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Review

Potential impact of filter-feeding invaders on temperate inland freshwater environments

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Abstract

Since the 1990s, biological invasions have captured the attention of the scientific community as an important element of global change and a major threat to biodiversity. The inland waters of South America provide two examples of biological invasions. This review examines bivalve invasions in South America, summarizes the research results for two species, the Asian clam (*Corbicula fluminea*) and the golden mussel (*Limnoperna fortunei*), and suggests further studies. The rapid expansion of invasive bivalves into these environments involves significant changes. Until now, *C. fluminea*, the Asian clam, did not produce generalized macrofouling in the Neotropical region, as is common in the Holarctic region. However, the first specific cases of macrofouling by *C. fluminea* were recently detected in heat interchangers of power stations in Brazil. On the other hand, *L. fortunei* is provoking new economic impacts in South American freshwaters through macrofouling. Before the invasion by the golden mussel, macrofouling was recorded only in the marine and estuarine environments of the Neotropical region. The impact caused by invasive bivalves in this region is not only economic, however. Rapid changes in the benthic community, favoring the presence of Oligochaeta and Hirudinea, as well as the displacement of native species of mollusks, are among the problems related to the presence of the golden mussel. Another issue is the settlement of golden mussels on native bivalves. This bivalve is now a new element in the diet of some native fish species, being the main food item in some cases.

Introduction

Although species distribution changes naturally over time, human activities greatly increase the rate and the spatial scale of these changes by accidentally or deliberately moving organisms across the world (Ricciardi and MacIsaac 2000). Many human activities, such as agriculture, aquaculture, recreation and transportation promote both the intentional and accidental spread of species across their natural dispersal barriers (Kolar and Lodge 2001). A non-indigenous species must overcome several sequential transitions (transportation, release and establishment) to continue the invasion process (Kolar and Lodge 2001). The first step for such species concerns the transport pathway (e.g. in the ballast water of a ship). During this stage, specimens can either die or survive. From the time of release, this species interacts with the invaded ecosystem. These interactions, along with other factors, determine whether the non-indigenous species becomes established.

The introduction of invasive species threatens native biodiversity, ecosystem functioning, animal and plant health and human economies. The best solution is to prevent the introduction, but, once produced, eradication may be feasible (Myers et al. 2000). However, the elimination of the entire invading population is seldom tackled for three reasons (Simberloff 2001): it is seen as not feasible; it is expensive; and it may have horrendous non-target impacts.

Among the aquatic ecosystems, lakes and estuaries are highly susceptible to invasion (Ricciardi and MacIsaac 2000). According to Morton (1996), an invasive species should have several characteristics to be successful in the new environment: a short life span (e.g. 2–3 years); rapid growth; rapid sexual maturity (a typically dioecious sexual strategy with occasional hermaphroditism); high fecundity; euryoecious (an ability to colonize a wide range of habitat types); eurytopic (possessing a wide range of physiological tolerances); gregarious behavior; some form of association with human activities (food sources; inhabitants of estuaries, rivers, lakes or canals, reservoirs, harbors, etc.); wide genetic variability and phylogenetic plasticity; suspension feeding; the ability to repopulate previously colonized habitats, following population crashes caused by extreme physical conditions. Invasive bivalves present many of the above characteristics. They are also able to overcome the sequential transitions successfully. Conspicuous examples are *Modiolus striatulus* Henley and *Mytilopsis sallei* Recluz in estuaries; *Corbicula fluminea* (Müller) and *Limnoperna fortunei* (Dunker) in rivers and lakes; and *Dreissena polymorpha* (Pallas) in canals and reservoirs (Morton 1996).

This review examines and summarizes the research results of the introduction, spread, biology and environmental and economical impacts of two invasive freshwater bivalves, *L. fortunei* and *C. fluminea* in the Plata Basin, South America, and suggests further studies. *C. fluminea* has been introduced throughout the world, while the range of *L. fortunei* is just beginning to expand beyond its indigenous distribution in Southeast Asia to other continents. This review presents an advance warning of this species' ecological and economic impacts for the likely future introduction of *L. fortunei* to the inland waters of the southern United States and southern Europe, where it could prove extremely costly as has the introduction of the zebra mussel.

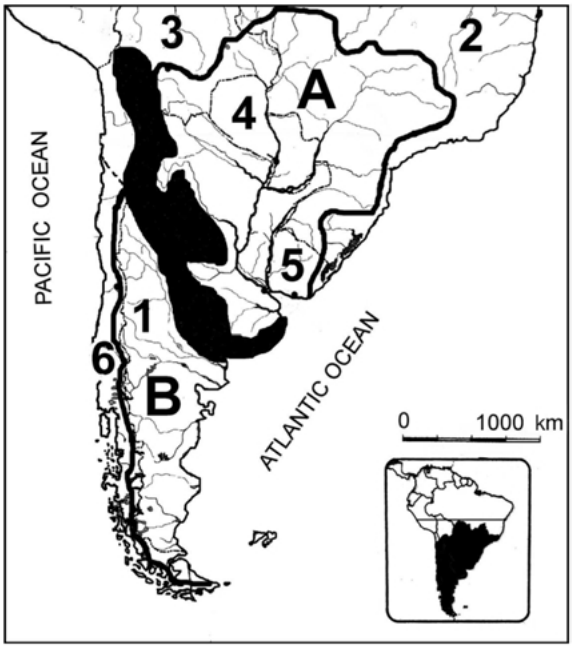

Figure 1. Austral South American rivers. A: The Plata Basin; B: Chilean–Patagonian Subregion of the Atlantic Versant. 1: Argentina; 2: Brazil; 3: Bolivia; 4: Paraguay; 5: Uruguay; 6: Chile. In black: arid diagonal (modified from Bonetto 1994).

Introduced bivalves: two case studies

Since the 1960s, three species of freshwater bivalves from Southeast Asia have reached the Neotropical region through the Argentinean coast of the Río de la Plata Estuary (Figure 1; Ituarte 1981; Pastorino et al. 1993): *C. fluminea* (Müller), or Asian clam, *Corbicula largillierti* (Philippi) (both Corbiculidae), and *L. fortunei* (Dunker), or golden mussel (Mytilidae). The Asian clam and the golden mussel have many of the characteristics mentioned above for invader species (Morton 1996; McMahon 2000). Their rapid growth, early maturity and high fecundity rate and adaptability to the different habitat conditions allow them to colonize new environments. Moreover, the associations of these species with human activities increase their dispersal capacity. On the other hand, *C. largillierti* was not successful in the invasion process (Darrigran 1992a; Ituarte 1994). Now, this species is rare and found only in restricted areas of the Plata Basin.

Corbicula fluminea shows the least recorded impacts, both to humans and to the natural environments. On the other hand, the environmental impact produced by *L. fortunei* is comparable to that of *D. polymorpha* (Pallas) in North America (Nalepa and Schoelesser 1993; Darrigran 2000). The life histories and the potentially different environmental and economic impacts of the two species are analyzed below.

Golden mussel or Limnoperna fortunei *(Dunker 1857)*

Life history characteristics

The golden mussel (Figure 2) is native to Chinese and southeastern Asian rivers and creeks. It invaded Hong Kong in 1965 (Morton 1977) and Japan (Kimura 1994) and Taiwan (Ricciardi 1998) in the 1990s. It was discovered in September of 1991 at Bagliardi Beach, Río de la Plata estuary (Pastorino et al. 1993). Darrigran and Pastorino (1995) described the transport and release of this species into South America as a non-intentional introduction through ballast waters of ocean vessels.

Morton (1973) provides a general description of *L. fortunei*. The yellow-brown shells look golden in clear water, for example in northern Argentina; for this reason *L. fortunei* is called 'golden mussel'. *Limnoperna fortunei* has an epifaunal mode of life, attaching to a wide variety of hard substrates, both natural (from trunks and aquatic plants to compact silt-sand) and artificial (docks, tubes, walls, etc.). Where hard substrates are rare, larvae settle on small pebbles, and new mussels grow on older specimens of this and other bivalve species (Ituarte 1997). In this way, they generate patches of hard substrate consisting of shells.

In South America, the golden mussel specially inhabits the large rivers of the Plata Basin and the release area, and the first established population inhabits temperate areas with water temperatures between 14 and 24 °C. Later, it invaded subtropical areas with shorter winters and a temperature range of 15.3–32.6 °C. It can also live in brackish waters where salinity does not exceed a mean value of 3 psu. This is the same salinity tolerance found in Japanese populations (Kimura et al. 1995). *Limnoperna fortunei* was found in environments with a wide range of pH conditions (6.2–7.4) and with 3.96 mg/l of Ca^{++}.

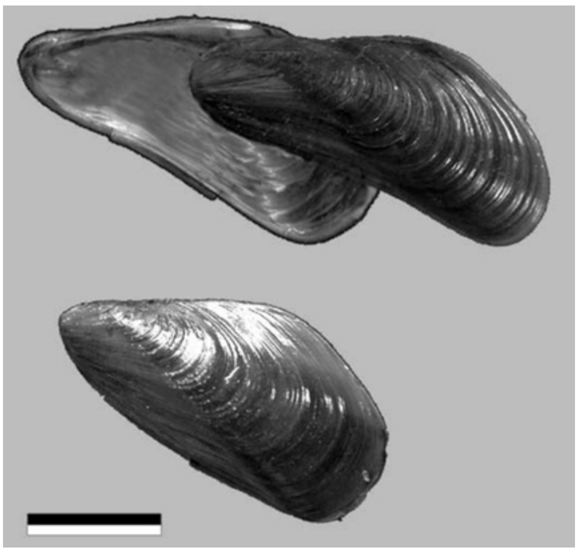

Figure 2. Limnoperna fortunei (Mytilidae). Bar: 1 cm.

The maximum recorded valve length of *L. fortunei* specimens in the Plata Basin is 40–45 mm (personal observation). It is an externally fertilizing dioecious species and, as for other mollusks, temperature is key to its reproductive cycle (Darrigran et al. 1999; Cataldo and Boltovskoy 2000). The threshold temperature associated with the onset of reproduction is about 15–17 °C. Furthermore, as other Mytilidae, the golden mussel has planktonic larval development, which facilitates wide dispersion by currents. The duration of the larval period varies. Choi and Kim (1985) estimate it at 15–20 days. These data agree with observations by Ezcurra de Drago for golden mussel populations of the Paraná River in the Plata Basin (Ezcurra de Drago, pers. comm.).

The reproductive biology of *L. fortunei* in South America is known only for the founding population in the Río de la Plata, Argentina. This study started a year after the first record (Darrigran et al. 1999). The minimum size of sexual differentiation was 5 mm in shell length, both for males and females, while gonadal maturity for both was attained when the shell was 6-mm long. The size at sexual maturity varied over time. The reproductive cycle of this population during the first period of study (1992 and the beginning of 1993) shows two gamete releases of low intensity. They were associated with a partially stable follicular occupation of the mantle and the proliferation was continuous. During the second period (from February 1993 to November 1994), two main spawning events per year were recognized. As *L. fortunei* is an invasive species introduced into South America in 1991, and the study has been carried out since mid-1992, this reproductive pattern probably responds to the lack of fitness and synchronization of the reproductive cycle of this population to the new environment. Also, as it frequently occurs in other mytilid species, 0.55% of individuals were hermaphrodites in the same population of *L. fortunei* from Río de la Plata (Darrigran et al. 1998a).

The combination of early sexual maturity, high fecundity, semelparity and wide environmental tolerance allows *L. fortunei* to overcome the transitions to be a successful invader into the new environment. Another characteristic, which contributed to the development of the golden mussel into an invasive species, is the absence of competitive interaction within the byssally attached epifaunal freshwater niche.

Spatial–temporal distribution
The first record of *L. fortunei* in South America occurred in 1991 (Pastorino et al. 1993), at Bagliardi Beach, on the coast of the Río de la Plata (34°55′ S; 57°49′ W). The density of organisms when first detected was 4–5 individuals/m^2. Their high biotic potential was evidenced by the massive density increase of the founding population during the following years (Figure 3). In 1995, golden mussel density was approximately 150,000 ind/m^2 (Darrigran and Ezcurra de Drago 2000).

The increase in the spatial distribution of the golden mussel from 1991 to 2001 (Figure 4) can be summarized as follows:

1. It invaded five large rivers of the Plata Basin. It was found only in the Río de la Plata in 1991 and is currently present in the Paraná, Paraguay, Pilcomayo and Uruguay Rivers.
2. Until 1991, the golden mussel was found only in Argentina. It is currently found in Uruguay, Paraguay and Brazil.

Several natural and human dispersal mechanisms can be mentioned (e.g. water currents, animals, ships, and fishing activities). The veliger larvae stage is a natural dispersal phase. However, in this case, the dispersal of *L. fortunei* in the Neotropical region occurred mainly upstream. The rapid dispersion along the Plata Basin is mainly due to the river navigability, especially for the Río de la Plata and the Paraná and Paraguay Rivers. In short, during the last 10 years, the golden mussel has advanced approximately 240 km per year along the Plata Basin since its introduction.

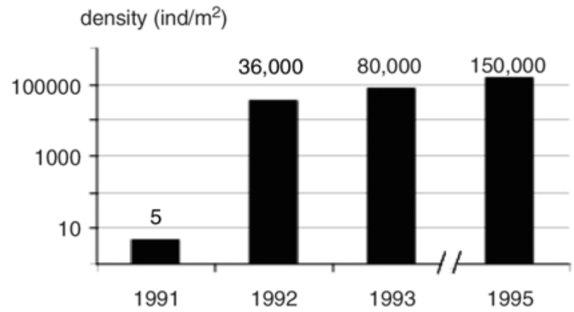

Figure 3. Temporal variation in density of the golden mussel of Bagliardi Beach (logarithmic scale).

Environmental impact
The impact caused by this species involves both human and natural environments, and is similar to the impact caused by the invasive bivalve species *D. polymorpha* in the Northern Hemisphere (Nalepa and Schoelesser 1993; Darrigran and Ezcurra de Drago 2000).

Impact on the human environment (macrofouling). Macrofouling is due to life forms (bigger or equal to 1 mm) which grow attached to solid non-living substrates, and which, in the case of man-made immersed structures, often interfere with human interests (Wahl 1997). Freshwater macrofouling is a new economic/environmental problem for South America.

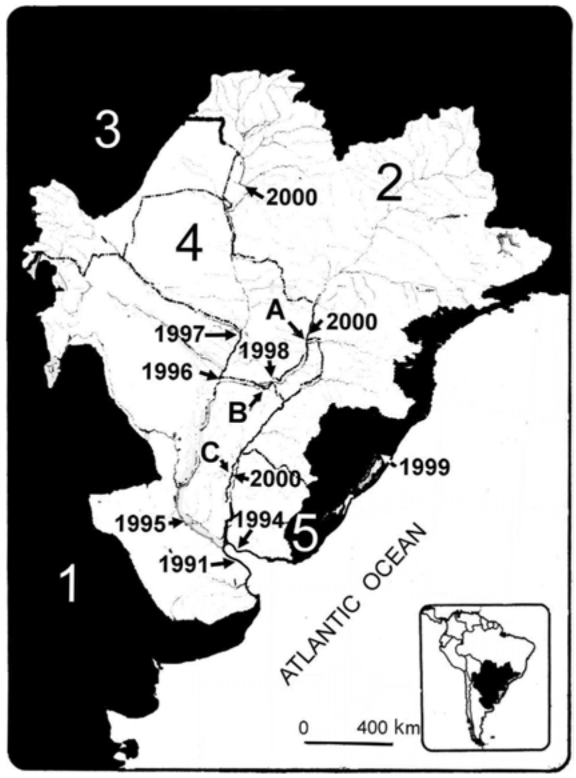

Figure 4. Plata Basin. Spatial–temporal distribution of the golden mussel. Binational hydroelectric power stations polluted by *L. fortunei*, A: Itaipú Hydroelectric Station (Brazil–Paraguay). B: Yacyretá Hydroelectric Station (Argentina–Paraguay). C: Salto Grande Hydroelectric Station (Argentina–Uruguay). 1: Argentina; 2: Brazil; 3: Bolivia; 4: Paraguay; 5: Uruguay (modified from Darrigran et al. 2000).

Until the beginning of the 1990s, macrofouling in the Neotropical region occurred only in marine and mixohaline waters. Since the introduction of *L. fortunei*, macrofouling has also extended to freshwaters in Argentina, Brazil, Paraguay and Uruguay (G. Darrigran, pers. obs.).

This kind of biopollution is caused by the appearance of larvae or juveniles of *L. fortunei*. It impacts the sources of water supply for many water-treatment plants, industrial refrigeration systems and power stations. Among the usual problems involved, the following are the most significant: pipe obstruction; reduction in flow velocity in pipes due to friction loss (turbulent flows); accumulation in empty valves and the pollution of water ways from massive mortality; filter occlusion and an increase in the corrosion of surfaces due to mussel infestation. This new economic and environmental problem for the Neotropical region (freshwater macrofouling) produces unexpected expenses, such as system shutdowns, the need for chemical or mechanical cleaning, and pipe and filter replacement. In Argentina, these cases of macrofouling occur in the industrial plants developed along the banks of the Paraná River, Uruguay River and the Río de la Plata estuary (Figure 5). The settlement and maturity of larvae and juveniles into water-distribution systems was detected in several of the southern power generation plants of the Plata Basin. Among these, the most important ones are the nuclear power plant Atucha (Argentina) and Yacyretá Hydroelectric Station (Argentina–Paraguay), one of the most important of South America. It has also been recently detected in the largest power station in the world, Itaipú Hydroelectric Station (Brazil–Paraguay) (Figure 4; Boltowskoy and Cataldo 1999; Zampatti and Darrigran 2001).

Impact on the natural environment. The impact of the golden mussel is not only restricted to economic aspects. Among the potential impacts associated with the presence of this invasive bivalve, the rapid change produced in benthic communities should be noted. Since its invasion of the Plata Basin, *L. fortunei* has modified the presence and abundance of species of several native macroinvertebrates (Martin and Darrigran 1994; Darrigran et al. 1998b).

Sandy beaches are the characteristic substrate in the Río de la Plata. The scarce, natural, hard substrate available (Darrigran 1999) is limited to caliche (compact silt-sand) beaches, aquatic vegetation, trunks and substrates of human origin (e.g. walls, tubes, docks). Before the invasion by *L. fortunei*, the benthic fauna associated with hard substrates was of low density and richness.

There is little quantitative information available about the composition of benthic freshwater fauna from the Plata Basin rivers. Several samples from Bagliardi Beach, Río de la Plata, were taken on March 20, 1988, during a study of the mollusk fauna from the Argentinean coast of Río de la Plata (Darrigran 1991a). At that moment, before the

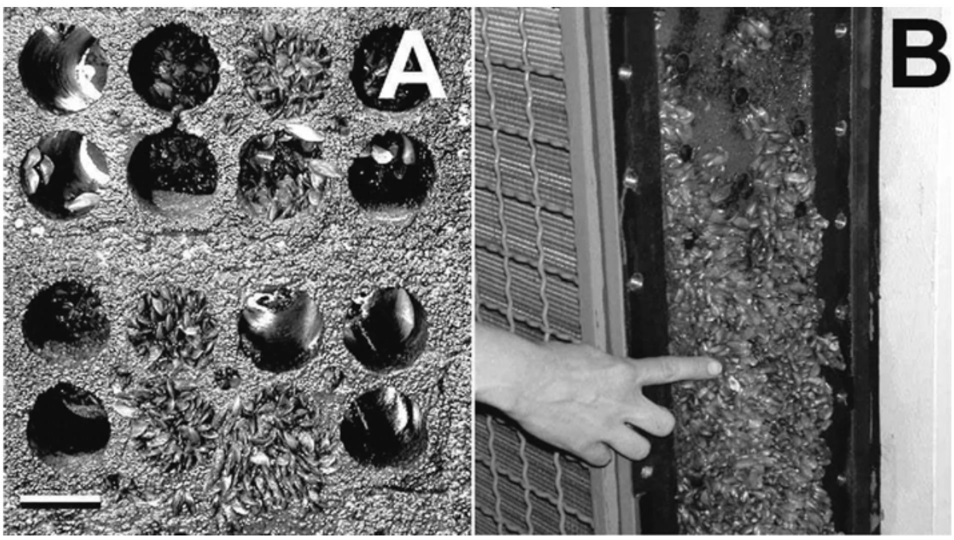

Figure 5. Two examples of macrofouling caused by *L. fortunei*. A: Parshall in a water-treatment plant. Bar: 5 cm. B: Heat interchanger of a hydroelectric power plant.

introduction of the golden mussel to Bagliardi Beach, three gastropods were common in the rocky environment: *Heleobia piscium* (d'Orbigny), *Chilina fluminea* (Maton) and *Gundlachia concentrica* (d'Orbigny). Only two species of Hirudinea (i.e. *Helobdela striata* (Ringuelet) and *Gloiobdella michaelseni* (Blanchard)) (Gullo and Darrigran 1991) and one species of Isopoda (*Pseudoesphaeroma platense* (Giambiagi)) (Darrigran and Rioja 1988), were found.

The same rocky environment of Bagliardi Beach was studied between 1992 and 1995, after the settlement of the golden mussel (Darrigran et al. 1998b). The high densities of golden mussel and their fixation to the substrate through byssal threads result in the formation of a new continuous microenvironment, which allows colonization by some epifaunal species and displaces others. The displacement of native mollusk species was recorded. After the introduction of *L. fortunei*, both *Ch. fluminea* and *G. concentrica* became rare, while other epifaunal macroinvertebrates were recorded for the first time (i.e. 8 species of Oligochaeta, 1 of Aphanoneura, 8 of Hirudinea, Amphipoda, Tanaidacea, Isopoda, Chironomidae, Turbellaria and Nematoda) (Darrigran 1991a) (Darrigran et al. 1998b).

Another example of impact on aquatic fauna is produced by the settlement of the golden mussel on native species, such as specimens of the bivalve *Anodontites trapesialis* (Lamarck) (Mycetopodidae), the crab *Aegla platensis* Schmitt (Anomura, Aeglidae) (Figure 6) and the introduced invasive bivalve *C. fluminea* (Darrigran et al. 2000).

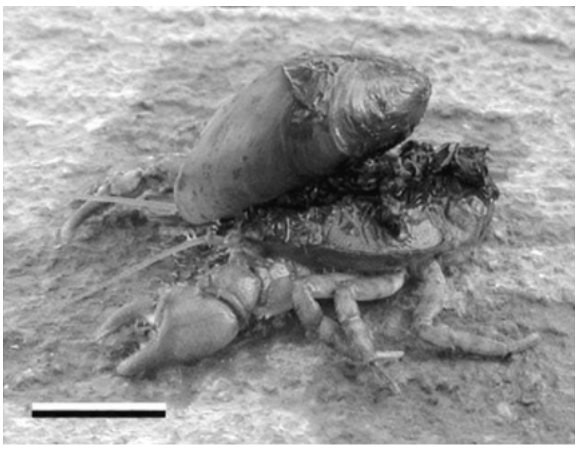

Figure 6. Infestation of *L. fortunei* on an endemic South American crustacean (*A. platensis*). Bar: 1 cm.

On the other hand, the large biomass, associated with high densities of *L. fortunei*, may impact aquatic food chains. Several species of native fish consume *L. fortunei* (López Armengol and Casciotta 1998; Montalto et al. 1999). For example, it constitutes the main food source for *Leporinus obtusidens* Valenciennes (Anostomidea) in the Río de la Plata (Penchaszadeh et al. 2000).

Asian clam or Corbicula fluminea *(Müller 1774)*

The genus *Corbicula* (Megerle) is another taxon whose range expanded rapidly after it was unintentionally introduced into the Neotropical region. *Corbicula fluminea* is the freshwater invader bivalve species with the most extensive distribution on the American continent. McMahon (2000) suggested that the introduction of *C. fluminea* into the Neotropical region occurred accidentally through the liberation of live specimens, which had been transported as a food source by Southeast Asian immigrants.

The morphological description of *C. fluminea* can be found in Ituarte (1994). It is a hermaphroditic species. The fertilization occurs inside the paleal cavity and larvae are incubated in branchial water tubes. After this protection period, larvae are released into the water. A short larval stage, the pediveliger, which is almost a juvenile stage (Cataldo and Boltovskoy 1999; McMahon 2000), is developed. These larvae settle and bury themselves in the substrate. The habit of this species is infaunal.

Ituarte (1981) first documented the presence of *C. largillierti* and *C. fluminea* for South America in the Río de la Plata, and estimated the date of introduction from Southeast Asia at the end of the 1960s and beginning of the 1970s. At that time, Veitenheimer-Mendes (1981) published the first record of this genus in Brazil and also estimated its introduction at the beginning of the 1970s. Veitenheimer-Mendes and Olazarri (1983) reported *Corbicula* sp. in Uruguay in 1979. The presence of *Corbicula* spp. in Bolivia and Peru is probable. The genus *Corbicula* is currently distributed along the main rivers of the Plata Basin, including the Río de la Plata, and the Paraná and Uruguay Rivers (Darrigran 1992b). In addition, the most southern distribution in America of this species is in a sandy shore of the Colorado River (39°01′ S–64°01′ W), in the Chilean–Patagonian subregion of the Atlantic versant, along the northern border of Patagonia (Cazzaniga 1997) (Figure 1).

Spatial–temporal distribution of the Corbicula *species in the Río de la Plata Basin*
At the beginning of the 1980s, *C. largillierti* occupied a continuous fringe along the littoral of the Río de la Plata, from its source Puerto Nueva Palmira (33°53′ S; 58°25′ W) to Magdalena Beach (35°01′ S; 57°31′ W), but it was not found in the tributary streams of the Río de la Plata (Ituarte 1981). Moreover, *C. fluminea* was only found to the north of Buenos Aires Port (34°29′ S; 58°28′ W) (Darrigran 1991a). Ten years later, Darrigran (1992b) described the variation in the distribution of the genus *Corbicula* along the Argentinean banks of the Río de la Plata; the distribution of *C. fluminea* was extended along all the littoral regions up to Punta Indio Beach (35°15′ S; 57°08′ W), while the distribution of *C. largillierti*, previously found in these littoral regions, declined. It is important to point out that *C. largillierti* predominated in density over *C. fluminea* in environments with muddy sediments (streams and lentic water bodies, close to the Río de la Plata), which clearly contrast with the typically sandy sediments of the coast of the Río de la Plata (Darrigran 1992a).

The advance in the distribution of *C. fluminea* may have lead to competition between the two species. Darrigran (1991b) analyzed the temporal variation of densities of both species in sympatric population at two locations in the Argentinean littoral of the Río de la Plata: Punta Blanca (34°56′ S; 57°40′ W) and Atalaya Beach (35°00′ S; 57°33′ W) (Figure 7). During 1985–1988, the density of the *C. largillierti* population in the Río de la Plata Basin decreased relative to that of *C. fluminea*. At present, *C. fluminea* is found in the littoral of the Río de la Plata and in many lotic and lentic environments associated with the Río de la Plata Basin, while *C. largillierti* is found only in some tributary streams, cohabiting with, but at lower densities than *C. fluminea* populations (Darrigran 1992b). Thus, I suggest that *C. fluminea* is potentially competitively superior to *C. largillierti*.

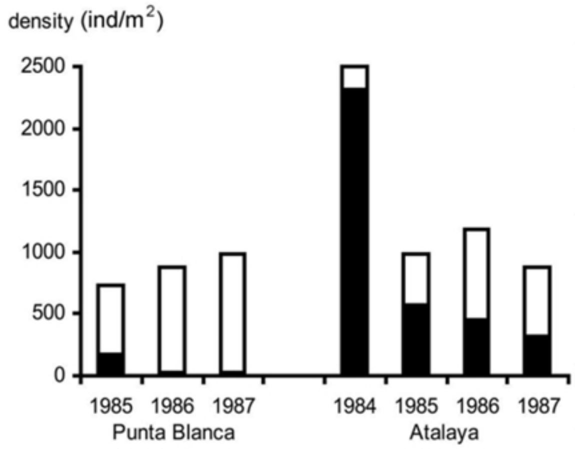

Figure 7. Densities of *C. fluminea* (white bars) and *C. largillierti* (black bars) at two localities of the Río de la Plata (taken from Darrigran 1991b).

Environmental impact
Impact on the human environment. The estimated date of introduction of *C. fluminea* into the Plata Basin is at the end of the 1960s in the Río de la Plata (Ituarte 1981) and at the beginning of the 1970s in Brazil (Veitenheimer-Mendes 1981). Up to now, no macrofouling cases have been recorded in Argentina. On the other hand, by the year 2000, the rapid increase in the distribution and abundance of *C. fluminea* in Brazil caused the first macrofouling cases to be reported from South America in power stations in the cities of Rio de Janeiro, Parana Panema and Minas Gerais, among others (Zampatti and Darrigran 2001).

Impact on the natural environment. The capacity of *C. fluminea* to thrive in a wide variety of environments and its high reproductive potential in North America and the Neotropical region (Correa et al. 1992; Darrigran 1992b) make this species an important component within the ecosystems of the Uruguay River and the Río de la Plata (Spinetti et al. 1992). Although we expect a displacement of the native mollusk fauna by *C. fluminea* in South America, there are no records on this subject.

Darrigran and Colauti (1994) described potential impacts of *C. fluminea* on the diet of the armado *Pterodoras granulosus* (Valenciennes), an omnivorous native fish of the Plata Basin (Hahn et al. 1992). Forty percent of the analyzed *P. granulosus* specimens had only *C. fluminea* in their gut (Darrigran and Colautti 1994).

Discussion

Invasive freshwater bivalves of the Neotropical region considered in this study, especially the golden mussel, produce significant abiotic and biotic changes either directly or indirectly:

(1) the introduction at specific coastal locations resulted in their dispersion through drainage systems with unpredictable consequences for the native biota (Darrigran et al. 2000);

(2) the alteration of natural ecosystems, since larval, juvenile and adult stages act at different levels of the same ecosystem, even producing changes in the diet of native species (Darrigran and Colautti 1994; Penchaszadeh et al. 2000); and
(3) not only the natural but also the human environment is altered, negatively impacting industrial operations and causing economic losses (Darrigran and Ezcurra de Drago 2000).

These introductions resulted in problems similar to those caused by the introduction of *C. fluminea* and *D. polymorpha* into the Northern Hemisphere.

Morton (1996) describes the characteristics of successful invader species to new regions. The golden mussel and the Asian clam have those characteristics in the Plata Basin, overcoming the sequential transitions of the invasion process successfully. However, no major problems were detected since the second species was introduced in South America at the beginning of 1970s. On the other hand, *L. fortunei* has demonstrated a great reproductive capacity, colonizing the wide variety of environments offered by the Plata Basin and causing several macrofouling problems within the region. These are similar to those described for *D. polymorpha* in the Northern Hemisphere, which create huge losses for companies that draw *raw* water from freshwater bodies for different purposes in Europe, Canada and the USA.

Corbicula fluminea is regarded as a 'pest species' in the USA (McMahon 1983), due to problems created for sand companies, watering channels and the raw water systems of factories and power stations near water bodies. This species entered North America in 1924 (McMahon 1983). The rapid spread of *C. fluminea* through North American freshwater has been the result of human activities (McMahon 2000): as fish bait (Goodchild 2000); as aquarium specimens or the transport of juveniles as a tourist curiosity (McMahon 1982), or the juvenile byssal attachment to boat hulls, which facilitates long-distance dispersal (McMahon 2000). Likewise, the Asian clam has extensive capacities for natural dispersal: downstream, the pediveliger and juvenile (<2 mm) are passively transported, and juvenile byssal attachment to floating vegetation or small specimens of *C. fluminea* secrete long mucous threads and their exhalant siphons act as draglines to buoy the animal into the water column (Prezani and Chalermwat 1984). However, the pediveliger larvae and juveniles are also transported on the feet or feathers of aquatic birds, downstream or upstream (McMahon 1982). Although no data are available on the dispersal of *C. fluminea* in South America, similar spread mechanisms to those observed into North America could occur.

Since the introduction of *L. fortunei* into South America through the Río de la Plata, it has infested a large geographic area representing a diversity of habitat types. The range of expansion through the freshwater ecosystems in the Plata Basin drainage has been extremely rapid, estimated at 240 km/year (Darrigran and Ezcurra de Drago 2000). This rate of dispersal is similar to that shown by *D. polymorpha* since its introduction into North America (Claudi and Mackie 1994). The dispersal of this last species in North America occurred quickly via natural downstream movement of veligers. However, other mechanisms may also contribute to the dispersion such as adult mussels attached to floating debris (Mackie and Schloesser 1996). The dispersal of *L. fortunei* throughout the Plata Basin is also quick, but it occurs upstream in the rivers. The main rivers of the Plata Basin are navigable and this results in intense commercial traffic. Therefore, the dispersal of the golden mussel is believed to occur primarily through the attachment to commercial and recreational ships. The dispersal rate of *L. fortunei* in Japan, which occurred after the release of imported *Corbicula* spp. into Japanese waters (T. Kimura, pers. comm.), is lower than in South America. In Japan, the golden mussel has been reported in three areas: Biwa Lake, Kiso Rivers (Kiso, Ibi, Nagara) and Yodo River (Kimura et al. 1999); after this, *L. fortunei* has never been reported in any other parts of Japan. The Japanese government promoted quantitative analysis of *L. fortunei* in Biwa Lake and Yodo River from 1994 to 1996, but the results have not been published yet (T. Kimura, pers. comm.).

Information about benthic communities, species richness and environmental characteristics of the water bodies of the Plata Basin is scarce. The epizoic colonization of native naiads (Hyriidae and Mycetopodidae) by the golden mussel is the most direct and severe ecological impact. This type of impact is similar to that caused by *D. polymorpha* on native bivalves of the Northern Hemisphere (Ricciardi et al. 1997). In cases of mussel infestation, displacement of the native species occurs due to their incapacity to open or shut their valves due to the presence of byssally attached mussels on the bivalve shells. Although in South America, the quantitative impact caused by *L. fortunei* on native naiads is unknown, in

North America infestation of bivalve native fauna by *D. polymorpha* may result in density reductions or even loss of species (Bogan 1994; Gillis and Mackie 1994; Ricciardi et al. 1995, 1996, 1998; Schloesser et al. 1998).

As occurred in North America with the introduction of *D. polymorpha* to the Great Lakes, the establishment of *L. fortunei* in the Plata Basin added the first epifaunal mussel to the freshwater communities. Both zebra mussel and golden mussel colonizations alter the abundance and composition of benthic macroinvertebrate communities. Dense golden mussel populations create habitats for diverse taxa and increase the benthic substrate heterogeneity. Some benthic native invertebrates (e.g. native bivalves) are adversely affected by *L. fortunei* (Darrigran 2000; Darrigran et al. 2000), whereas others, including Oligochaeta and Hirudinea, exploit structures associated with high, dense infestations of the golden mussel (Darrigran and Ezcurra de Drago 2000; Darrigran et al. 2000). The increase in macroinvertebrates' diversity associated with the golden mussel is similar to that recorded for *D. polymorpha* infestations in the Northern Hemisphere (Ricciardi et al. 1998). It is expected that where golden mussel populations exist, independently of regional climates, they would associate with species of benthic macroinvertebrates with similar habits to those recorded by Darrigran et al. (1998b). *Limnoperna fortunei* infestations could result in the elimination of regional differences (Westbrooks 2000) in epifaunal species.

Darrigran et al. (1999) described the reproductive biology for the founding population at Bagliardi Beach, in Rio de la Plata, Argentina, and reported some differences from the Hong Kong population described by Morton (1982), the other known reproductive study. The main difference is that the spawning periods (both spring and summer ones) in South America are longer than in Hong Kong populations and larvae are absent only during two winter months (Cataldo and Boltovskoy 2000). Darrigran et al. (1998a) first reported hermaphroditism in this species, whereas Morton (1982) did not find hermaphrodite specimens in the Hong Kong population. The golden mussel life span is highly variable, estimated to be up to 3 years in the Neotropical temperate region (Boltovskoy and Cataldo 2000), up to 2 years in the Uji River, Japan, and up to 4–5 years in Korea (Iwasaki and Uriu 1998).

In South America, adult golden mussels have been found in the stomachs of several native fishes (Montalto et al. 1999), but the relative contribution of the fish to predation *on* golden mussel is unknown. Only *L. obtusidens* has been studied in detail (Penchaszadeh et al. 2000).

It is important to note the filtering capacity and bioaccumulation of xenobiotics of these bivalves, as well as their potential use as bioindicators of environmental conditions in South America (Colombo et al. 1990; Darrigran 1994; Cataldo et al. 2001). Both invader species can be regarded as biological monitors, similar to the Asian clam in freshwater environments of North America (Belanger et al. 1987; Doherty 1990).

Since the introduction of the golden mussel into the Plata Basin, several research lines have been started, such as population dynamics and their impact on native species (Darrigran et al. 1998b); distribution and impact (Darrigran 2000; Darrigran et al. 2000; Darrigran and Ezcurra de Drago 2000); reproductive biology (Darrigran et al. 1998a, 1999) and predation (Penchaszadeh et al. 2000). Others are in progress (e.g. larval development and individual growth) as well as the biotest (e.g. resistance to air exposition and poisoning). The aim of this research is to provide the necessary information for the control of current bivalve invasion and the prevention of their economic impacts.

Many other aspects are completely unknown, for instance, the filtering capacity of the golden mussel. Because of its high density in the Plata Basin, this species could increase water clarity as the zebra mussel has done in the Northern Hemisphere. An increase in water clarity could stimulate the growth of benthic plants (MacIsaac 1996). In this respect, to counteract the adverse economic impact of their macrofouling, the application of 'biomanipulation' programs for these invasive bivalve species could prove beneficial, for example, in fish production, reduction of algal biomass, increased water clarity, use as environmental bioindicators, etc.

Due to the different life strategies, the two case studies have different environmental and economic impacts. *Corbicula fluminea* has less reproductive capacity than *L. fortunei* and the branchial incubation slows down the dispersal rate mechanisms. The spread rate of the Asian clam also depends mainly on human activities, especially related to fishing (McMahon 2000). This species shares the habitat with native bivalve species. On the other hand, the natural and economic impacts of *L. fortunei* in the Plata Basin are substantial. This species has a greater reproductive capacity. The byssally attached epifaunal freshwater niche was free before its invasion into the Plata Basin, so it has no habitat competitors. In addition, the long, free larval development and the unintentional dispersal via ships allows the golden mussel to be quickly and widely spread along the Plata Basin. These facts allow *L. fortunei* to have a great economic impact on human environment.

Genetic variation and test alleles are other aspects that could be studied. This research could analyze populations' genetic variation and allele heterozygosity of the golden mussel from South America, Japan and Southeast Asia. Similar analyses would be done for the Asian clam, between Southeast Asian, North and South American populations. Lee and Bell (1999) consider that the application of molecular tools can provide insight into pathways, timing, sources and direction of invasions. This study should be directed to detect invasion corridors (transportation systems and pathways that facilitate the long-distance dispersal of species to particular regions) (Ricciardi and MacIsaac 2000). This kind of knowledge may be incorporated into predictive models.

Finally, although *C. fluminea* has been found in North America since the beginning of the twentieth century (McMahon 2000), the golden mussel has not yet entered that subcontinent. It is expected that the absence of international legislation and effective control of vessel ballast waters would eventually lead to the introduction of this species into North America (Ricciardi 1998). The probability of invasion by *L. fortunei* into North America is now greater than in South America, since this last subcontinent can be affected only by vessels coming from Southeast Asia, while vessels from both Southeast Asia and South America are potential agents of the species introduction into North America. The same reasoning can be applied to Europe. Considerable commercial trade exists between South America and southern Europe (e.g. Spain), especially during this last decade. For this reason, higher control on ballast water must be enforced to avoid the dangerous spread of *L. fortunei* into Europe and North America.

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