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## Byssal hairs in the invasive Asian freshwater bivalve *Limnoperna fortunei* (Mytilidae) in the Paraná River system with comments on this species in South America

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We recorded, for the first time, byssal hairs in the Asian freshwater bivalve *Limnoperna fortunei* from the Paraná River system. We analysed the presence of hairs and their distribution on the shell in relation to habitat and shell size in 12 sites. Hairs were present in lentic habitats associated with macrophytes or organic matter, but were absent in lotic environments. The proportion of mussels with hairs was negatively correlated with current velocity. Hairs were more frequent and abundant in larger mussels. In general, the hairs are a similar length over the bivalve and almost entirely cover the shells in  $\geq 60\%$  in lentic habitats. The projections allow *L. fortunei* to be camouflaged among the roots of macrophytes or coarse organic matter, assisting in avoiding visual predators. The clear-cut separation of *L. fortunei* populations into two different groups could be associated with phenotypic plasticity in this species.

**Keywords:** golden mussel; non-native species; phenotypic plasticity; byssal hairs; camouflage; bivalve

### Introduction

It has been more than 20 years since the invasive freshwater mussel *Limnoperna fortunei* (Dunker, 1857) (golden mussel) was first recorded in South America. This species is a native of southern Asia, including China, Thailand, Korea, Laos, Cambodia, Vietnam and Indonesia (Ricciardi and Rasmussen 1998). *Limnoperna fortunei* first appeared in Hong Kong in 1965 (Morton 1975), and between 1980 and 1990 it spread to Taiwan and Japan (Ricciardi and Rasmussen 1998; Magara *et al.* 2001). In 1991, *L. fortunei* settled in South America, in the Río de la Plata estuary in Argentina (Pastorino *et al.* 1993) and, in 1996, in the Middle Paraná River floodplain habitats (Darrigran and Ezcurra de Drago 2000). The arrival of this species was unintentional, probably through larvae or juveniles via ballast water released from ships into the Río de la Plata basin. *Limnoperna fortunei* has since spread to Argentina, Brazil, Uruguay, Bolivia and Paraguay (Darrigran 2002; Boltovskoy *et al.* 2006).

The globalisation of economics and trade has facilitated the spread of exotic species. The golden mussel is considered to be one of the most significant suspension feeding freshwater invaders, and it has successfully overrun different aquatic habitats, benefiting from biological and ecological features such as free-swimming planktonic larvae, high rate of reproduction, rapid development time and epifaunal habit. The presence of a byssus

allows it to attach to almost any available natural substrate such as tree trunks, rocks, aquatic macrophytes, other organisms and compacted silt-sand and artificial substrates such as piers, filters, pipes and walls (Darrigran 2002; Karatayev *et al.* 2007a). *Limnoperna fortunei* shares these traits with another invasive Asian freshwater species *Dreissena polymorpha* (Pallas, 1771) (zebra mussel) that has spread through much of Europe and North America. Both species are very tolerant of a broad range of physicochemical conditions and different habitat characteristics. In this respect, both species have a similar impact on habitat structure, biomineralisation, oxygenation, and benthic and planktonic community structure as ecosystem engineers (summarised by Darrigran 2002; Karatayev *et al.* 2007a, b; Darrigran and Damborenea 2011; Rojas Molina *et al.* 2012). Another invasive Asian species that has spread in Europe and North America is *Dreissena rostriformis bugensis* (Andrusov, 1897) (quagga mussel), which is a similar life strategist and is becoming dominant in habitats of the Great Lakes (Peyer *et al.* 2010).

Due to its biotic potential, *L. fortunei* has a significant economic and ecological impact. The first substantial impact on human activities in the neotropical region was related to macrofouling by golden mussels in industrial and power plants. The consequences include the reduction or blocking of pipe diameters, filters, heat exchangers and water flow as well as occlusion by accumulation of empty

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shells, or water pollution inside the system due to mussel mortality (Cataldo *et al.* 2003; Darrigran and Damborenea 2006).

The arrival of *L. fortunei* in Argentina has resulted in different biotic interactions. This species has been incorporated into the diet of many fish species (Montalto *et al.* 1999; Ferriz *et al.* 2000; Pentchaszadeh *et al.* 2000; García and Montalto 2006; Paolucci *et al.* 2007), and has been recorded as one of the trophic options for crabs in Portunidae and Trichodactylidae (César *et al.* 2003; Torres *et al.* 2012). The impact of the filtering activity of this bivalve on planktonic animals, protozoans and algae can modify plankton density and structure, and can transfer energy and material from the water column to the benthos, thus serving as a link between the planktonic and benthic components of the ecosystem (Rojas Molina and José de Paggi 2008; Boltovskoy *et al.* 2009; Rojas Molina *et al.* 2010, 2012; Frau *et al.* 2013). Some authors have mentioned that *L. fortunei* beds represent a new habitat for benthic invertebrate development (Darrigran *et al.* 1998; Sardiña *et al.* 2011).

In this study, we report the presence of byssal hairs on juveniles and adults of *L. fortunei*. This feature does not seem to have been previously reported for *L. fortunei*, but similar structures have been found in some marine mytilids including *Mytilus* Linnaeus, 1758 (Dixon *et al.* 1995) and *Modiolus* Lamarck, 1799 (Carter and Aller 1975; Bottjer and Carter 1980; Ockelmann 1983). We analyse the presence of byssal hairs and their distribution on the shell surface in relation to *L. fortunei* size and habitat in several environments of the Paraná River.

## Materials and methods

### Study area and sampling

The Paraná River is the second largest hydrographic system in South America and drains an area of 26,106 km<sup>2</sup> along its length of 3800 km (Paoli *et al.* 2000). Along its right bank, in the middle stretch, a wide floodplain extends comprising numerous permanent and temporary water bodies as well as a great number of islands and banks (Drago 1989; Ramonell *et al.* 2000). The annual phases of flood and drought, and the complex hydrological connectivity between lotic and lentic environments, are the main factors that characterise lateral and longitudinal exchanges of sediments, organic matter and organisms structuring the ecosystems (Junk *et al.* 1989; Neiff 1990; Drago 2007). Thus, in these systems, *L. fortunei* populations are subjected to flood pulses; during high water levels, this species colonises different floodplain habitats and during drought phases mussels can be affected by desiccation (Montalto and Ezcurra de Drago 2003; Ezcurra de Drago *et al.* 2006).

From November 2009 to March 2012, mussel samples were collected in different aquatic environments of

the middle Paraná River floodplain (covering approximately 300 km; Fig. 1). Sites included the main channel and other habitats with different degrees of connectivity, with some of them being connected permanently or temporarily to the main channel of the Paraná River. Lotic environments included a site in the main channel which is 603 km upstream from its mouth (PMC), two sites in the secondary channels: San Gerónimo (permanent flow, SC1) and Colastinecito (low intermittent flow, SC2), and a site at the entrance of the channel leading to the harbour of Santa Fe city (EC). Other sampled sites included a minor channel (MCa and MCb) with low current velocity and a site in a small standing water area located in the main channel of the Paraná River up to Corrientes city (SWA). In the lentic environment, six lakes with different connectivity were sampled (L1, L2, L3, L4, L5, and L6—see Fig. 1).

Mussels were collected from: a marker buoy in PMC; coarse particulate organic matter (CPOM) of the bottom sediment in SC1, SC2, MCb and L3; the roots of *Eichhornia crassipes* (Martius) Solms-Laubach, 1883 in MCa, SWA, L1, L2, L4, L5, and L6; and the rhizome of *Paspalum* Linnaeus, 1759 in EC. In all the sampled sites, mussels were manually removed, placed in containers, and fixed and preserved in a 10% formaldehyde solution. The environmental characterisation of each site and the substratum from which the specimens were taken are shown in Table 1.

### Biological material and data analysis

Bivalves were counted and their maximum valve lengths were measured with a digital caliper ( $\pm 0.01$  mm precision). When the mussels were small and their manipulation difficult, the measurement was performed using a compound binocular microscope with an ocular scale. In each site, when the mussels sampled were fewer than 200 individuals, the organisms were completely analysed. When the sample pools of *L. fortunei* were abundant, individuals were selected at random and analysed, until reaching a count of c. 200 individuals. The presence or absence of hairs on the shell was recorded. We followed the criteria of Ockelmann (1983) who considers that the hairs of mytilids are secretions of byssus glands, shaped and applied by the foot to the exterior part of the shell. These structures are proteinaceous, non-calcified flexible projections, and lack internal vacuolisation (Bottjer and Carter 1980).

Organisms with hairs were observed under a binocular stereoscopic microscope and grouped into five patterns that were defined in relation to spatial distribution and the proportion of the shells covered by hairs (Fig. 2): (1) bivalves with isolated hairs; (2)  $\leq 20\%$  of the shell covered by an area of hairs in the dorsal-posterior shell margin; (3)  $> 20\%$  to  $50\%$  of the shell covered by hairs from the dorsal edge (without the umbo) to the centre of the shell; (4)  $> 50\%$  to  $70\%$  of the shell covered in the posterior

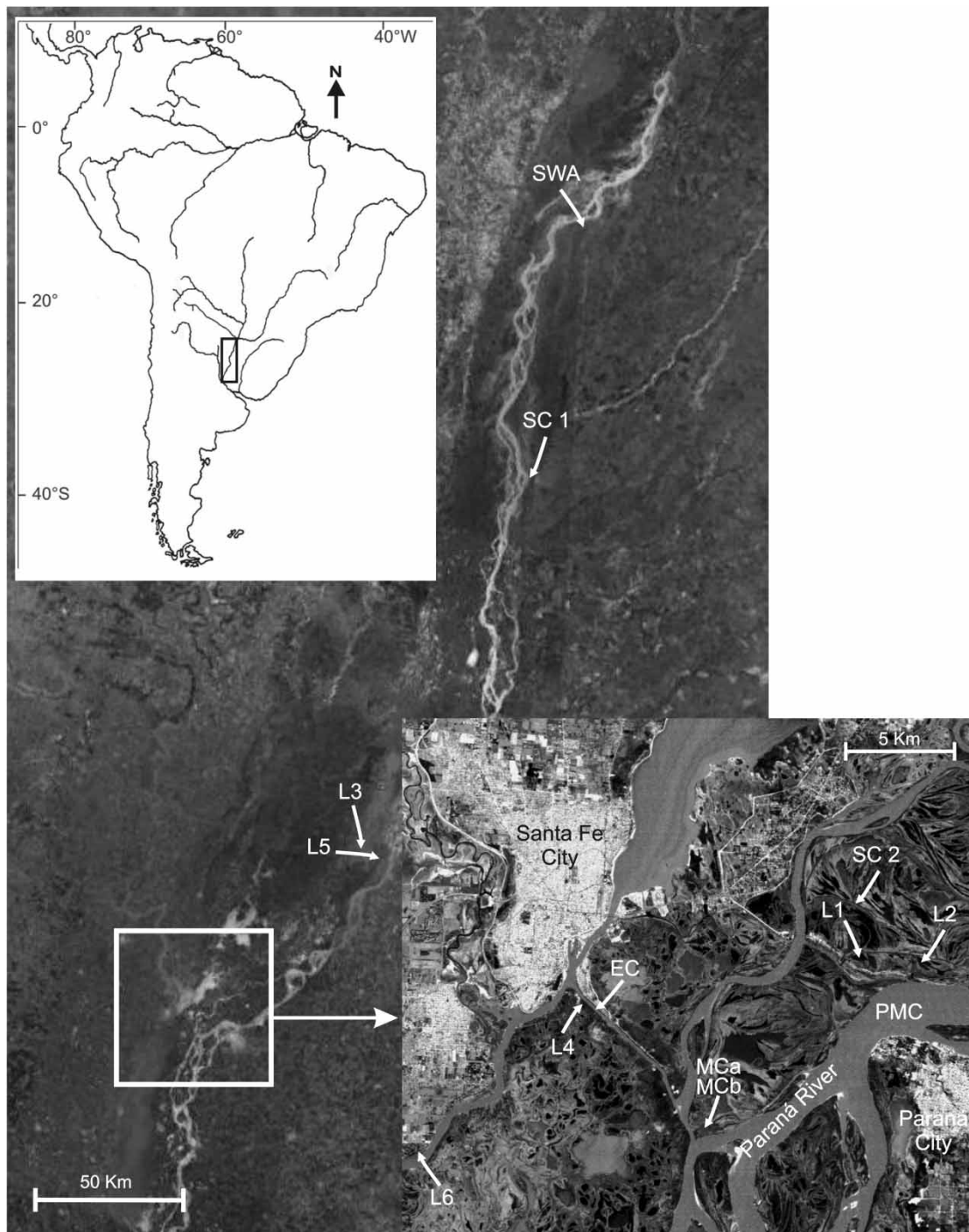


Figure 1. Study area showing sample sites in the Paraná River system (Argentina). Abbreviations: PMC—Paraná River main channel; SC1—San Gerónimo secondary channel; SC2—Colastinecito secondary channel; EC—entrance channel to the harbour of Santa Fe city; MCa—minor channel where mussels were attached to macrophytes; MCb—minor channel where mussels were attached to coarse particulate organic matter; SWA—small standing water area in main channel; L1, L2, L3, L4, L5, and L6, Lakes.

region of the shell (without the umbo); and (5) > 70% to 95% of the shell covered by hairs (with or without the umbo), with the antero-ventral extreme being hairless.

The non-parametric Kruskal-Wallis (KW) and Mann-Whitney (MW) tests were applied (transformation of the

data failed to improve their normality, so non-parametric tests were required) to compare the sizes of the organisms among the sites studied and between the mussels, with and without hairs. The multiple Dunn test was employed for the post-test analysis. Relationships between

Table 1. Physical and chemical parameters recorded in the sampled sites.

Site	Abbrev.	Location	Date	Secchi (cm)	Depth (m)	Temp. (°C)	pH	Cond. (µS)	DO (ppm)	Current velocity (m/s)	Substrate
Paraná River (603 km)	PMC	31°44'30" S 60°39'51" W	13/05/2011	26.1	5.2	19.0	7.9	75.5	8.5	1.3	Marker buoy
San Gerónimo River	SC1	29°10'23" S 59°29'03" W	04/11/2011	59.0	4.0	24.8	7.2	ND	7.5	0.65	CPOM
Colastinecito River	SC2	31°39'13" S 60°34'16" W	23/03/2012	11.0	2.5	25.2	7.3	88.0	6.7	0.4	CPOM
Entrance channel to the harbour of Santa Fe city	EC	31°40'37" S 60°41'43" W	13/05/2011	30.0	7.0	20.0	6.7	82.5	7.1	0.36	<i>Paspalum</i> rhizome
Minor channel <sup>a</sup>	MCa and MCb	31°43'37" S 60°39'27" W	13/05/2011	49.0	7.8	21.9	7.3	96.0	8.1	< 0.1	<i>E. crassipes</i> roots (MCa) and CPOM (MCb)
Standing water area (Paraná River)	SWA	30°00'59" S 59°32'15" W	21/10/2011	ND	ND	26.7	7.7	270.0	4.5	< 0.1	<i>E. crassipes</i> roots
Lake 1	L1	31°40'22" S 60°34'17" W	05/11/2009	88.0	3.0	24.0	6.6	49.0	4.7		<i>E. crassipes</i> roots
Lake 2	L2	31°40'32" S 60°32'43" W	25/11/2009	80.0	5.7	27.0	6.7	64.2	1.1		<i>E. crassipes</i> roots
Lake 3	L3	31°10'50" S 60°05'26" W	06/10/2010	99.0	2.1	18.4	ND	ND	6.4		CPOM
Lake 4	L4	31°40'40" S 60°42'44" W	13/05/2011	38.0	3.4	19.0	6.8	109.9	6.0		<i>E. crassipes</i> roots
Lake 5	L5	31°10'38" S 60°02'23" W	04/10/2011	100.0	2.1	19.1	ND	ND	6.3		<i>E. crassipes</i> roots
Lake 6 <sup>b</sup>	L6	31°43'14" S 60°47'29" W	11/10/2011	37.4	2.0	19.9	6.9	201.7	7.1		<i>E. crassipes</i> roots

Notes: Abbrev.—Abbreviations; Cond.—conductivity; DO—dissolved oxygen; ND—no data; Temp.—temperature.

<sup>a</sup>Average of the environmental variables measured during April 2005–March 2006 (Zilli and Marchese 2011).

<sup>b</sup>Average of the environmental variables measured during January 1995–December 1995 (Collins 2000).



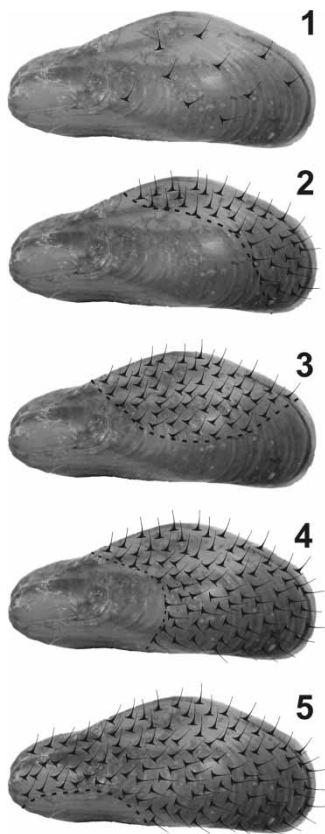


Figure 2. Spatial distribution patterns of byssal hairs on the shells (1 to 5) (lateral view of left valve). Hairs are represented by symbols.

the proportion of mussels with hairs and the environmental parameters, and between the size of the bivalves with hairs and the patterns of hair distribution, were analysed using the Spearman rank correlation coefficient ( $Rho$ ). A significance level of 95% was used for all statistical analyses. The statistical analyses were performed using SPSS software (version 18).

## Results

In the present study, 2524 bivalves from 12 sampled sites were analysed. Overall, 42% of the total bivalves ( $n = 1063$ ) had hairs. The byssal hairs were simply pointed, slightly curved, with a widened base and presented a similar size in each individual (Fig. 3). The hairs were similar in form and structure to those described for *Mytilus edulis* Linnaeus, 1758; *Modiolus rectus* (Conrad, 1837) and *Modiolus thorsoni* Ockelmann, 1983 (Bottjer and Carter 1980; Ockelmann 1983; Dixon *et al.* 1995).

The presence of hairs was observed in lentic habitats (lakes, MCa, MCb, and SWA). In L6 and SWA, only individuals with hairs were recorded, while in lotic environments (PMC, SC1, SC2, and EC) only mussels without hairs were registered. In the sites in which both kinds of

mussels were present, in general more than the 50% had hairs (except in L3) (Fig. 4). The proportion with hairs was negatively correlated with the current velocity of the sampled sites ( $Rho = -0.6451$ ;  $P = 0.0173$ ), whereas the other environmental parameters exhibited no correlation.

The size of all the analysed mussels ranged between 0.05 to 19.7 mm in length, with the highest mean size in the sites L3, L6, and SC2 (11.7 mm for L3, and 11.1 mm for the others) and the smallest mean size (1.6 mm) in EC. The size variation was significant among the sites (KW = 1170.6,  $P < 0.0001$ ; Fig. 5).

The size of the mussels without hairs was between 0.05 to 19.4 mm with a mean length of 7.3 mm. Mussels with hairs ranged from 0.2 to 19.5 mm in all datasets. The variation in the shell size was significant among the sites (KW = 292.7;  $P < 0.0001$ ), with L3, L6 and SWA being the sites that had the highest mean size (11.7, 11.1 and 10.8 mm respectively; Fig. 5).

In sites with low current velocity (lakes and minor channels, except L3), 70%–95% of the total number of mussels without hairs were smaller than 5 mm (pre-reproductive). In lotic sites, post-reproductive organisms ( $> 5 - 10$  mm and  $> 10 - 15$  mm) without hairs were in a higher proportion than in lentic sites (except EC). On the other hand, in lentic sites, mussels with hairs  $< 5$  mm represented less than 50% (except MCb), with the largest being dominant (Fig. 6).

Among all datasets of mussels with and without hairs, a comparison of the valve size indicated no significant difference (MW = 760172,  $P = 0.366$ ). On the other hand, there was a significant difference between the sizes of the hairy and smooth mussels at each site (MW = MCa: 288.0,  $P < 0.001$ ; MCb: 1963.5,  $P < 0.001$ ; L1: 947.5,  $P < 0.001$ ; L2: 806.0,  $P < 0.001$ ; L3: 3334.5,  $P = 0.001$ ; L4: 308.5,  $P < 0.001$ ; L5: 247.5,  $P = 0.008$ ; Fig. 5).

In each site, all patterns were observed, with the exception of pattern 4 which was evident in only three lakes, but with a different frequency (Figs 2 and 7). Pattern 5 has a higher occurrence in all sites (except for MCb). This pattern was represented by  $\geq 60\%$  of the sampled mussels in sites where they were associated with macrophytes. Bivalves associated with CPOM (MCb and L3) showed a higher frequency of the patterns of hair coverage ( $\leq 50\%$  of the shells—patterns 1 to 3), with MCb being significantly different from the rest of the sites (KW = 97.4;  $P < 0.001$ ; Dunn: vs L1, L2, L4, L5, L6, SWA, and MCa =  $P < 0.001$ ; vs L3 =  $P < 0.05$ ). In the lakes studied, L4 was different from L1 ( $P < 0.05$ ) and L3 ( $P < 0.01$ ).

The size of mussels was associated with the hair coverage patterns of shells, with the largest individuals presenting a higher percentage of coverage. The Spearman correlation coefficient showed a significant direct relationship between them, apart from L3 and L6 sites (Fig. 8).

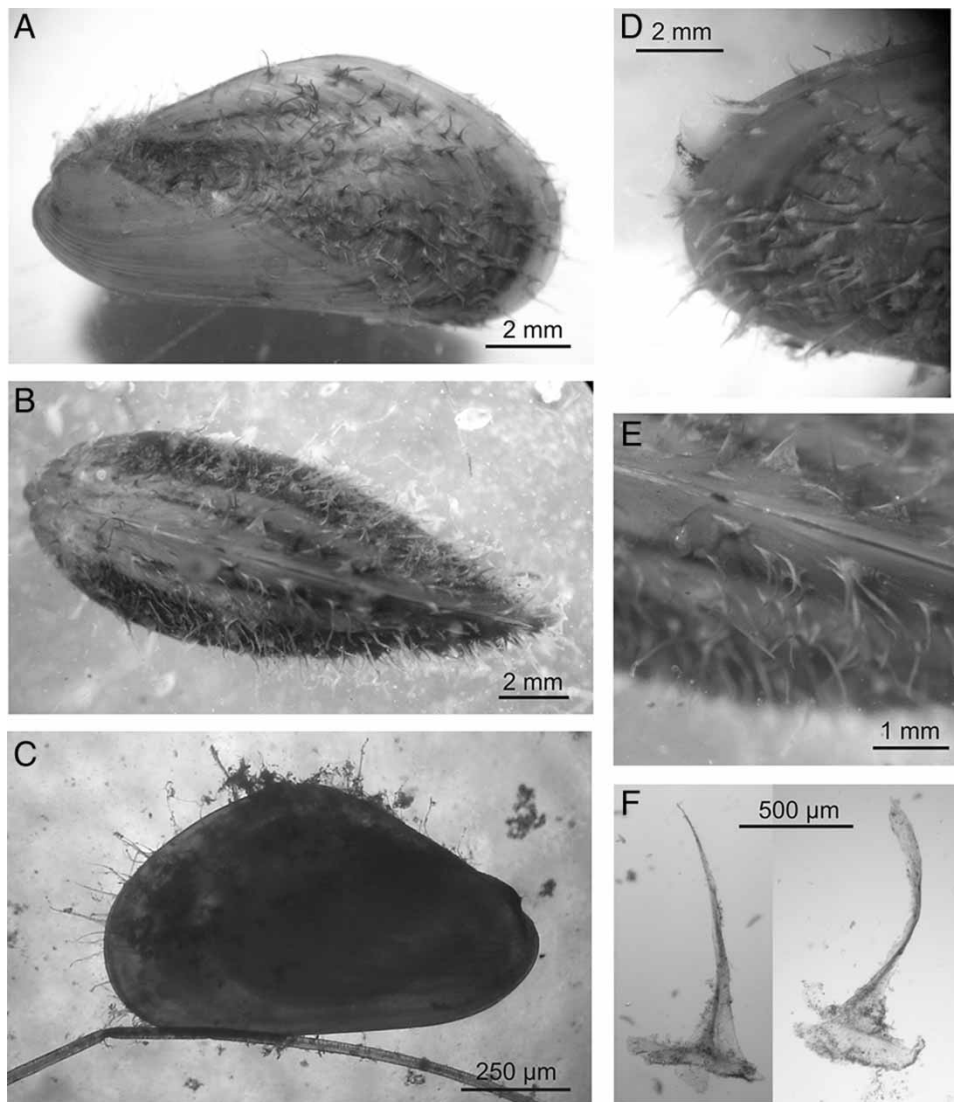


Figure 3. Byssal hairs of *Limnoperna fortunei* from the Paraná River floodplain, Argentina. **A**, Lateral view of left valve; **B**, dorsal view of a specimen; **C**, lateral view of juvenile attached to *Eichhornia crassipes* root; **D**, and **E**, details of the byssal hairs; **F**, individual byssal hairs under optic microscope.

## Discussion

### Byssal hairs

Projecting structures such as hairs, shingles and thorns are features of several bivalve superfamilies such as Arcoidea, Mytiloidea and Veneroidea (Vance 1978; Bottjer and Carter 1980; Ockelmann 1983; Feifarek 1987; Dixon *et al.* 1995; Harper 1997; Willman 2007).

In morphological studies of *L. fortunei*, there is no reference to byssal hairs (Dunker 1856; Morton 1973). Morton (1973) described a smooth and shiny periostracum for this species and he made no reference to any projections. Although there have been many ecological and biological studies in native and invaded locations about this species, byssal hairs do not appear to have been reported (Morton 1973, Montalto *et al.* 1999; Montalto

and Ezcurra de Drago 2003; Montalto and Marchese 2003; Rojas Molina and José de Paggi 2008; Rojas Molina *et al.* 2010, 2011, 2012). However, images of individuals with this characteristic can be found on the web (<http://ecology.woweb.net/x/15240>) and in at least one paper (Avelar *et al.* 2004).

In accordance with Ockelmann (1983), we observed that the projections of *L. fortunei* can be considered byssal hairs similar in form to those described for marine species of *Modiolus*, *Mytilus* and *Trichomya* Ihering, 1900 (Bottjer and Carter 1980; Ockelmann 1983; Dixon *et al.* 1995).

Considering the gregarious byssal epifaunal habits of *L. fortunei*, it is common to observe byssus threads attached to shells of conspecifics, which could be confused

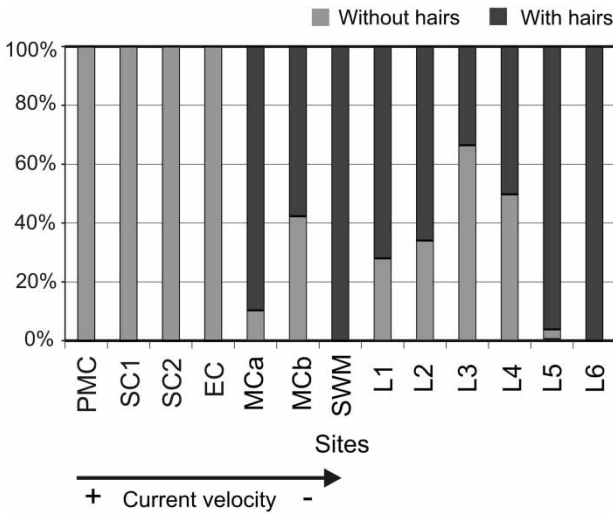


Figure 4. Relative proportion of molluscs with and without byssal hairs in each sampled site.

with these projections. However, as it was mentioned by Ockelmann (1983) and Dixon *et al.* (1995) for Mytiloidea, adventitious hairs are clearly different and distinguishable from byssus threads, which have a more uniform diameter and, in general, are longer and have typical plaque areas.

Byssal hairs in the golden mussel *L. fortunei* were found in both pre-reproductive and adult individuals, being more frequent and abundant in adults of a larger size. In general, the hairs show a similar length in the bivalve and cover the shells almost completely.

**Hairs and environmental characteristics**

Invasive species tend to be phenotypically plastic (Pigliucci 2005), and acclimatisation can be important, responding to biotic and abiotic changes (Strayer *et al.* 2006). These can be manifested as changes in morphology, physiology, life history or behaviour, as well as an improvement in the invasiveness of the exotic species that have been introduced into new habitats (Engel *et al.* 2011).

The correlation between habitat characteristics and morphological changes in bivalves, including invasive species (shell form, weight, periostral projections, etc.), has been analysed by several authors (Bottjer and Carter 1980; Watters 1994; Hornbach *et al.* 2010; Peyer *et al.* 2010). For *Dreissena polymorpha* and *Corbicula fluminea* (Müller, 1774), significant differences in palp and gill area ratios were mentioned in relation to the suspended solid concentration, and they showed larger palps and smaller gills in habitats with a high suspended solid concentration (Payne *et al.* 1995). In the case of *L. fortunei*, similar changes in the relationship between gill and shell areas, associated with variations in environmental factors, have

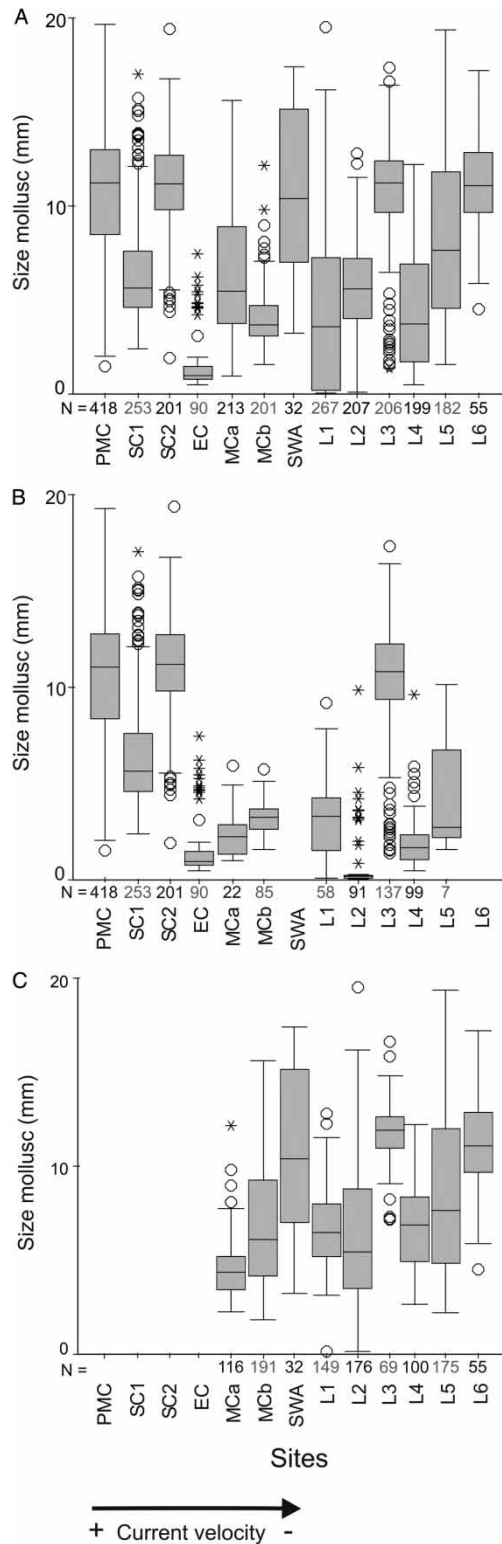


Figure 5. Variation of the mussel sizes registered in each site. **A**, All dataset of sampled bivalves; **B**, mussels without hairs; **C**, molluscs with byssal hairs. Outer lines are the 95th percentiles; upper and lower boundaries of the box are the 90th percentiles; and the horizontal line in the box interior is the median value. Circles and asterisks are atypical and extreme values, respectively.



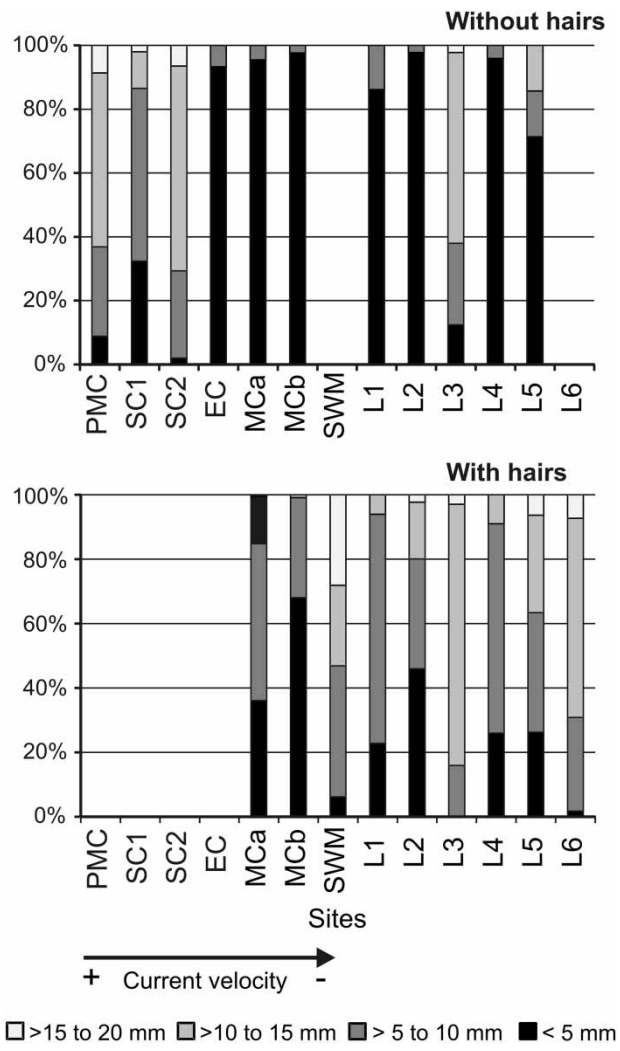


Figure 6. Relative number (%) of mussels for four size ranges: < 5 mm; > 5 – 10 mm; > 10 – 15 mm; > 15 – 20 mm.

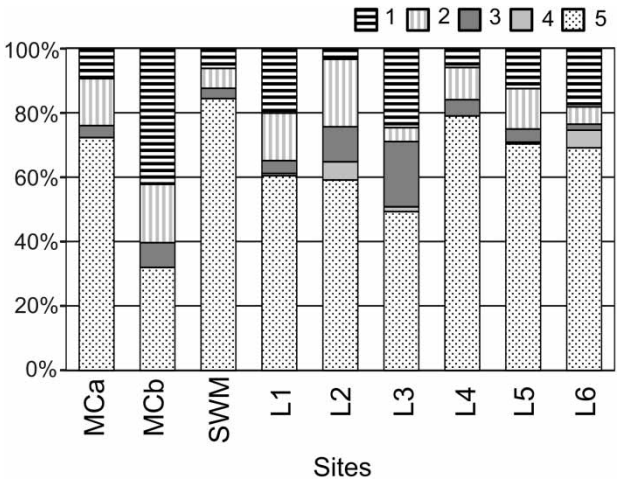


Figure 7. Relative frequency (%) of byssal hair distribution patterns (1 to 5) in each site.

recently been described (Paolucci *et al.* 2011). Another example is that recorded by Peyer and collaborators (2010) and Pavlova (2012), in which different shell morphology in *Dreissena rostriformis bugensis* could be caused by environmental variables resulting in two morphotypes, one typical of shallow water conditions and the other present in deep habitats. This plastic response might confer competitive advantages to *D. rostriformis bugensis*, allowing the species to colonise a wider range of habitats than another invasive species, *D. polymorpha*.

Ockelmann (1983) suggests that the deposition of byssal hairs does not happen at random and seems to be influenced by conditions in the immediate habitat of the mussel. In this respect, Bottjer and Carter (1980) found that the presence of hairs is related to low external abrasion and low general energy in the environment, as was recorded in the present study. These authors mentioned that hairs were more common in infaunal/semifaunal bivalves, or in epifaunal species that attach to hard substrates (shells, coarse gravels, rocks) than in soft ones (mud, sand, plants). Contrary to Bottjer and Carter (1980), in *L. fortunei* a higher proportion of hairs was found in specimens associated with soft substrates such as roots of floating macrophytes or bottom necromass. During the first period of invasion, *L. fortunei* was observed to be more commonly attached to different hard substrates such as rocks, submerged trunks and man-made structures (Boltovskoy *et al.* 2006; Darrigran and Damborenea 2006, 2011); however, later, this bivalve used mobile soft substrates such as standing macrophytes or bottom necromass. The use of macrophytes as habitats in lentic environments was observed in the Paraná River habitats (Darrigran and Ezcurra de Drago 2000; Rojas Molina *et al.* 2010), the La Plata River (Boltovskoy *et al.* 2006), Paraguay River (Marçal and Callil 2008) and in the Jacuí Delta (Dreher Mansur *et al.* 2003), being *Eichhornia crassipes*, *E. azurea* (Swartz) Kunth, 1843, and *Scirpus californicus* (Meyer) Steud, 1981 the species cited.

We observed a relationship between the presence and coverage percentage of hairs and the type of habitat. *Limnoperna fortunei* individuals with hairs were associated with floating macrophyte or bottom organic matter in lentic habitats with low current velocity (lakes, standing water areas, minor channels, etc.) where their proportions were very high (up to 100% of individuals). In contrast, in lotic habitats (main and secondary channels of the Paraná River), mussels with hairs were not recorded. We can argue that the development of hairs occurs in lentic habitats with macrophytes or CPOM.

**Possible function of adventitious hairs**

Various studies have been conducted about the function of rigid shell projections, but these flexible extensions have

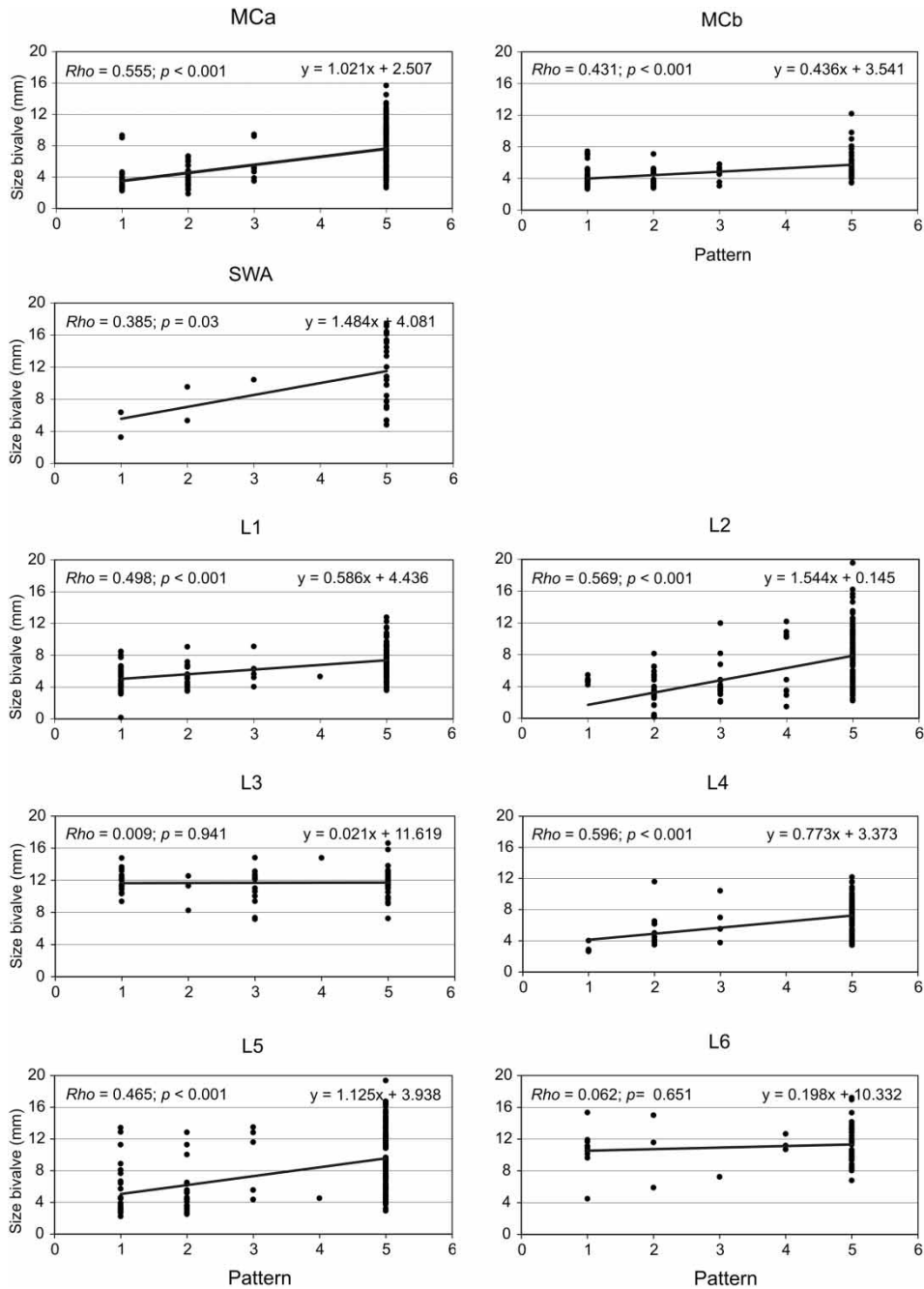


Figure 8. Byssal hair distribution patterns as a function of shell size in each site.

been poorly studied, and their functions are still unclear. [Bottjer and Carter \(1980\)](#) proposed possible roles of hairs in mussels: (1) protection of the shell from encrusting and boring organisms; (2) stabilisation of the shell in the substratum in burrowing forms; (3) camouflage and protection of the mantle margins from predators; and (4) extension of the range of tactile perception away from the mantle margins. This classification was enlarged by [Dixon et al. \(1995\)](#) who added: (5) a buoyancy aid for young during secondary settlement; (6) a spacing mechanism to

reduce competition during filter feeding; and (7) a mechanism to prevent fouling by byssus threads produced by conspecifics.

Shell projections in some species of *Bivalvia* may have been assumed to function as an anti-predator defense. Experimental studies demonstrated that spines in *Spondilus americanus* Hermann, 1781 and rough areas in *Chama pellucida* Broderip, 1835 may serve to attract epibionts so that they settle on the shell and thus provide camouflage ([Vance 1978](#); [Feifarek 1987](#)). [Dixon](#)

*et al.* (1995) suggests that hairs in *Mytilus edulis* are often adaptive, as they probably reduce predation by boring organisms and may inhibit fouling, particularly conspecifics during the primary settlement phase. The fact that *L. fortunei* shows individuals with more hairs when they are attached to macrophyte roots during its ontogeny can serve as a strategy for camouflage in these microhabitats, and thus assist in avoiding predation. Floodplain lentic habitats are important places for feeding and refuge for fishes and crabs, in particular in those areas covered with floating vegetation (Welcomme 1979; Fuentes and Espinach Ross 1998, Collins *et al.* 2006). Predation on *L. fortunei* by several species of fishes (larval, young and adult stages) and crabs has been well documented (Lopez Amengol and Casciotta 1998; Montalto *et al.* 1999; Ferriz *et al.* 2000; Pentchaszadeh *et al.* 2000; Rossi 2004; García and Protoginio 2005; García and Montalto 2006; Paolucci *et al.* 2007; Torres *et al.* 2012). It could be argued that greater hair frequency and abundance as a camouflage strategy could be more effective in larger mussels because these are more visible among roots, increasing the effectiveness of camouflage to avoid visual predators, such as fishes and crabs. Smaller mussels attached to roots are less obvious, and they may not require a substantial development of hairs.

### Closing remarks

In our study, the presence of two clear alternative developmental pathways in relation to habitat conditions reflect the phenotypic plasticity of *L. fortunei*.

Native predators may play an important role in regulating the long-term dynamics of invasive species, affecting their abundance, morphology and behaviour (Carlsson *et al.* 2009; Kobak and Kakareco 2009, 2011). It is likely that morphological changes with the incorporation of hairs in *L. fortunei* can influence the predator–prey dynamic because these projections allow *L. fortunei* to be camouflaged among the roots of macrophytes or CPOM to avoid visual predators. This defensive strategy can be an advantage of *L. fortunei* over native prey as has been found in other invasive species.

Studies on invasive species usually only include the early phase of invasion when species arrive in new habitats, and these can lead to wrong conclusions about the magnitude of environmental and economic future effects of this species. In this respect, there is a necessity for comprehensive long-term studies, which may be relevant to understand the decisive effects that an invasive species has on ecosystem processes and functional diversity (Strayer *et al.* 2006, 2011; Pace *et al.* 2010; among others). Laboratory and field experiments regarding the possible functions of byssal hairs in *L. fortunei* are required to test the ideas presented in this study.

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