere have spurred an increase in bioinvasions and their subsequent impacts on ecosystems (Lockwood et al., 2007), which entail the structural transformation of natural environments. The geographic scale, frequency, and number of species involved in such changes have increased enormously over the past few decades as a consequence of the expansion of worldwide commerce and fluvial transport of goods (IUCN, 2000).

Presently, introduction of foreign species is the main cause of biodiversity loss, followed by habitat destruction (IUCN, 2000). This negative impact on the environment affects three essential components of biodiversity: landscape, species, and genetic structure (Carlton, 1996). Continental invading bivalves are similarly important due to their impacts on man-made structures and on natural systems.

The invasion by *Limnoperna fortunei* (Dunker, 1857), the golden mussel (Bivalvia: Mytilidae) is one exemplary model of bioinvasion in the Neotropical region. This species is an epifaunal freshwater mussel, filter-feeding, gregarious, with planktonic larvae, short life span, rapid growth, early sexual maturity, and high fecundity. It is native to rivers and creeks in China and Southeast Asia. It invaded Hong Kong in 1965 (Morton, 1973), Japan (Kimura, 1994) and Taiwan (Ricciardi, 1998) in the 1990s. It was first recorded in America in 1991 along the Argentine Bagliardi Beach, on the southern margin of the Río de la Plata estuary (35°55′S-57°49′W) (Pastorino et al., 1993). Darrigran and Pastorino (1995) suggested that the non-intentional introduction of this species into the area was via ballast water of ocean vessels.

Since the invasion, it has dispersed upstream within in the Plata and Guaíba basins (Mansur et al., 2003) at a rate of 240 km yr^{-1} (Darrigran et al., 2007). Human activity and the hydrosedimentological and chemical conditions of the environment necessitated assessment of the potential spread of *L. fortunei* in the area (Belz, 2009).

Several non-native freshwater mollusk species have been introduced to South America (Darrigran and Pastorino, 2004). Some of these are considered invasive species, e.g. *Corbicula fluminea* (Müller, 1774) (Darrigran, 2002). However, of these *L. fortunei* is the most aggressive freshwater invader in South America. It is the only freshwater bivalve in this region with a planktonic larval stage that attaches in high densities to hard substrates (Darrigran, 2002). Similar to *Dreissena polymorpha* (Pallas, 1771) (Karatayev et al., 2002), its life history enhances its ability as an invader and allows it to become enormously abundant when introduced into a new water body. This invasive species also impacts on man-made structures, both in South America (Darrigran and Damborenea, 2005, 2006; Darrigran, 2010) and Japan (Ohkawa et al., 1999; Matsui et al., 2001; Nagaya et al., 2001; Goto et al., 2001; Matsui et al., 2002).

Ecosystem engineers are organisms that change the abiotic environment by physically altering its structure. As a consequence, they often – but not invariably – have effects on other members of the biota and their interactions, and consequently on overall ecosystem processes. The ecosystem engineering concept connects a number of important ecological and evolutionary concepts, and is particularly rel-

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evant to environmental management (Gutiérrez and Jones, 2008).

Based on such concepts, and on the fact that the invaders that will have the largest impacts are those that directly modify ecosystems, and thus have cascading effects on the resident biota (Crooks, 2002), this article describes *L. fortunei* as an important ecosystem engineer in freshwater systems. Although little is known about its biology and interactions, it is estimated that – like *D. polymorpha* in the northern Hemisphere (Karatayev et al., 2007) – this species aggregates into beds, thus modifying the nature and complexity of the substrate in a way similar to its related marine taxa (Borthagaray and Carranza, 2007). Upon invading the Plata basin, the golden mussel had an impact on different communities, altering the composition of the benthic fauna (Darrigran et al., 1998; Sylvester et al., 2007; Sardiña et al., 2008), predator diets (Penchaszadeh et al., 2000; García and Protogino, 2005; Sylvester et al., 2007), and physical conditions of the soil and water column (Sylvester et al., 2005, 2006).

ECOLOGICAL IMPACTS

To accurately assess the ability of the golden mussel as an ecosystem engineer, we should consider both spatial and temporal variables (Fig. 1). Local effects (e.g., on the benthic community and on predatory fish) should first be assessed and then extrapolated to system-wide effects (Karatayev et al., 2007). Likewise, the impact on the ecosystem derived from the filtering rate of golden mussel populations should also be considered (Sylvester et al., 2006).

The system-wide effects depend not only on the characteristics of the water bodies (invasibility), but also of the invasiveness of the golden mussel (Hicks, 2004.). The impact produced at the beginning of the invasion will be modified over time. In the case of the golden mussel, the impact does not seem to be capable of attaining temporal stability. The highest density is recorded during the early invasion period; it then fluctuates prior to reaching stability at lower density (Mansur et al., 2003). This process takes about ten years (Darrigran et al., 2003).

Impact of *L. fortunei* on benthic communities

Dense *L. fortunei* populations have a major impact on the structure of macroinvertebrate communities (Fig. 1). Studies carried out in different climate regions and on different substrates (Darrigran et al., 1998; Sylvester et al., 2007; Sardiña et al., 2008; Marçal and Callil, 2008) have shown that habitat differences exert less influence on community structure than the presence of dense populations of golden mussel.

The great majority of mussels are important ecosystem engineers in benthic systems because they aggregate into beds, thus modifying the nature and complexity of the substrate (Borthagaray and Carranza, 2007). Communities of benthic invertebrates recorded in the areas invaded by *L. fortunei* (Darrigran et al., 1998) are therefore similar to those developed on experimental frameworks (Sylvester et al., 2007). The results of these studies suggest that the changes occurring in these communities are characterized by an increment in macroinvertebrate richness species – dominated by Oligochaeta, Nematoda and Hirudinea – with the development of mussel beds. Higher densities of live mussels show an increase in the density of some associated taxa– Oligochaeta, for instance, especially benefit from the feces and pseudofeces produced by the *L. fortunei* (Sardiña et al., 2008), and Hirudinea species benefit from the greater food supply (Darrigran et al., 1998).

These studies agree in pointing out that some of the species associated with *L. fortunei* are more abundant (e.g. *Heleobia piscium*, *Nais variabilis, Helobdela adiastola* and *H. hialina*), and also that there is an increase of some taxa at the expense of others (Darrigran et al., 1998; Sylvester et al., 2007).

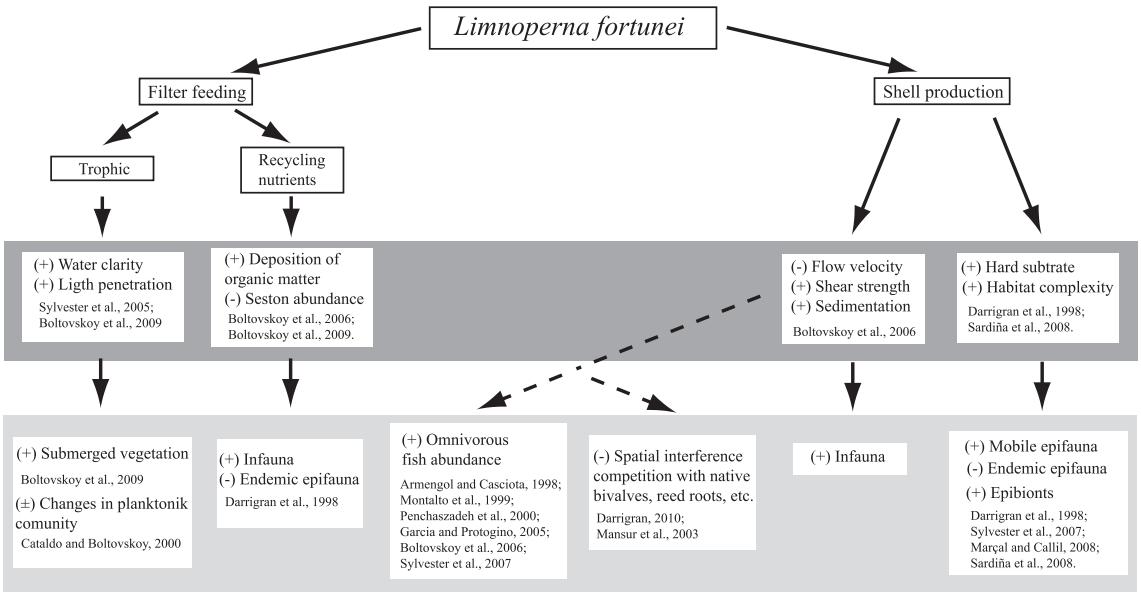


Fig. 1. General pathways of engineering effects by the golden mussel. Positive (+) and negative (–) effects are indicated. Direct (solid arrows) and indirect (dashed arrow) impacts of *Limnoperna fortunei* on invaded aquatic ecosystems. Dark gray: Effects on abiotic variables; light gray: Effects on biotic variables (modified from Sousa et al., 2009).

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The golden mussel shows a suite of physical and biological attributes that influence the structure of macroinvertebrate assemblages. It deposits sediments as agglutinated feces and pseudofeces. These biodeposits provide a food source for other invertebrates, and this organic enrichment of substrata alters the local distribution and abundance of benthic faunas. Mollusk shells are abundant, persistent, and ubiquitous physical structures in aquatic habitats (Gutiérrez et al., 2003). These authors state that colonization of a shelled habitat depends on individual shell traits and the spatial arrangement of shells, which in turn are determinant of the access of organisms to resources, and of the degree to which biotic or abiotic forces are modulated.

The invasion of South American basins by *L. fortunei* increases the colonizable substrate with interstitial spaces as well as the amount of organic matter in the sediments. Sardiña et al. (2008) carried out an experimental study in order to examine the influence of this newly created habitat on benthic invertebrate communities. They showed that the lowest abundance and diversity of benthic invertebrates are recorded in substrates lacking golden mussels. Abundance and diversity increase on surfaces with empty valves. On these surfaces, the macroinvertebrate taxa have the highest diversity and abundance. Oligochaetes are an exception to this rule, as they are significantly more abundant on substrates with live mussels (Sardiña et al., 2008), where oxygen levels are probably low within the interstitial spaces of the mussel shells due to bacterial decomposition of the accumulated biodeposits. This favors the presence of oligochaete populations. High biomass values of benthic invertebrates – showing no significant difference – are recorded on both surfaces, *i.e*., those with dead and live mussels. This indicates that physical attributes of the environment, as much as biological attributes of the golden mussel, influence the structure, diversity, and abundance of the benthic community. Spatially complex surfaces and lower organic matter content of the sediments associated with the filter-feeding mussels tend to support richer faunal communities as they provide a higher number of microhabitats and niches. Clumped mussels have abundant interstitial spaces that serve as disturbance and predation refugia for small organisms (Darrigran, 2002).

It should be mentioned that dense coverage of hard surfaces by mussels may reduce or displace native species (Fig. 1) (Darrigran and Damborenea, 2005). Darrigran et al. (1998) studied in the field the alteration in abundance and species richness of communities of benthic invertebrates, and concluded that some endemic species that were abundant before the invasion (e.g., Gastropoda, such as *Gundlachia concentrica* and *Chilina fluminea*) decreased in numbers over time. The abundance of other species (the gastropod *Heleobia piscium* and annelid species) increased in direct proportion to the densities of *L. fortunei.*

It is expected that species of benthic macroinvertebrates with similar habits may associate with mussels, regardless of regional climate. Invasion by *L. fortunei* may result in elimination of regional differences in epifaunal species (Darrigran, 2002). If we consider human activity on biotas, the result would be a more homogenized biosphere with lower diversity at regional and global scales (McKinney and Lockwood, 1999; Olden et al., 2004). Most species are declining as a result of human activity ('losers'), while a much smaller group is becoming more numerous ("winners") (Lockwood et al., 2007). Homogenization is defined as an increase in biota similarities over time (Rahel, 2002).

Biotic homogenization often exhibits scale dependence (Rooney et al., 2007). Studies on communities of benthic macroinvertebrates associated with *L. fortunei* populations evidence "loser" and "winner" species at a local scale (Darrigran et al., 1998) in a way similar to what occurs in communities associated with *D. polymorpha* in the northern hemisphere (Ward and Ricciardi, 2007); an increase in the number of ecologically similar species in the invaded environment is noticed. However, total species richness (ecologically similar and non-similar species) tended to decline in large water bodies (regional scale).

The impact of *L. fortunei* on fish communities

Dense populations of *Limnoperna fortunei* in the Plata basin (Orensanz et al., 2002; Boltovskoy et al., 2006) introduce a new element in the diet of some fish. According to García and Montalto (2006), the first record of predation on this species is by *Micropogonias furnieri* (López Armengol and Casciotta, 1998). After this initial record, several other species of fish were reported to be consumers of the golden mussel (Table 1). Likewise, Penchaszadeh et al. (2000) – in a study on the diet changes occurring in adult specimens of *Leporinus obtusidens* – corroborated the selective predation of this species on adult specimens of the golden mussel. Paolucci et al. (2009) experimentally studied the feeding selectivity of larvae of *Prochilodus lineatus* Valenciennes, 1836 in relation to veligers of *L. fortunei*. Veligers are preferred by the early developmental stages of the fish, as the slower swimming of veligers makes them easier to capture than are planktonic crustaceans. However, as fish larvae grow, veligers become too small a prey for their energetic needs, and they switch to larger elements, such as cladocerans and copepods. This study suggests that this new and abundant food resource may have an important impact on the survival and growth of *P. lineatus*.

Generally, species of omnivorous fish studied (Table 1) have altered their diets to become malacophagous (García and Montalto, 2006). This is evident in the feeding habits of both adult (Penchaszadeh et al., 2000) and larval (Paolucci et al., 2007) stages of fish development.

This situation suggests that there may be environmental changes in two directions: a) one relative to population densities of the prey that was part of the diet of fish prior to the golden mussel invasion (García and Montalto, 2006), and b) the other related to fish populations that, in a relatively a short period of time, came to coexist in the environment with a density and availability of over-abundant food that led them to modify their feeding habits, using the energy they previously spent in finding food, to grow and reproduce instead. Currently, the adults of some of the species that eat invasive bivalves are considered the most abundant in commercial and sport fishing (García and Montalto, 2006). In the Paraná River, colonization by *L. fortunei* has been associated with very significant increases in commercial fish catches (Boltovskoy et al., 2006). *Limnoperna fortunei* is thus a new and abundant food resource, having an important impact on the populations of all predatory species that

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Table 1. Fish species that predate on populations of *Limnoperna fortunei* in environments of the Plata basin. 1, Boltovskoy and Cataldo, 1999; 2, Ferriz et al., 2000; 3, García and Protogino, 2005; 4, García and Montalto, 2006; 5, López Armengol and Casciotta, 1998; 6, Montalto et al., 1999; 7, Montalto, 2000; 8, Penchaszadeh et al., 2000.

SPECIES	DIET	REFERENCE
Leporinus obtusidens (Valenciennes, 1847)	Omnivorous (seeds, other plants, invertebrates and small fish)	1; 2; 3; 6; 8
Schizodon borellii (Boulenger, 1900)	It feeds on different plants	5
Piaractus mesopotamicus (Holmberg, 1887)	Omnivorous (crustaceans, insects and plants)	7
Pterodoras granulosus (Valenciennes, 1833)	Omnivorous (crustaceans , mollusks, otros invertebrates, fruit and plants)	1; 3; 6
Rhinodoras dorbigny (Kröyer, 1855)	Omnivorous	6
Oxydoras kneri (Bleeker, 1862)	Omnivorous	4
Pimelodus maculatus (Lacépède, 1803)	Omnivorous (small insects and crustaceans, plant and fish remains)	6
Pimelodus albicans (Valenciennes, 1840)	Omnivorous	1; 6
Pimelodus argenteus (Perugia, 1891)	Omnivorous (small insects, and plant and fish remains)	4; 7
Brochiloricaria chauliodon (Isbrücker, 1978)	Iliophagous (substrate algae)	3
Hypostomus laplatae (Eigenmann, 1907)	Iliophagous	6
Paraloricaria vetula (Valenciennes, 1836)	Detritivorous	1
Megalancystrus parananus (Peters, 1881)	Omnivorous	4; 7
Pseudohemiodon laticeps (Reghan, 1904)	Omnivorous	6; 7
Cyprinus carpio (Linnaeus, 1758)	Iliophagous and plants	4
Potamotrygon brachyura (Güther, 1880)	Small mollusks, crustaceans, larvae of aquatic insects and fish in adults	6
Micropogonias furnieri (Desmarest, 1823)	Carnivorous	5

have been favored by the invasion.

It is noteworthy that the original concept of ecosystem engineering does not include trophic interactions (Jones et al., 1994, 1997). Even though the trophic relationships described cannot be considered ecosystem engineering activities, the impact caused by this invasion on the predator community is significant and should be emphasized.There is a great predator diversity in the region (Table 1) and these species have totally or partially changed their regular prey preferences and now eat *L. fortunei* too, so that the density of these prey species increases in the absence of predation limit forces. Future research should explore whether increases in macrobenthic abundance and biomass due to *L. fortunei* ecosystem engineering activities indirectly enhance fish abundance and biomass.

The impact of *L. fortunei* on the water column

Several non-native bivalve species colonized aquatic ecosystems worldwide, in some cases with great ecological and economic impact (Sousa et al., 2009). Souza et al.(2009) stated that engineering activities of bivalves can meaningfully alter ecosystem structure and function (*e.g.*, changes in sediment chemistry, grain size, and organic matter content via bioturbation, increased light penetration into the water column due to filter-feeding, changes in nearby bed flows).

Most bivalves feed by filtering water through their gills. These are structures specialized in retaining particles suspended in water, part of which are drawn into the digestive system through the mouth. The amount of nutrient material suspended in freshwater is normally very low, generally less than 1 mg/liter (Sylvester et al., 2006). Hence, filtering organisms are required to process large volumes of water in order to fulfill their living and reproductive needs. Consequently, high densities of filtering organisms substantially modify their environment. Firstly, filtration draws particles from the water column and transfers them to the sediments as feces or pseudofeces (Ricciardi et al., 1997) such that mussels contribute toward more transparent water and bottom environments more enriched in organic matter. Clearer water and higher nutrient concentrations favor the growth of underwater vegetation. Benthic animals, in particular detritivorous ones, are favored by the higher content of organic matter in the bottom sediment (Karatayev et al., 2007).

Limnoperna fortunei grows in high densities in the invaded areas. It can reach 150,000 specimens.m^{-2} in natural environments (Darrigran and Pastorino, 2004), and 240,000 specimens.m^{-2} in man-made structures (Darrigran and Dreher Mansur, 2009). This, added to their great filtering ability (Sylvester et al., 2005), generates a particularly important impact on the water column. As described for other species of invading bivalves, they alter the abundance and composition of plankton (Cataldo and Boltovskoy, 2000), modify trophic interactions and food availability of benthic and pelagic species, increase the depth of the photic zone, and favor macrophytic growth (Boltovskoy et al., 2009). They also influence the mineralization of nutrients, availability of oxygen, and rates of sedimentation and nutrient recycling (Karatayev et al., 2007).

Information on the filtering ability of *L. fortunei* is poor. The first contribution assessing its filtering ability was carried out under controlled conditions (Sylvester et al., 2005). Knowledge of the filtering rate of *L. fortunei* will be crucial to assessing the potential impact on seston. Specimens can fulfill their energetic requirements using only phytoplankton and seston. According to estimates by Sylvester et al. (2005), abundance of phytoplankton in the lower Paraná River is not high enough to cover such energy demands, which vary by season and specimen size (Pestana et al., 2009). Therefore, *L. fortunei* must filter particulate organic matter. Sylvester et al. (2006) indicated that due to: 1) the high densities shown by golden mussels, 2) the energy requirements of the mussel, and 3) the fact that most particulate matter flows from the upper reaches of the rivers in the Plata basin towards the sea, important quantities of particu-

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late organic matter are retained in the freshwater bodies by filtration activities of *L. fortunei*. Thus, besides the local impacts due to filtration mentioned above, there are long-range impacts that can only be detected in the medium and long terms. These include modifications in the amount of particles spilling into the sea from one of the most important hydrographic basins in South America.

A study in the Río Tercero water reservoir, Cordoba, showed that water transparency, seston and chlorophyll a concentrations, and primary production suffered statistically significant modifications after the introduction and settlement of *L. fortunei* in the reservoir (Boltovskoy et al., 2009).

GENERAL REMARKS

Limnoperna fortunei is not only an aggressive invasive species, it is also a very effective ecosystem engineer, altering both ecosystem structure and function. Although first recorded in the American continent about twenty years ago, there are still too few studies to achieve an appropriate description of the bioinvasion pattern, especially considering the great adaptive capacity that allows such a vast dispersion distribution into different environments (from a temperate to subtropical ones). In a way similar to that detailed by Karatayev et al. (2002) for *Dreissena polymorpha*, the impact of *L. fortunei* invasion varies over time. This species responds in a way similar to that of most species involved in biological invasion. On one hand, in this kind of process there is interaction between the environmental characteristics (invasibility) and those of the invading species (invasiveness). On the other, population growth of an invading species changes through time (Hicks, 2004). Growth is exponential immediately after invasion. During this stage, impact on the environment is mainly direct. Later, when population density stabilizes at lower values, it acts as an ecosystem engineer, and its impact is mainly indirect. Predictability of the effects of *L. fortunei* on the aquatic community after the initial stages of invasion is lower.

According to Karatayev et al. (2007), in the near future *L. fortunei* may colonize the southern and central parts of North America, much farther north than previously predicted (Ricciardi, 1998). *L. fortunei* has wider ecological tolerances (e.g. high temperature, low pH, low calcium content, water pollution) than *D. polymorpha.*

This should allow the golden mussel also to invade freshwater environments unsuitable for zebra mussels (Karatayev et al., 2007). The same reasoning can be applied to Europe. Considerable commercial trade exists between South America and southern Europe (e.g. Spain), especially in the past two decades. These facts suggest that bivalve introductions between these two areas are likely to increase in the future. *Dreissena polymorpha*, for instance, may be transported and released into South American acquatic systems and *Limnoperna fortunei* may be transported and released into south European freshwater systems. Therefore, understanding the ecosystem engineering roles of *L. fortunei* is critical for its management and/or control. Such an understanding could serve to alert governments and private institutions about a potential environmental and economical regional bionvasion problem, consequently allowing them to generate measures relating to management, control, and awareness of the magnitude of the problem. Accurate knowledge on the pattern of activity of ecosystem engineers is essential for designing preventive management strategies to handle bioinvasion processes.

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