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RESEARCH ARTICLE

Effects of conspecifics on settling juveniles of the invasive golden mussel, *Limnoperna fortunei*

Paula Sardiña · Daniel H. Cataldo ·
Demetrio Boltovskoy

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Abstract We conducted a field experiment to assess the influence of conspecific adults on recruitment success of the golden mussel *Limnoperna fortunei*. Tiles, 225 cm^2 surface area, were used as artificial substrates in four treatments: control (blank tiles), low (800 mussels m^{-2}), medium (4,000 mussels m^{-2}) and high (12,000 mussels m^{-2}) density treatments. Results indicated that recruitment was strongly affected by the presence and density of conspecifics. After one and 3 months of exposure, numbers of recruits were significantly higher on tiles with conspecific adults than on blank tiles, and there was a positive and significant relationship between the number of recruits and the number of adults in the three treatments assayed. Also, after 3 months of exposure, recruits in all treatments with adults present were larger than recruits in the control treatment. Our results suggest that conspecific adults have a positive effect on recruitment success and growth of newly settled juveniles through factors that enhance larval settling or that contribute to the survival of settlers in areas colonized by adult conspecifics.

P. Sardiña · D. H. Cataldo · D. Boltovskoy
Consejo Nacional de Investigaciones Científicas y Técnicas
(CONICET), Buenos Aires, Argentina

P. Sardiña (✉) · D. H. Cataldo · D. Boltovskoy
Museo Argentino de Ciencias Naturales "Bernardino
Rivadavia", Av. Angel Gallardo 470, C1405DJR Buenos Aires,
Argentina
e-mail: psardina@gmail.com

D. H. Cataldo · D. Boltovskoy
Departamento de Ecología, Genética y Evolución,
Facultad de Ciencias Exactas y Naturales,
Universidad de Buenos Aires,
C1428EHA Buenos Aires, Argentina

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Introduction

Investigations carried out in the last decade show that the structure and composition of benthic communities of the Río de la Plata watershed is being profoundly altered by the presence of the exotic mussel *Limnoperna fortunei*. *L. fortunei* is a freshwater bivalve native to southeastern Asia that colonized the Río de la Plata in the early 1990s, most probably as a result of ballast water discharge. This mussel forms large aggregations of intraspecific suspension feeders that strongly enhance community diversity, abundance and biomass by providing food and structural habitat for other species (Sylvester et al. 2007a; Sardiña et al. 2008).

L. fortunei is unique among the Río de la Plata watershed freshwater bivalves in possessing free-swimming larval stages and byssate adults. These unusual life history characteristics have facilitated rapid dispersal and the exploitation of unused solid benthic substrates to the point that it became the dominant macroinvertebrate on hard substrates along a >3,000 km stretch of the Río de la Plata-Paraná-Paraguay River system. During the reproductive period (September through April), when recently settled juveniles are abundant, densities can exceed 200,000 mussels m^{-2}, but adult and subadult individuals (>7–10 mm in length) usually range around 5,000–10,000 m^{-2} (Darrigran 2002; Boltovskoy et al. 2006; Sylvester et al. 2007a).

Recruitment dynamics of planktonic larvae are critical determinants of population structure and dynamics in marine and freshwater benthic communities (Lewandowski 1982; MacIsaac et al. 1991; Browne and Zimmer 2001; Hadfield and Paul 2001). Abundant literature attests that larvae of many marine species are influenced by specific chemical cues to settle and metamorphose in an appropriate site for juvenile growth and eventual reproduction (see in Hadfield and Paul 2001). Such cues may be waterborne or adsorbed to surfaces and associated with conspecific individuals, specific prey, or the surfaces of substrata. In gregarious settlement, conspecific adults may be the source of specific chemical cues. However, risk of predation may be especially pronounced for larvae settling among dense aggregations of potentially cannibalistic adults (Highsmith 1982; Pawlik 1988). In their selection of hospitable adult habitat, gregarious settlers actively choose a seemingly dangerous environment when recruiting into dense populations of suspension feeders (Okamura 1986; Young 1988). For the zebra mussel, *Dreissena polymorpha*, the severity of mortality between planktonic veliger and settled subadult phases has been described as a major factor governing populations dynamics (Lewandowski 1982; Sprung 1989), and intraspecific predation by adults was identified as a major source of mortality (MacIsaac et al. 1991).

To understand and predict changes in the spatial and temporal distributions, abundances, population growth rate, and population structure of a species with such a complex life cycle (involving a sessile adult and a dispersing larval stage), it is necessary to understand the relative importance of the physical, chemical and biological properties and processes that govern settlement dynamics. In this study, we examined the effects of adult *L. fortunei* on settlement success of larvae. Three main research questions were tested using field experiments: (1) Does the presence of conspecific adults influence recruitment? (2) Is there any relationship between adult population density and recruitment success? and (3) How does population structure influence settlement over time or is recruitment influenced by recently settled juveniles? To answer these questions, artificial tiles colonized with different adult mussel densities were used, and the relationship between adult density and number and size of recruits was analysed after 1 and 3 months of exposure.

Materials and methods

The study was conducted in the Carapachay River, lower Paraná River delta, Argentina (33°23′55″S, 58°35′41″W) between December 2007 and March 2008. The experimental site has a freshwater tidal regime of approximately, ±0.5 m, but wind-induced water level variations can occasionally increase this range to over 2 m for short periods. Water temperature ranges between 28 and 29°C in January and 10–11°C in July. Sediments are mainly composed of sand (98–99%), with very little silt and clay, and with small amounts of organic matter (3–6%; Boltovskoy et al. 1995). Stretches of compacted sediments are common, and tree remains, waterfront defenses, piers, various other man-made structures, construction debris spread along the shoreline and hulls of sunken ships provide abundant hard surfaces for the settling of *L. fortunei*.

Ceramic tiles 225 cm^2 in surface area were used as artificial substrates in four treatments with six replicates each: control (blank tiles), low-density (800 mussels m^{-2}), medium-density (4,000 mussels m^{-2}), and high-density treatment (12,000 mussels m^{-2}). The mussels used (adults with shell lengths between 15.87 and 31.45 mm) were manually collected in the lower delta of the Paraná and transferred to aquaria with aerated, dechlorinated tap water, on the bottom of which the tiles were previously placed. Animals were left in the aquaria for 2 weeks in order to allow firm bysal attachment to the tiles. When necessary, mussels were added or eliminated during colonization in order to achieve equal replicates for all treatments. Control tiles were also kept in the aquaria to allow a biofilm to develop.

Before deployment, tiles were individually protected with plastic screens with 5 mm meshes to prevent predation of mussels (previous experiments in the same area showed that predation eliminates up to 80% of the mussels, Sylvester et al. 2007b). Although meshed substrates may not perfectly mimick natural field conditions, the potential bias involved was homogeneously distributed throughout all experimental and control tiles and should therefore not affect the results.

All tiles were deployed on 28 December 2007. They were suspended from a pier vertically at about 1–1.5 m from the surface (depending on tide and wind conditions), and secured by means of 20 kg moorings. Three replicates of each treatment were recovered on 31 January 2008 (after 1 month of exposure), and the other three replicates were recovered on 28 March 2008 (after 3 months of exposure). Upon recovery, tiles were carefully placed in a bucket and covered with a lid. Buckets were transported to the laboratory and preserved frozen until the samples were processed. Densities of *L. fortunei* larvae (samples collected with a 26-μm mesh plankton net) and water temperature at the experimental site were assessed monthly.

In the laboratory, all mussels (adults + recruits) were carefully removed from the tiles with a sharp blade and tile surfaces were rinsed to remove adhering sediment. Recruits were isolated using a 200-μm mesh sieve and mussels >2–3 mm were picked out from the samples, counted and measured with a digital caliper to the nearest 0.01 mm. The remainder of the sieved sample was subsampled by means of a Folsom plankton sample splitter (McEwen et al. 1954) until a fraction containing at least 50 juveniles was obtained. All mussels in the subsample were counted and measured with a micrometric eye-piece using a compound microscope.

Single-factor ANOVAs and Tukey's multiple comparison tests were used to assess treatment effects on the densities and sizes of recruits. Data transformations (square root, logarithmic) were applied whenever parametric assumptions were not fulfilled. The relationship between the number of adult mussels and the number of recruits was assessed by means of simple regression analysis using all experimental tiles and both sampling dates.

Results

During the experiment, water temperature ranged between 25 and 26°C and densities of *L. fortunei* larvae in the water column varied between 4,267 and 16,667 ind. m^{-3} (Fig. 1).

After 1 month of exposure (January), the numbers of juveniles were lower on control tiles than on tiles with adults present (Fig. 2). There was also a strong positive relationship between the number of adults and the corresponding number of recruits ($P < 0.01$, Fig. 3). Significant differences between the numbers of recruits were found for the control treatment versus the medium and high-density treatments, and for low versus high-density treatments (Table 1). Low versus medium-density treatments yielded a strong, although statistically non-significant ($P = 0.06$) difference. After 3 months of exposure (March), densities of juveniles increased strongly on all tiles, but they remained lower on blank tiles than on tiles with adults present. The relationship between the numbers of adults and the corresponding numbers of recruits remained positive and significant ($P < 0.01$), although the rate of increase (i.e., the slope of the regression) was slightly lower than in January (Fig. 3). Significant differences between the numbers of recruits were restricted to control versus high-density treatments (Table 1).

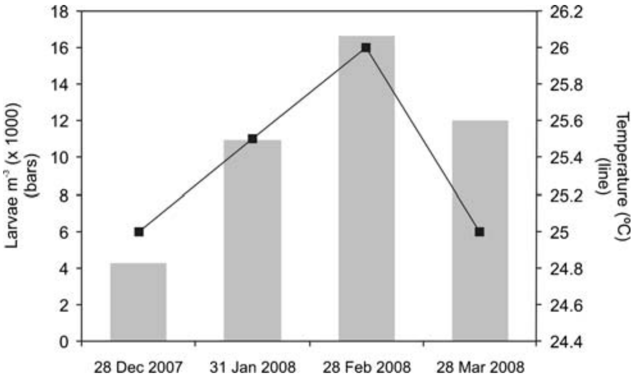

Fig. 1 Water temperature and densities of *Limnoperna fortunei* larvae in Carapachay River, lower Paraná River delta

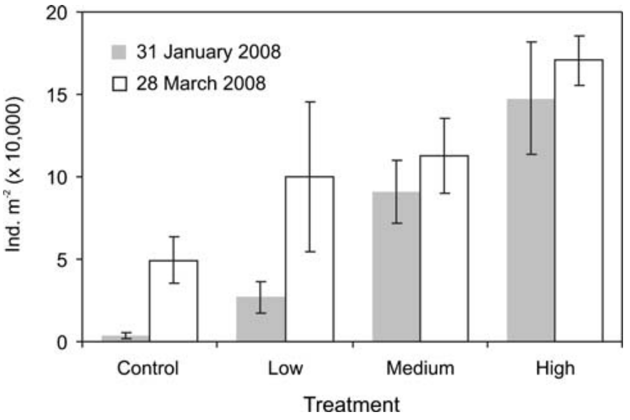

Fig. 2 Densities of *L. fortunei* recruits (mean ± SE) in the four treatments assayed (control: blank tiles, low: 800 mussels m^{-2}, medium: 4,000 mussels m^{-2}, and high-density: 12,000 mussels m^{-2}) after 1 month (January) and 3 months (March) of exposure in the Carapachay River, lower Paraná River delta

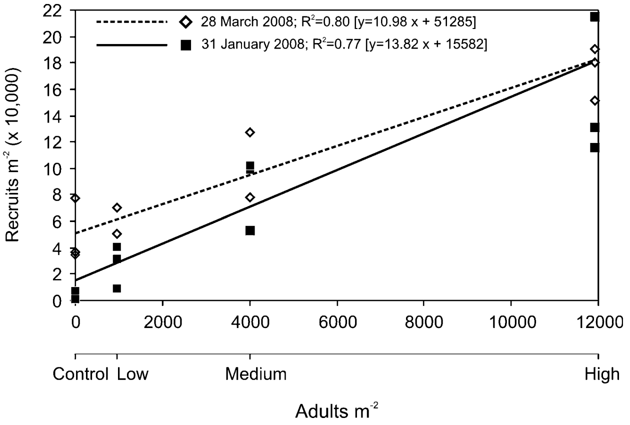

Fig. 3 Regression curves for densities of *L. fortunei* recruits in the four treatments assayed (control: blank tiles, low: 800 mussels m^{-2}, medium: 4,000 mussels m^{-2}, and high-density: 12,000 mussels m^{-2}) after 1 month (January) and 3 months (March) of exposure in the Carapachay River, lower Paraná River delta

After the first month of exposure, the numbers of recruits kept increasing in all treatments, but the rates of growth were uneven, with highest values on control tiles and lowest on high density tiles (Figs. 2, 3). Thus, in March 2008, the numbers of juveniles were still highest in the high-density treatment, but their increase with respect to January 2008 was only 15%, whereas on blank tiles they went up by 1,200%. Increases in the other two treatments were intermediate between the above (23% for the medium-density tiles, and 270% for the low-density tiles) (Figs. 2, 3).

Size-frequency distributions for each retrieval date are shown in Fig. 4. In January, all treatments were colonized

Table 1 Single-factor ANOVA and Tukey's multiple comparison test results for juvenile *Limnoperna fortunei* abundances among treatments (control: blank tiles, low: 800 mussels m^{-2}, medium: 4,000 mussels m^{-2}, and high-density: 12,000 mussels m^{-2}) and for 1 month (January) and 3 months (March) of exposure

	Control	Low	Medium
ANOVA among treatments, $P < 0.001$ (January)			
Low	0.21		
Medium	0.004 ($P < 0.01$)	0.06	
High	0.001 ($P < 0.01$)	0.006 ($P < 0.01$)	0.36
ANOVA among treatments, $P < 0.05$ (March)			
Low	0.58		
Medium	0.41	0.99	
High	0.05 ($P < 0.05$)	0.33	0.48

by a single cohort of juveniles, characterized by >98% of early, recently settled juveniles <1.5 mm in length. In March, at least two distinct cohorts were evident in the four treatments. The first one composed of early juveniles ≤1.8 mm (35–48% of all recruits), and a more heterogeneous population of older mussels >1.8 mm (65–52% of all recruits) (Fig. 4).

Treatment-dependent differences in mussel growth were evaluated using the larger (>1.8 mm) animals retrieved in March. In the control, the mean size of these recruits was significantly lower than in all treatments with adults ($P < 0.01$ for all comparisons, Fig. 5). Also, a weak trend suggesting a decreasing recruit size with increasing adult density was observed, but the differences involved were not significant (Fig. 5).

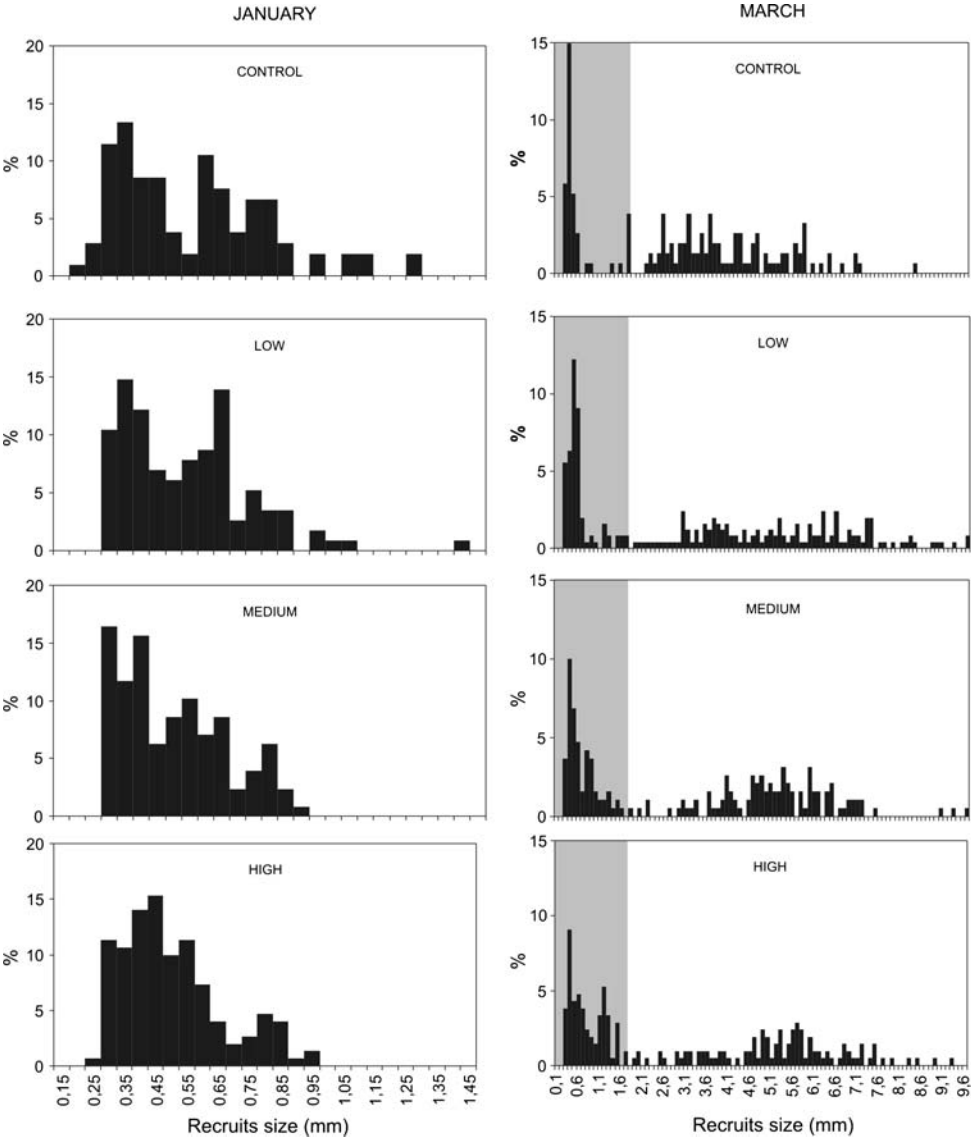

Fig. 4 Size frequency distributions (%) of *L. fortunei* recruits in the four treatments assayed (control: blank tiles, low: 800 mussels m^{-2}, medium: 4,000 mussels m^{-2}, and high-density: 12,000 mussels m^{-2}) after 1 month (January) and 3 months (March) of exposure in the Carapachay River, lower Paraná River delta. In March, the first cohort of small juveniles (≤1.8 mm) is highlighted in *grey*

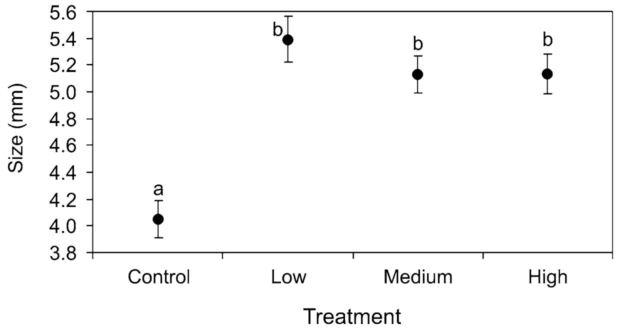

Fig. 5 Size of recruits of the second cohort of *L. fortunei* (mean ± SE) recovered after 3 months of exposure (March) in the four treatments assayed (control: blank tiles, low: 800 mussels m^{-2}, medium: 4,000 mussels m^{-2}, and high-density: 12,000 mussels m^{-2}). *Different letters* indicates significant differences

Discussion

Larval recruitment has sometimes been described as a passive process dependent upon hydrodynamic forces (Harvey et al. 1995), but abundant literature attests that for many species, larval behavior is influenced by the distribution of adults (Burke 1986; Chase and Bailey 1996; Browne and Zimmer 2001; Tamburri et al. 2006; Werner and Rothhaupt 2007). While studies of larval settlement are available for a variety of marine invertebrates (Hadfield and Paul 2001), almost nothing is known for freshwater organisms. The fact that free-swimming larval stages are comparatively rare among freshwater invertebrates (Lopez 1988; Thorp and Covich 2001) (which partly explains the scarcity of reports), makes studies of larval settlement in freshwater habitats particularly interesting. Because the loss of these free-swimming stages in fresh waterbodies is associated with the risk of expatriation into hostile habitats, including the ocean (Thorp and Covich 2001), analysis of larval settling modes can yield valuable information on the evolutionary adaptation processes that govern the colonization of freshwater habitats.

Our results with *L. fortunei* indicate that recruitment was strongly affected by the presence and density of conspecifics on the substrate. After 1 and 3 months of exposure, numbers of recruits were significantly higher on tiles with conspecific adults than on blank tiles, and there was also a strong positive relationship between the number of recruits and the number of adults in the treatments assayed. Comparison with other freshwater bivalves with planktonic larval stages is inconclusive. Chase and Bailey (1996) found that recruitment of the zebra mussel *D. polymorpha* is significantly higher in areas where conspecific adults were present, whereas Mörtl and Rothhaupt (2003) found the opposite, concluding that adults influence negatively the settlement of juveniles. A similar result was also obtained by Werner and Rothhaupt (2007) for the freshwater clam *Corbicula fluminea* (which broods its larvae through early development in marsupial sacs of the gill), who found that densities of juveniles were higher in areas lacking live adults. In both cases, the authors concluded that competition for food resources and cannibalism (in the case of *D. polymorpha*) may be responsible for the results obtained.

Our results can be due to either or both of two potentially synergistic mechanisms: (1) colonized areas receive more settlers, and (2) the numbers of settlers in colonized and barren areas are alike, but survival is higher in colonized areas. While the outcome of these two processes may be very similar, they involve subtle conceptual differences. Separation of the two, however, is not an easy task, especially because enhanced survival rates among conspecifics is the reason that leads to the evolutionary development of mechanisms that attract the larvae toward the sessile adults.

Among the factors that enhance larval settling in areas colonized by adult conspecifics are flow conditions, presence of a microbial film, and chemical cues produced by the sessile individuals or by organisms in the biofilm (Wainman et al. 1996; Hadfield and Paul 2001; Kavouras and Maki 2003). Tamburri et al. (2006) found that gregarious Pacific oyster larvae successfully settle among conspecifics due to a combination of biological and physical processes. They concluded that adult feeding (weak ciliary currents) and larval settlement behaviors (larvae control their descent upon contact with an adult chemical cue) contribute to minimize cannibalism.

Evidences of chemical communication have been found for several marine and freshwater species, including cnidarians, molluscs, annelids and arthropods (Hadfield and Paul 2001; Browne and Zimmer 2001; Burke 1986; Tamburri et al. 2006). Attraction by chemical cues has been documented for *D. polymorpha* (Chase and Bailey 1996; Hebert et al. 1991; Wainman et al. 1996; Mörtl and Rothhaupt 2003). Attracting substances operate either in solution or are adsorbed on a surface (Hadfield and Paul 2001; Zimmer-Faust and Tamburri 1994), and are often produced by conspecifics (Browne and Zimmer 2001; Pearce and Scheibling 1990; Zimmer-Faust and Tamburri 1994; Matsumura et al. 1998), or by bacterial and algal films associated with the substrate (Morse and Morse 1991; Leitz and Wagner 1993; Wainman et al. 1996; Hadfield and Paul 2001; Kavouras and Maki 2003). Although for *L. fortunei* the existence of chemical cues mediating settlement has not been investigated, the fact that more settlers were found in the high-density treatment may be in part the result of chemical cues released by the adults. Alternatively, if attracting chemicals are produced by the biofilm, enhanced settlement on the high density tiles may be due to the fact that the overall surface covered by this biofilm is considerably higher where adult shell densities are higher. Chemical cues may not only be released to the medium, but may also act on contact of the larva with the sessile conspecific. Morton (1977) and Uryu et al. (1996) found a strong thigmotaxis in *L. fortunei* larvae, stressing the importance of stimulus of contact for larval settlement.

A combination of chemical cues and carrying capacity may explain why blank tiles had a 1,200% increase of new colonizers after 3 months of exposure (as opposed to 15–270% for tiles pre-colonized by adults; Fig. 2). It is conceivable that individuals established earlier had influenced settlement of the new recruits through a conspecific or a biofilm-mediated cue. On the other hand, low population growths in the medium and high-density treatments may indicate that these substrates had reached the population carrying capacity (around 112,000–170,000 ind. m^{-2}) between the first and third months of the experience. The fact that these density figures are close to the highest ever reported for the species (ca. 200,000 ind. m^{-2}, Sylvester et al. 2007a) supports this assumption. One can envision that chemical cues governing larval settlement have threshold concentrations above which settlement is hindered signaling that the site is no longer advantageous for establishment. Such a mechanism was suggested for *D. polymorpha* (Hebert et al. 1991), as well as for many marine invertebrates (Browne and Zimmer 2001).

Protection from predators, currents and wave-generated disturbance, as well as enhanced food supply, are among the factors that can significantly contribute to the survival of settlers in beds of conspecifics. Several investigations on marine invertebrates (Bertness and Grosholz 1985; Okamura 1986; Côté and Jelnikar 1999) showed that living in close proximity to conspecifcs reduces the rate of predation, and that risk of predation decreases with increasing group size. It is conceivable that in our experiment recruits settling on the control tiles, devoid of the protection of the adults, were subjected to a greater grazing pressure thus yielding lower population densities. Higher numbers of recruits in association with higher densities of adults may also support this assumption: in our low-density treatment recruits tended to colonize the edges of the mussel clusters, where they may have been more accessible to predators than within the matrix of the group, where protection was higher (Okamura 1986). Although our experimental tiles were protected with a 5 mm mesh screen, for many small predatory invertebrates this protection is ineffective (Sylvester et al. 2007b). Paraná-Río de la Plata waters host many crustaceans that can conceivably graze on juveniles of *L. fortunei*, such as several isopods and crabs (Boschi 1981; Lopretto 1995; César et al. 2000; Sylvester et al. 2007b), and early juveniles can be consumed by leeches, gastropods, copepods, and insect larvae (Liebig and Vanderploeg 1995; Molloy et al. 1997), all of which are abundant in the area (César et al. 2000). It should be noted, however, that the mechanisms responsible for the protection of recruits by adult mussels against these small invertebrates is not clear. Indeed, while it is easy to envision how a recruit hidden between the crevices of a cluster of adults becomes less available to large predators like fish, the protection they offer to small invertebrates that can crawl into these restricted spaces is not obvious.

Nevertheless, the importance of enhanced protection, rather than attraction, is also supported by the fact that pre-colonized tiles not only hosted more recruits, but also favored their growth. After 3 months of exposure, recruits in all treatments with adults present were larger than recruits in the control treatment (Fig. 5). This result can be attributed to the fact that juveniles settled among conspecifics benefit from an enhanced food supply derived from the more active water movement due to the filtering activity of the adults. This interpretation disagrees with several findings in that bivalve recruits settled among dense clusters of conspecifics are subject to higher pressure, competition for food in particular, leading to lower growth rates (Okamura 1986; Bertness and Grosholz 1985; Chase and Bailey 1996). However, most of these studies were conducted in food-limiting environments, whereas in the Paraná delta particulate organic matter is abundant and does not represent a limiting factor (Sylvester et al. 2005; Boltovskoy et al. 2006).

Many benthic invertebrates produce planktonic larvae that gregariously colonize habitat occupied by cannibalistic adults. In our experiment, *L. fortunei* larvae successfully settled among conspecifics, which may have put larvae at risk of predation within the dense aggregation of adult suspension feeders. Adult *L. fortunei* are able to ingest particles up to 1 mm in length (e.g., nematodes) and readily cannibalize their larvae (Rojas Molina et al. 2008 and unpublished data). When adults indiscriminately consume their young, barriers to cannibalism and/or some kind of benefit derived from gregarious settlement are required (Polis 1981; Tamburri et al. 2006). However, pinpointing the benefits to gregarious settlers can be elusive. Benefits can be immediate (e.g., increased survival due to physical protection from predators), or more or less delayed (e.g., faster growth and maturation, enhanced chances of reproduction), thus outweighing the costs of larval loss due to cannibalism (Tamburri et al. 2006). On a broad perspective, at the population level, evolution of sufficiently high larval productivity, which seems to be the case of *L. fortunei*, would maintain the populations despite moderate cannibalism (Chase and Bailey 1996).

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