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A South American bioinvasion case history: *Limnoperna fortunei* (Dunker, 1857), the golden mussel*

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Abstract: Two factors combine in this age of globalization to favor the establishment of alien species in natural environments: human activities and global climate change. This paper reviews the recent invasion of the golden mussel, *Limnoperna fortunei,* in South America, including its impacts in natural and human environments. This case study allows the identification of the likely impacts that morphologically and functionally similar invasive species will have in similar environments, such as in North America, which is considered to be at high risk of invasion by *L. fortunei.*

Key words: Mytilidae, biological invasion, South America, macrofouling

Two factors combine in this age of globalization to favor the establishment of alien species in natural environments. First, through intentional or non-intentional activities of people, non-native species are introduced into and distributed within areas beyond their natural historical range (Johnson and Carlton 1996, Ricciardi and MacIsaac 2000, Ruiz *et al.* 2000). Second, global climate change may result in new regions becoming potentially available for colonization, especially for those species able to adapt to the newly accessible environment (Leach 2000).

Many human activities, including agriculture, aquaculture, recreation, transportation, the aquarium trade, and construction of canals and other aquatic diversions, promote the spread of species beyond their natural dispersal barriers (Ruiz *et al.* 1997, Benson 2000). This entails alterations in the composition and functioning of ecosystems (Grosholz 2002). Although there are many mechanisms for non-intentional introduction of species, for aquatic species, discharge of ballast water in foreign waters is recognized as the most common cause of such introductions (National Research Council 1996, Mackie 2000, Fofonoff *et al.* 2003 [and references therein]). Carlton and Geller (1993) described the increasing introduction of aquatic species via the ballast water of cargo ships as “ecological roulette.”

Human activities during the last decades of the twentieth century resulted in the emission of substantial amounts of anthropogenic greenhouse gases. However, these may not be solely responsible for the steep rise in the earth’s temperature and may only be accelerating a process of natural change (Broecker 2001). Two global events strongly influenced biotas during the past millenium: the Medieval Thermal Maximum (800-1200 A.D.) and the Small Ice Age (1450-1850 A.D.) (Jones *et al.* 2001, Deschamps *et al.* 2003). Dispersal of a species into a region beyond its existing range, as well as its establishment and adaptation within the new range, are due not only to chance but also depend on the presence of appropriate environments within the new region. Climate change may enhance the invasibility of such regions. Global climate change affects the distribution of species as well as resource dynamics in both terrestrial and aquatic ecosystems, thereby modulating biological invasions. Stachowicz *et al.* (2002) relate the establishment of introduced ascidean species in New England to the increase in winter water temperatures from the 1970s to the 1990s. Dukes and Mooney (1999) mentioned that increased CO_2 levels might slow the process of succession in grasslands, which would increase the dominance of non-native species in many ecosystems. They also suggested that the temperature increase, resulting from climate change, might benefit the Argentine ant (*Linepithema humile* [Mayr, 1868]) in its invaded area to the detriment of native ant species. Likewise, both the increased global transport of species and increased coastal ocean temperatures in the past few decades may provide an explanation for the increasing rate of invasion by alien species (Stachowicz *et al.* 2002).

Within these general contexts (invasion and global change), Dukes and Mooney (1999) addressed whether some ecosystems are more or less prone to invasion than others, whether certain alien species will become invasive, and whether the impacts caused by invading species will be

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severe or mild. Integration of theoretical principles with the scarce studies on how biological invaders respond to global change led to the conclusion that the most important elements of global change seem to increase the prevalence of biological invasions.

From an agricultural point of view, the Argentine pampas is one of the most productive areas in South America. One of its main waterways, the Río de la Plata, was the entrance point – during the past three decades – of at least three alien molluscan species, i.e., *Corbicula fluminea* (Müller, 1774), *Limnoperna fortunei* (Dunker, 1857) (Darrigran 2002), and *Rapana venosa* (Valenciennes, 1846) (Pastorino *et al.* 2000); the first two have already been acknowledged as invasive in the region. This may be an example of an invasion involving not only human maritime activity (through the port of Buenos Aires) but also, although highly speculatively, a global climate change that took place during the past few decades. This climate change included a 100% increase in rainfall in the region (Fig. 1) (Deschamps *et al.* 2003), an alteration that carried manifold consequences for freshwater ecosystems. Enhanced commercial links during recent decades, together with rapid climatic change, could have facilitated the arrival and establishment of the three alien species.

Dukes and Mooney (1999) also commented on the feedback interaction connecting the impacts of new invading species on the environment, global change, and human action through commerce on a global scale (Fig. 2). All this points to a future in which “foreign ecosystems” will be the rule. Single elements of global change might affect biological invasions. For instance, the rising concentration of carbon dioxide could increase the dominance of invaders in some ecosystems. Climate change might favor the many alien spe-

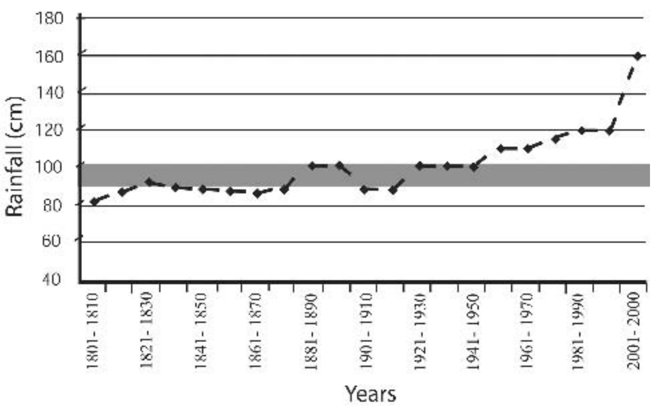

Figure 1. Rainfall in Buenos Aires from 1801 to 2002 (modified from Deschamps *et al.* 2003). In gray, range used for public works planning at the end of the 19th century and for much of the 20th century.

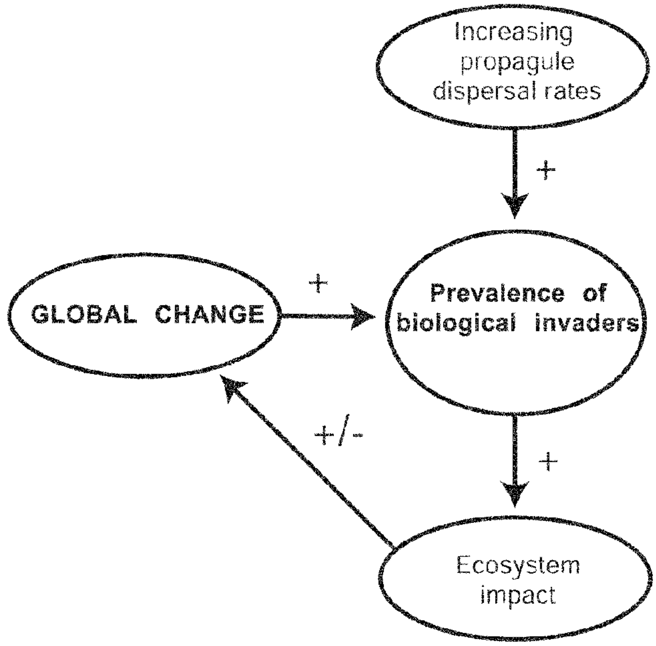

Figure 2. Forces that may affect the prevalence of invasive species. Elements of global change and changes in global commerce increase the rate of arrival of alien species. The invader species alter ecosystem processes and properties; many of them may interact (positively or negatively) with elements of global change (modified from Dukes and Mooney 1999).

cies that can shift range quickly and/or tolerate a wide range of environments. Land-use patterns that increase habitat fragmentation can increase the prevalence of non-native species. The interactions among the elements of global change that affect the prevalence of biological invaders remain unstudied.

Levine and D’Antonio (2003) suggested that the ecological and economic costs associated with human-caused biological invasions may continue to rise substantially over the next decades. Numerous international meetings organized by diverse organizations have had the underlying aim of preventing the realization of such predictions. Two such meetings, focused on molluscs, were recently held: a workshop on “Freshwater invading bivalves in southern South America” during the Fifth Latin American Malacological Congress (São Paulo, Brazil, 2002) and the symposium during the 69th Annual Meeting of the American Malacological Society (Ann Arbor, USA, 2003) to which this paper is a contribution. Independently, similar discussions arose and the same conclusions were drawn at these meetings, essentially: (1) there is a lack of public awareness of the problem; (2) this leads to a lack of control over human activities that cause introduction/dispersal of foreign species; and (3) there is a general lack of interest in generating knowledge to prevent the economic/environmental problems at a regional scale.

In order to establish *a priori* criteria for the prevention or treatment of an invasion – knowing that studies on populations in their natural ranges are inadequate – patterns of impact for species with an invasion history should be identified. This could lead to the ability to predict the impacts of morphologically and functionally similar species in similar environments (Bij de Vaate *et al.* 2002, Ricciardi 2003). Comparative studies of these patterns, which serve as major sources of understanding of the processes involved in invasion capacity and the consequences of invasions, require the collection of comparable data sets (Orensanz *et al.* 2002). However, currently available quantitative data on the history of bioinvasions are inadequate for comparison of similar ecosystems (Ricciardi 2003). Although the number of scientific publications on bioinvasions has increased over the past decade (Kolar and Lodge 2001), Orensanz *et al.* (2002) concluded that the literature on estuarine or marine invasions is unevenly distributed, with a majority from the USA, Western Europe, and Australia. Much of the little that is known about the issue in South America is either unpublished or reported in relatively obscure sources not normally available to the international scientific community (Orensanz *et al.* 2002).

An alternative approach to predicting the impact of an introduced species is to infer it from the invasion history of functionally similar organisms. Therefore, knowledge of the biology of invasive bivalves such as *Dreissena polymorpha* (Pallas, 1771), *Limnoperna fortunei, Mytilopsis sallei* (Récluz, 1849), *Modiolus striatulus* (Hanley, 1853), *Perna viridis* (Linneaeus, 1758), and *Xenostrobus securis* (Lamarck, 1819) could serve as a template to set priorities in the study of other potential pest bivalves that do not yet have an invasion history (Ricciardi 2003).

This paper presents a synthesis of a bioinvasion case history: the invasion of *Limnoperna fortunei* in South America. Enhanced knowledge about this species may be of value in predicting and preventing potential impacts of invasions by bivalve species with similar morphological and functional features.

LIMNOPERNA FORTUNEI: A CASE HISTORY

Numerous alien species have arrived in the Americas during the recent past. Among them are three freshwater bivalves that became invasive: *Corbicula fluminea* (Asian clam), *Limnoperna fortunei* (golden mussel, Fig. 3), and *Dreissena polymorpha* (zebra mussel). The zebra mussel has been present in North America since the 1980s but is absent from the Neotropical Region (Ricciardi 2003).

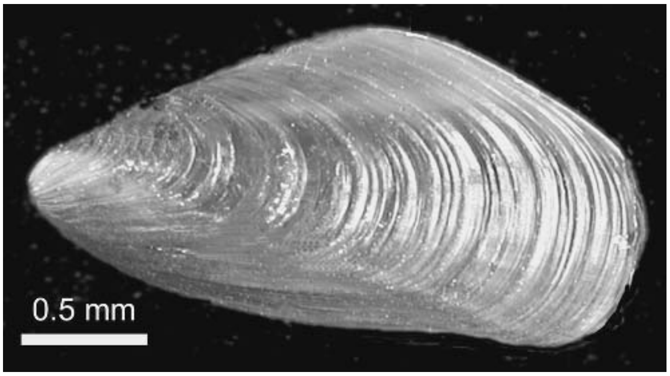

Figure 3. External view of left valve of *Limnoperna fortunei.*

The golden mussel, *Limnoperna fortunei,* is native to southeast China and Korea (Iwasaki and Uryu 1998). It was introduced to Hong Kong in 1965 (Morton 1977) and to Japan (Kimura 1994) and Taiwan (Ricciardi 1998) in the 1990s. It was found for the first time in the Americas in 1991 in the Argentine pampas at Bagliardi Beach, Río de la Plata estuary (35°55'S, 57°49′W) (Pastorino *et al.* 1993) (Fig. 4), having been introduced in the ballast water of ocean-going vessels (Darrigran and Pastorino 1995).

Several factors enabled *Limnoperna fortunei* to spread rapidly and to have a severe impact on natural and human environments in South America, including its short life span, rapid growth, early sexual maturity, high fecundity, ability to colonize a wide range of habitat types, wide range of physical tolerances, gregarious behavior, suspension feeding, and planktonic larvae (Morton 1996). In addition, the South American native freshwater bivalves, which include unionids, corbiculids, and sphaeriids, are predominantly infaunal in soft substrates and lack planktonic larvae. Thus there was an open opportunity for the epifaunal, hard substrate-dwelling alien (Darrigran 2002). Because its initial introduction was in an industrialized area with heavy river trade, it was immediately associated with human activity, settling on surfaces of commercial and/or recreational ships and boats, on artificial structures such as piers and wharves, in pipes supplying water for industry, and in water purification plants, refrigeration systems, etc. These characteristics have rendered *L. fortunei* the environmentally and economically most harmful freshwater invading bivalve in South America, similar to *Dreissena polymorpha* in North America.

Distribution and dispersal

The Río de la Plata is part of one of the major hydrographic systems in South America, the Plata basin. This system covers a drainage area of 3,000,000 km^2 (Fig. 4), with the richest freshwater molluscan diversity of the Patagonian

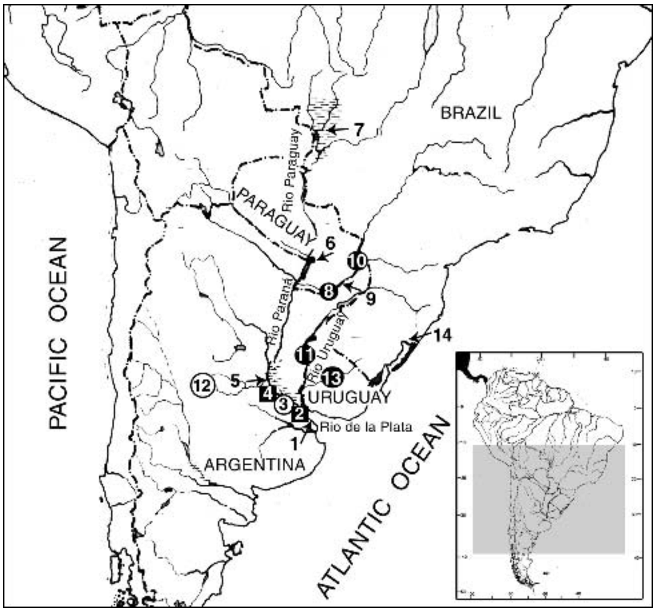

Figure 4. Distribution of *Limnoperna fortunei* in South America. 1, Bagliardi Beach (Argentina); 2, Buenos Aires Harbor (Argentina); 3, Atucha (Argentina); 4, San Nicolás (Argentina); 5, Santa Fe (Argentina); 6, Asunción Harbor (Paraguay); 7, The Pantanal (Brazil-Bolivia); 8, Yacyretá (Argentina-Paraguay); 9, Posadas Harbor (Argentina); 10, Itaipú (Brazil-Paraguay); 11, Salto Grande (Argentina-Uruguay); 12, Río Tercero (Argentina); 13, Río Negro (Uruguay); 14, Guaiba Basin (Brazil). Black circles, hydroelectric power plants; black squares: thermal power plants; white circles, nuclear power plants.

subregion of the Atlantic slope (Darrigran and Pastorino 2004) and good navigability in some of its rivers (Paraná, Río de la Plata, Paraguay), which sustain intense commercial traffic.

Since its first appearance in the Río de la Plata in 1991, the distribution of *Limnoperna fortunei* has been constantly expanding. In 1994 it was present only in the Río de la Plata, on both the Argentine and Uruguayan coasts (Scarabino and Verde 1994). Since 1995 it has been recorded in the industrialized area along the lower Paraná River, causing the earliest cases of macrofouling (Darrigran 1995). Two years later it was recorded in Asunción (Paraguay) on the Paraguay River. In 1998 it was collected in the Pantanal (Dreher Mansur *et al.* 2003), a World Ecological Sanctuary. It continued its northward dispersal along the Paraná River and in 1998 was recorded in Posadas and at the Binational Hydroelectric Power Plant at Yacyretá (Darrigran and Ezcurra de Drago 2000). By 2001 it had reached the Binational Hydroelectric Plant of Itaipú (Darrigran 2002, Zanella and Marenda 2002). It also dispersed up the Uruguay River (I. Ezcurra de Drago pers. comm.), being recorded in 2001 at the Binational Hydroelectric Power Plant of Salto Grande. Also in 2001, it was recorded in the reservoir and at the nuclear power plant in Río Tercero, Córdoba, Argentina (unpublished data). This large region encompasses widely varying environmental conditions and temperate to subtropical climates.

Limnoperna fortunei was also detected in Río Grande do Sul (Brazil) in November 1999 (Dreher Mansur *et al.* 1999). This is considered to be the outcome of a separate invasion event, probably resulting from commerce between Argentina and Brazil (M. C. Dreher Mansur pers. comm.). In Brazil it has invaded the states of Río Grande do Sul, Paraná, Mato Grosso, and Mato Grosso do Sul (R. J. Calixto pers. comm.). Several of these areas sustain important industries and their water cooling systems have been invaded by *L. fortunei* or are under imminent threat of invasion.

Planktonic larvae provide the natural dispersal mechanism of *Limnoperna fortunei*. However, in contrast to the spread of *Dreissena polymorpha* in North America (Mackie and Schloesser 1996), in the Plata basin *L. fortunei* dispersed mainly in a countercurrent direction, at an average rate of 240 km/yr (Darrigran 2002). This rapid countercurrent dispersal is probably related to human activities including commerce, fishing, and recreation, which are enhanced by the navigability of the rivers.

In South America, *Limnoperna fortunei* first occupied environments with water temperatures of 14-24°C. At a later stage it invaded areas with shorter winters and temperatures of 15-33°C. It can also inhabit brackish waters (salinity <3 ppt), and tolerates pH values of 6.2-7.4 and Ca^{++} concentrations of 3.96 mg/l (Darrigran 2002).

Density

When first detected in the Río de la Plata, the density of *Limnoperna fortunei* was 4-5 individuals per m^2 (Darrigran and Pastorino 1995, Darrigran 2000). Density peaked at the same locality in 1995 with ~150,000 per m^2, subsequently stabilizing at ~40,000 per m^2 (Darrigran *et al.* 2003) (Fig. 5). A similar trajectory was observed in populations in the Guaiba basin (Brazil) in 1999 (Dreher Mansur *et al.* 2003).

Impact on natural environments

The rapid increase in density and distribution of this invading bivalve added a widespread and abundant epifaunal mussel to freshwater benthic communities of the Plata basin. Dense populations of golden mussels create new habitats that can be colonized by other taxa, thereby modifying the specific richness and composition of the native benthic communities.

Little quantitative information is available regarding the original composition of the benthic freshwater fauna of the

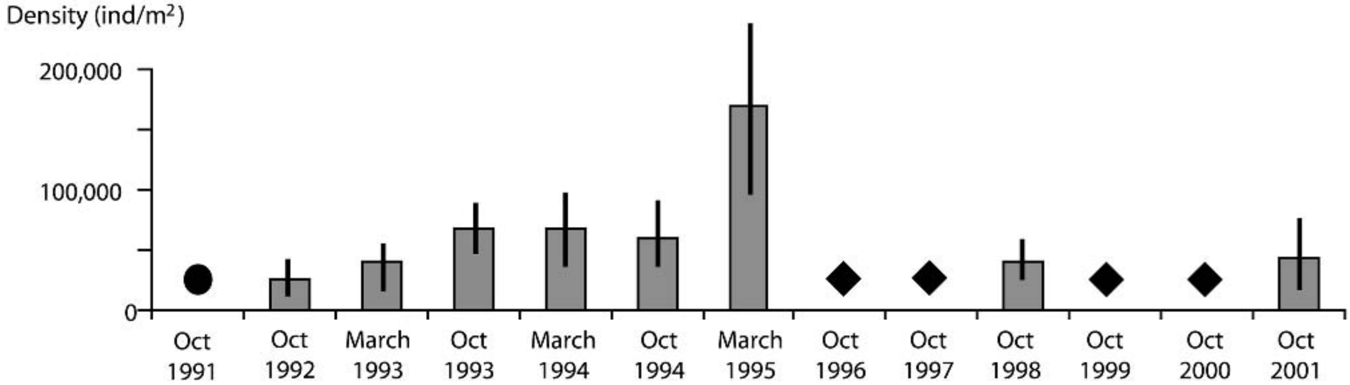

Figure 5. Temporal variation of density (mean and standard deviation) of *Limnoperna fortunei* in Bagliardi Beach, Río de la Plata, between 1991 and 2001. Black circle, 4-5 individuals per m^2; black rhombus, no data (modified from Darrigran *et al.* 2003).

Plata basin. In 1988, at Bagliardi Beach, before the introduction of *Limnoperna fortunei,* three gastropods were common in the rocky environment: *Heleobia piscium* (d'Orbigny, 1835), *Chilina fluminea* (Maton, 1809), and *Gundlachia concentrica* (d'Orbigny, 1835) (Darrigran 1991). Only two species of Hirudinea (Gullo and Darrigran 1991) and one species of Isopoda (Darrigran and Rioja 1988) were found. By 1992-1995, high densities of *L. fortunei* at this location had created a new microenvironment; *C. fluminea* and *G. concentrica* had become rare, while other epifaunal macroinvertebrates were recorded for the first time: eight species of Oligochaeta, one Aphanoneura, eight Hirudinea, and other species of Amphipoda, Tanaidacea, Isopoda, Chironomidae, Turbellaria and Nematoda (Darrigran *et al.* 1998b).

The most direct and severe ecological impact has been the epizoic colonization of native naiads (Hyriidae and Mycetopodidae) by *Limnoperna fortunei,* similar to the impact of *Dreissena polymorpha* on native bivalves in North America (Ricciardi *et al.* 1997). The displacement of the native naiads resulted from their inability to open and shut their valves because of the byssally-attached mussels on their shells. The quantitative impact of *L. fortunei* on native naiads in South America is unknown. Golden mussels also settle on other native fauna, such as *Pomacea canaliculata* (Lamarck, 1822) (Gastropoda, Ampullariidae) and *Aegla platensis* Schmitt, 1942 (Anomura, Aeglidae), as well as on the introduced *Corbicula fluminea* (Bivalvia, Corbiculidae) (Darrigran *et al.* 2000, Darrigran 2002).

The large biomass associated with high densities of *Limnoperna fortunei* impacts aquatic food chains. Several species of native fish consume *L. fortunei* (López Armengol and Casciotta 1998, Montalto *et al.* 1999) and it has become the main food source for *Leporinus obtusidens* (Valenciennes, 1836) (Anostomidea) in the Río de la Plata (Penchaszadeh *et al.* 2000).

Impact on human environment

The introduction of *Limnoperna fortunei* impacts not only natural environments. Freshwater macrofouling, caused by *L. fortunei,* is a novel economic problem in South America. Previously, macrofouling was only a problem in coastal and estuarine localities. Now, however, major industries in Argentina, Brazil, Uruguay, and Paraguay are faced with problems including reduction of water-pipe diameter, blockage of pipelines, decrease of water velocity, accumulation of empty shells, contamination of water by dead mussels, and blockage of filters by larvae and juveniles and their settlement in different parts of the processing plants (Darrigran 2000). These problems have been recorded in numerous installations, including water purifying plants, hydroelectric plants, thermal plants, freezing plants, and oil factories. As a consequence, costs rise because of shutdowns caused by pipeline obstructions and the need for periodic mechanical or chemical cleaning as well as the replacement of pipes and filters. Most information on this issue is contained in technical reports that are not widely available.

The global importance of invasion by *Limnoperna fortunei*

The climate in the native range of *Limnoperna fortunei* is humid subtropical, without a dry season and with a warm summer. Many parts of the world have similar climates, including parts of Japan and the Plata basin, both already invaded by this bivalve. Ricciardi (1998) has alerted us to the possibility of invasion of North America. In particular, the Gulf of Mexico and the Mississippi basin also have a similar climate and are therefore probably susceptible to invasion. Two important ocean navigation routes are also associated with this area: the Atlantic coast, with 30% of the USA traffic, and the Gulf of Mexico, with the major port of New Orleans. Invasion could be in ballast water of ships from southeast Asia or South America. European harbors are also susceptible to invasion.

Research on *Limnoperna fortunei* in South America

Introduction of the golden mussel in the Plata basin has resulted in extensive research activities, including: impacts on native species (Darrigran *et al*. 1998b); individual growth rates (Boltovskoy and Cataldo 1999, Maroñas *et al.* 2003); distribution and impacts (Darrigran 2000, Darrigran *et al.* 2000, Darrigran and Ezcurra de Drago 2000); reproductive biology (Darrigran *et al*. 1998a, 1999, 2003a); predation (Penchaszadeh *et al*. 2000); larval development and larval ecology in natural environments (Cataldo and Boltovskoy 2000; Irurueta *et al.,* in press) and in human environments (Darrigran *et al*. 2003b); resistance to exposure to air under different conditions of relative humidity, aimed at developing low environmental impact control methods and at determining the mussel's capacity for further spread (Darrigran *et al.* 2004); preliminary bioassays to determine the lethal effect of copper and zinc in order to formulate antifouling paints and coatings for freshwater environments (Caprari and Lecot 2001); and bioassays with a polymeric quaternary ammonium, tested on larvae (Darrigran *et al.* 2001) and adults (Darrigran and Damborenea 2001).

Most of these studies of *Limnoperna fortunei* are ongoing and will permit comparison with the abundant information on the invasion of *Dreissena poymorpha* in North America, as they are morphologically and functionally similar species. However, many other aspects of the biology of *L. fortunei* are still unknown, including its filtering capacity. Because of its high density in the Plata basin, *L. fortunei* could increase water clarity in a manner similar to that caused by *D. polymorpha* in North America (Fanslow *et al.* 1995).

The overall aim of the research activities outlined above is to provide the necessary information for effective control of the invasion and for mitigating its economic impact. Likewise, the results obtained should provide valuable information for prediction of future invasions (Ricciardi 2003), the impact this species may have in other regions, and basic information for the design of sustainable strategies of prevention and control.

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