*The invasive freshwater bivalve Limnoperna fortunei in South America: multiannual changes in its predation and effects on associated benthic invertebrates*

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# The invasive freshwater bivalve *Limnoperna fortunei* in South America: multiannual changes in its predation and effects on associated benthic invertebrates

**Daniela Duchini · Demetrio Boltovskoy · Francisco Sylvester**

**Abstract** The invasive golden mussel *Limnoperna fortunei* is known to strongly affect benthic communities in South American freshwaters, but the evolution of these effects after the early invasion stages is poorly understood. Using predator exclusion (covered with 15- and 40-mm meshes) and inclusion (unprotected) substrates, we investigated the interaction between golden mussels and benthic invertebrate communities at different levels of exposure to predators in the Paraná River delta. Colonization of the substrates was largely dominated by the mussels. Oligochaeta, Nematoda, and Hirudinea were the most abundant accompanying groups, while Rotifera, Tardigrada, Copepoda, Cladocera, Chironomidae, Gastropoda, Hydracarina, Amphipoda, and nauplii appeared sporadically. Regardless of their different trophic modes and functional attributes, the numbers and biomass of associated invertebrates were not only enhanced by protection against predators, but also by the presence of mussel colonies. Enhancement of invertebrate densities associated with mussel colonies was higher on unprotected than protected substrates, suggesting that invertebrate facilitation increases with increasing predation pressure. Comparisons with a similar study carried out a decade earlier suggest that, after two decades of invasion, the reproductive potential of the mussel, the predation pressure on its colonies, and its facilitation effects on other invertebrates have increased in the Paraná River delta.

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## Introduction

Since its introduction in the Río de la Plata estuary (Argentina) around 1990 (Pastorino et al., 1993), the golden mussel, *Limnoperna fortunei* (Dunker, 1857), has rapidly spread northwards and westwards upstream the Uruguay and Paraná-Paraguay rivers, and is

presently a dominant component of benthic communities throughout two major watersheds (Río de la Plata and São Francisco), as well as several smaller basins (Guaíba, Tramandaí, Patos–Mirim, Mar Chiquita) in Argentina, Bolivia, Brazil, Paraguay, and Uruguay (Oliveira et al., 2015; Barbosa et al., 2016). Colonization of other large South American river systems, including the Amazonas, Orinoco, and Magdalena, as well as Central and North America, is probably only a matter of time (Kluza & McNyset, 2005; Oliveira et al., 2010; Boltovskoy, 2015). In the lotic and lentic environments invaded, *L. fortunei* can reach densities > 200,000 ind. $m^{-2}$ (Sylvester et al., 2007a; Spaccesi & Capitulo, 2012), and strongly interacts with the local ecosystems through multiple pathways (Boltovskoy & Correa, 2015).

Several previous studies showed that the impacts of *L. fortunei* on the benthic fauna are particularly strong (Sylvester & Sardiña, 2015), but so far no information has been available on the temporal evolution of these impacts. This issue is critical for our understanding of the long-term influences of invasive species in general, and of mussels in particular, because their populations and the interactions they establish with resident organisms change significantly with the time elapsed after introduction (Stanczykowska, 1977; Burlakova et al., 2006; Strayer & Malcom, 2006, 2014). Further, the effects of mussel beds on resident invertebrates have been shown to change as a function of several variables (Sardiña et al., 2011; Boltovskoy & Correa, 2015), including protection against predators. In South America, *L. fortunei* has encountered a large array of predators that crop significant fractions of its production (Sylvester et al., 2007a; Cataldo, 2015). This high level of consumer pressure likely plays a role in the modulation of other interactions of the mussel with different ecosystem compartments, including its facilitation of benthic invertebrates (Bruno & Bertness, 2001), but these relationships have so far not been examined.

The invasion of the golden mussel in South America has traditionally been compared with that of the zebra mussel in North America and Europe, largely because the two species share several salient traits (Karatayev et al., 2015), and because of the bulk of knowledge gathered during decades of intensive zebra mussel research (Nalepa & Schloesser, 2014). While using the experience on the zebra mussel was a useful starting point that guided the progress of
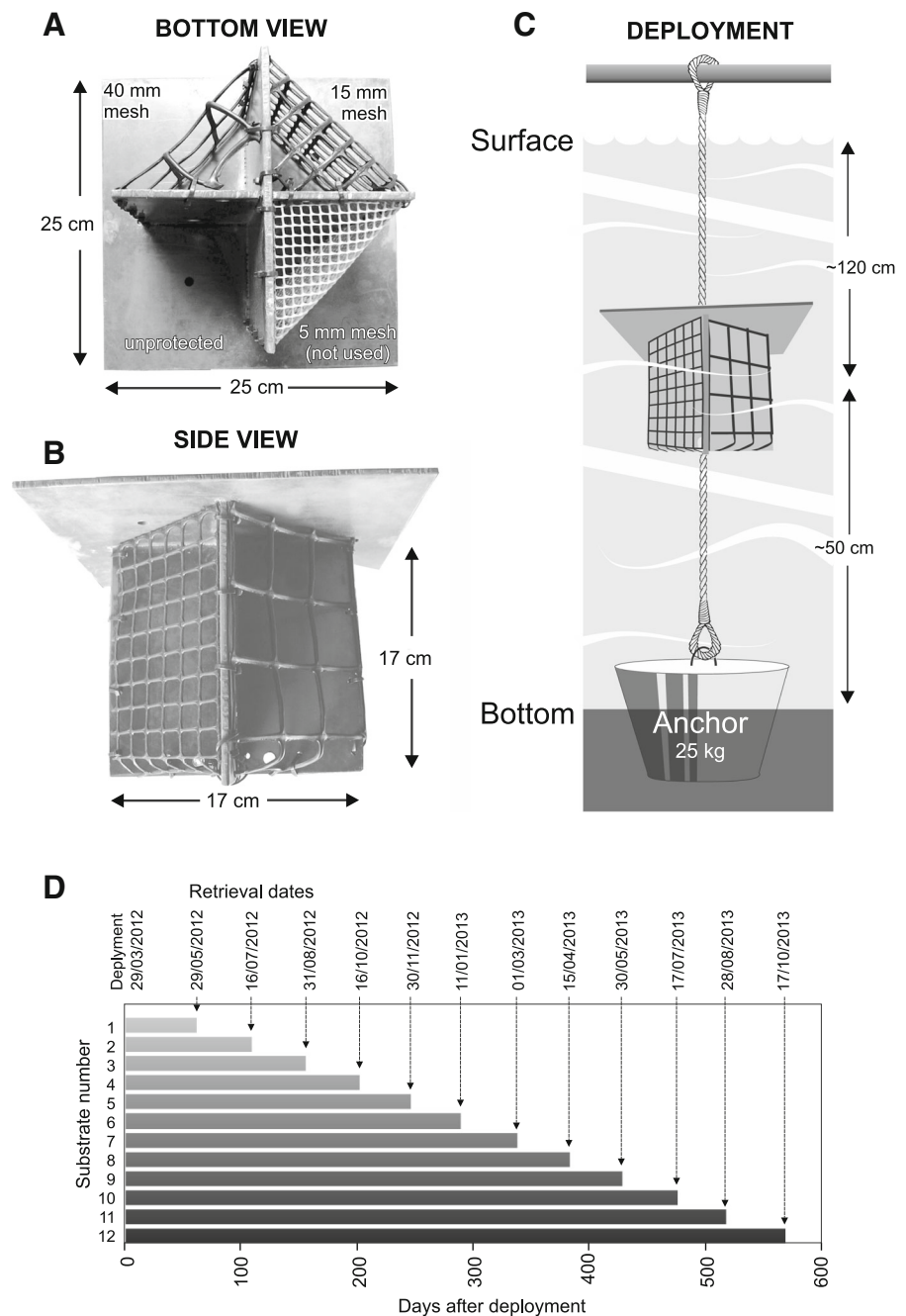
research on the golden mussel, mounting evidence indicates that some of the effects caused by the two bivalves can be very dissimilar, partly because of species-specific differences, and partly because of differences between the ecosystems invaded (Boltovskoy & Correa, 2015; Marçal et al., 2015), underscoring the need for first-hand experimental work on *L. fortunei* in the waterbodies invaded.

In the present work, we use artificial predator exclusion/inclusion substrates deployed for over a year in the lower Paraná River delta, and compare these data with a similar experiment conducted 10 years earlier to investigate changes in *L. fortunei* population densities and their facilitation effects on resident benthic invertebrates under different conditions of protection against predators ∼ 10 and 20 years after the mussel was introduced in South America. Our primary goal was testing whether facilitation of invertebrate fauna by *L. fortunei* is greater as predation pressure increases, as predicted by current hypotheses that propose stronger positive interactions under more stressful conditions (e.g., Bruno & Bertness, 2001). We also assess whether in the time elapsed the predation pressure on the introduced species and its facilitating effects on the invertebrates associated with its colonies had changed, and, if so, attempt to identify the sign of the trend, its magnitude, and its probable causes. Finally, we explore hypotheses that evaluate the importance of the enhanced food and shelter conferred by the mussel's beds to other organisms under different conditions of exposure to predation. In this context, two opposing effects are analyzed: (1) *L. fortunei* provides shelter and food for other invertebrates, which are therefore more abundant among the mussels than elsewhere, vs. (2) *L. fortunei* beds are themselves an attractor for predators, which feed on the mussels and on the fauna associated with them, and therefore the hazards involved in seeking refuge and nourishment in the colonies outweigh the benefits.

## Materials and methods

Twelve experimental cages (Fig. 1) were deployed for colonization by *L. fortunei* mussels in the Carapachay River (lower section of the Paraná River delta, Argentina; 34°23′51″S, 58°38′41″W) on 29 March

**Fig. 1** Experimental cages used (**A**, **B**), general scheme of their deployment (**C**), and deployment-retrieval dates (**D**)

**A** BOTTOM VIEW

40 mm mesh  15 mm mesh

25 cm

unprotected  5 mm mesh (not used)

25 cm

**B** SIDE VIEW

17 cm

17 cm

**C** DEPLOYMENT

Surface

~120 cm

~50 cm

Bottom  Anchor 25 kg

**D** Retrieval dates

Deployment 29/03/2012

29/05/2012
16/07/2012
31/08/2012
16/10/2012
30/11/2012
11/01/2013
01/03/2013
15/04/2013
30/05/2013
17/07/2013
28/08/2013
17/10/2013

Substrate number

Days after deployment

2012. Substrates consisted of PVC frameworks delimiting three 300 cm² sections: two areas protected from predators by plastic meshworks with pores of 15 and 40 mm, and one unprotected. Each substrate had a fourth section protected by a 5-mm mesh, but these sections were clogged by extensive siltation $\sim$ 3–4 months after deployment, and were therefore not used in our analyses. Mesh-protected areas were assumed to represent conditions where predation on benthic organisms was restricted to a degree proportional to the size of the potential predators, whereas unprotected areas were representative of "natural" conditions of unrestricted predation. A potential shortcoming of a predator inclusion–

exclusion field experiment such as conducted here is that predation was inferred from differences in mussel population densities in protected and unprotected cages, rather than based on direct observations of predation. It could be argued that the protective meshes could have affected mussel densities through mechanisms unrelated with predation, such as changes in the water flow, food availability, sediment retention, and larval settlement. While these effects cannot be ruled out, field observations (e.g., Correa et al., 2015) and experimental results (Sylvester et al., 2007a; Nakano et al., 2010) clearly show that physical protection from predators has a dramatic effect on mussel densities. Thus, even assuming that the protective meshes on our substrates might have had some accessory effects, we contend that their major influence was by far precluding the access of predators to the mussels.

Substrates were suspended at approximately 1.2 m from the water surface and 0.5 m from the river bottom. The tidal regime at this site is around ± 0.5 m, although wind action occasionally increases this range to 2–3 m. Thus, throughout the study, the substrates spent a few short (up to 4–5 h) periods outside of the water, but such situations are common for natural substrates colonized by the mussel in the area, with no apparent harmful consequences.

After deployment, substrates were retrieved at 42- to 61-d intervals; thus, the last of the 12 cages, retrieved on 17 October 2013, had spent 567 days in the water (Fig. 1D). Upon retrieval, we photographed all three sections of the cages before and after removal of the protective nets to assess mussel coverage on the substrates. We used the AutoCAD software (Autodesk 2007) to measure the surface area of zones covered by large (> 1 mm) mussels and of zones barren of them to the naked eye (henceforth termed zones with and without large mussels, respectively; Fig. 2) from the pictures.

Immediately after the protective nettings were removed, adhering mud and biological material was collected from all three sections. Collection was performed by gently scraping with a blade the surface of zones with and without large mussels separately (Fig. 2). Often no > 1-mm animals were visible in the "no large mussels zone," but upon processing the corresponding materials for counts of the small mussels and other invertebrates a few *L. fortunei* > 1 mm and up to ~ 5 mm were detected



**Fig. 2** Image of a partly colonized substrate; line separates area with large (> 1 mm) mussels from area without them. Substrate protected by a 40-mm mesh (removed in the photograph) recovered on 30 March 2013

(~ 40 per sample, on average < 6% of all large individuals on the substrates). Also, occasionally the "no large mussels zones" hosted one or a few isolated large mussels, but these were never clumped together forming a colony. Thus, mussels > 1 mm are often reported for the areas without large mussels, and the values may seem rather high (see Supplementary material), but it should be borne in mind that our figures are all expressed in individuals m$^{-2}$, whereas the surface of our substrates was only ~ 3% of 1 m$^2$.

All samples were preserved in 70% ethanol immediately after collection. The first three retrieval dates yielded no large (> 1 mm) mussels, and therefore their entire surfaces were considered as areas without large *L. fortunei* (Fig. 3D). Cages protected by 15-mm meshes were totally colonized by large mussels after ~ 200 days in the water, thus leaving no areas without *L. fortunei* (Fig. 3D). These samples (i.e., first three dates and cages protected by 15-mm meshes) were therefore excluded from the analyses comparing invertebrate colonization in areas with and without large mussels.

In the laboratory, samples were wet-sieved through a 75-µm mesh to get rid of silt and fractioned into small (< 1 mm) and large (> 1 mm) organism size classes using sieves. In samples with up to ~ 300 large (> 1 mm) *L. fortunei*, all mussels were counted

**Fig. 3** Temporal changes in the abundance (**A**, **B**), biomass (**A**, **C**), and experimental substrate coverage by the mussels (**D**) in protected and unprotected cages
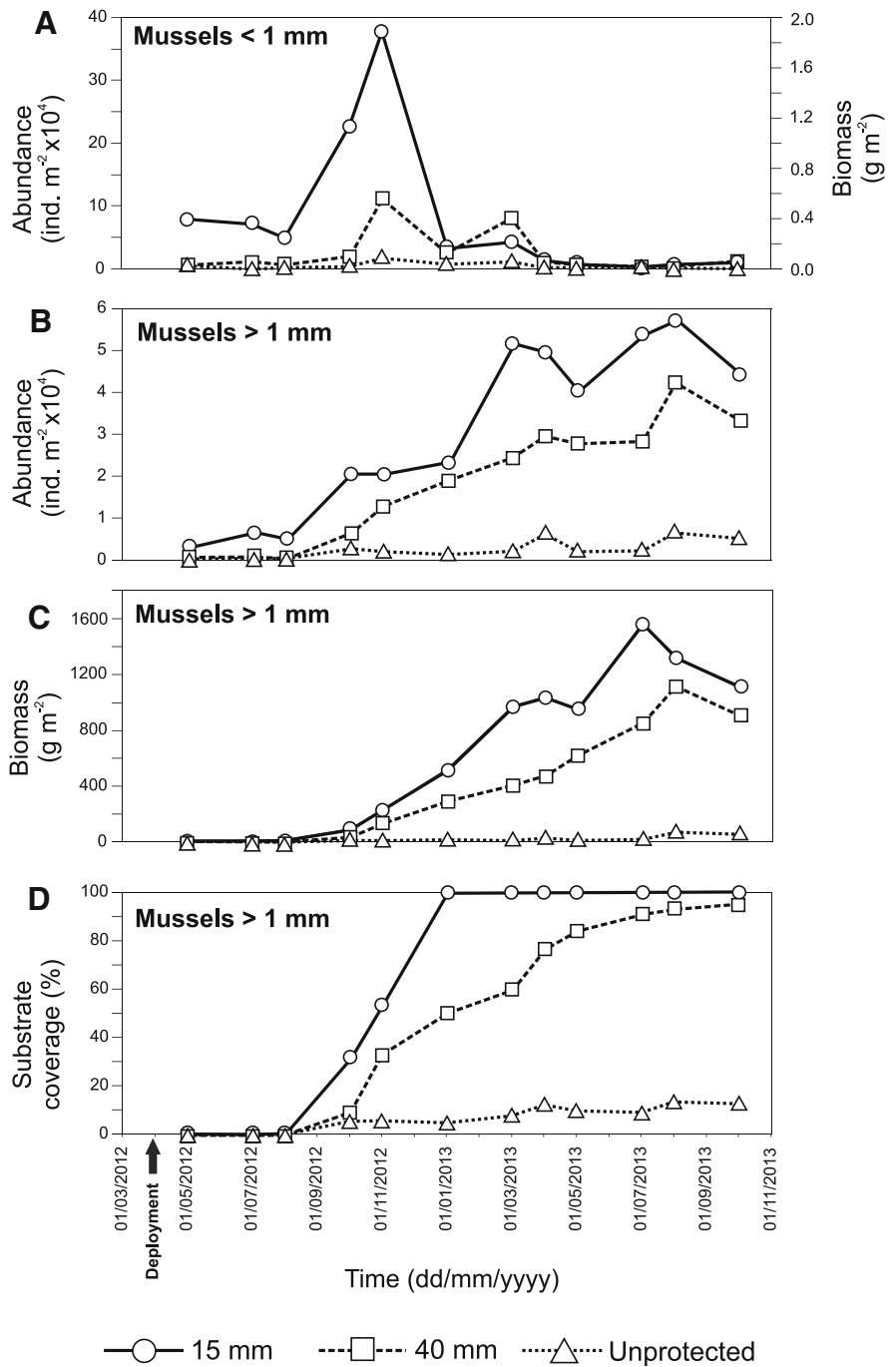


and measured, whereas in more abundant samples density estimates were based on gravimetrically calibrated splits containing ∼ 300 large animals. Small mussels (< 1 mm) were quantified using sub-samples (Folsom sample splitter, McEwen et al., 1954) containing ∼ 50 individuals. Mussels were measured to the nearest 0.1 mm with a digital caliper (large individuals), or under a binocular microscope (small individuals). Following Sylvester et al. (2007a), for mussels < 1 mm, a single conversion factor to biomass was used (4.78 μg tissue dry weight ind.$^{-1}$), whereas for those > 1 mm biomass was estimated in

two size classes according to the following relationships (Sylvester, 2006):

Mussels < 10 mm: Tissue dry weight (g)
$= 0.000119 \times e^{0.416 \times \text{mm shell length}}$

Mussels > 10 mm: Tissue dry weight (g)
$= 0.00396 \times e^{0.113 \times \text{mm shell length}}$.

Invertebrates collected from areas barren of mussels were assessed using subsamples with at least 50 individuals of each dominant taxon (see below), or one half of the sample for samples with fewer organisms. Invertebrates were classified into major taxonomic units (family to phylum). The biomass of the accompanying invertebrates was estimated on the basis of published data for biovolume or size to dry weight conversions. Biovolumes (in cm$^3$, and their corresponding volume to dry weight conversions) were used for Oligochaeta (0.1695; Sylvester et al. 2007b), Nematoda (0.2825), Hirudinea (0.2260), Rotifera, Copepoda, Tardigrada, and Hydracarina (0.226) (Feller & Warwick, 1988). For the remaining groups, we used the length to dry weight conversions proposed by Benke et al. 1990 (Chironomidae), Smock, 1980 (Gastropoda and Amphipoda), and Bottrell et al. 1976 (Cladocera and Nauplii). The latter are probably less precise because they are based on northern hemisphere species, but all these groups were very scarce in our samples, for which reason they were not used in our detailed analyses of seasonal and protection-related variations, and therefore the uncertainties involved are of minor importance for our conclusions.

Between-cage differences in the abundance and biomass of *L. fortunei* were analyzed with Generalized Linear Models (GLM) and LSD Fisher contrasts. Differences in the abundance and biomass of accompanying invertebrates between cages and zones with and without *L. fortunei* were also tested using GLMs. A Poisson distribution of errors, recommended for count data and confirmed graphically and with the dispersion parameter (McCullagh & Nelder, 1983), was used in most cases, except when data were over- or sub-dispersed, in which cases quasi-Poisson distributions were used. A significance level of $\alpha = 0.05$ was used in all statistical analyses.

Temporal comparisons were hindered by the fact that all cages retrieved on each sampling date were part of the same framework, and therefore potentially

not independent. Assessments of the effects of the presence of *L. fortunei* (areas with vs. without large mussels) on the abundance and biomass of accompanying invertebrates were based on unprotected cages and cages protected by the 40-mm mesh and the nine retrieval dates when these two areas were present and clearly distinguishable (mussels visible to the naked eye, i.e., areas with large *L. fortunei*, did not appear until after the third retrieval date; Fig. 3D). The 15-mm-mesh cages were excluded from this analysis as they were entirely colonized by mussels for > 50% the experimental period (i.e., no areas without large *L. fortunei* were present; Fig. 3D).

Although our data were unreplicated because the feasibility of setting up true replicates in our experimental conditions was questionable, in our experimental design the result of each successive retrieval is the outcome of the cumulative effects of all previous periods (recorded in previous retrievals), plus those of the period elapsed since the last retrieval (Fig. 1D). In this respect, each data point "replicates" the past history of each parameter. Gross errors in these measurements would obviously have appeared as discontinuities in our time series, which did not happen (see below). Thus, we contend that uncertainties associated with the lack or replicates did not affect the overall trends reported, although because of this caveat our conclusions should be considered as provisional.

## Results

Temporal changes in mussel populations

All cages were colonized by *L. fortunei*. The size of the bivalves ranged from < 1 mm to > 28 mm. On average, small mussels (< 1 mm) were more abundant (57–71%) than larger ones, but, as opposed to the latter, their numbers showed a very marked seasonality. In the cages protected by 15 and 40 mm meshes, early recruits peaked between October 2012 and March 2013, dropping sharply thereafter (Fig. 3A). These reproductive peaks were very conspicuous in the protected cages, but hardly noticeable in the unprotected ones, where the densities of early recruits were very low and lacked a seasonal trend (Fig. 3A). In contrast to small mussels, the abundance and biomass of large (> 1 mm) mussels increased

throughout the experimental period yielding similar profiles in both protected cages (Fig. 3B, C). The 15-mm cage was completely colonized by large *L. fortunei* towards half of the experimental period, leaving no areas free of mussels. In the 40-mm cage, colonization was more gradual, yet after $\sim 400$ days of deployment it reached 80–90% of the space available, leaving only a few, small isolated spots without mussels (Fig. 3D). In sharp contrast with the protected cages, in the unprotected ones colonization was always practically restricted to crevices around the angles of intersection between the plates (Fig. 3A–D, 4).

### Predation on *L. fortunei*

After $\sim 4$ months in the water, protected cages hosted significantly higher abundances and biomass of *L. fortunei* than unprotected cages, suggesting a strong predation impact in the latter (Table 1, Figs. 3, 4). On average for the entire experimental period, in the unprotected cages densities of small ($< 1$ mm) mussels were 5 and 17 times lower than in the 40- and 15-mm-mesh cages, respectively (Table 1). Large ($> 1$ mm) animals were 7–12 (40- and 15-mm meshes, respectively) times more abundant in protected than in unprotected cages. Biomass values for small mussels were based on a single conversion factor (see Materials and methods) and therefore their abundance and biomass temporal profiles were identical (Fig. 3A). On the other hand, for large mussels (whose biomass was based on size-frequency values),
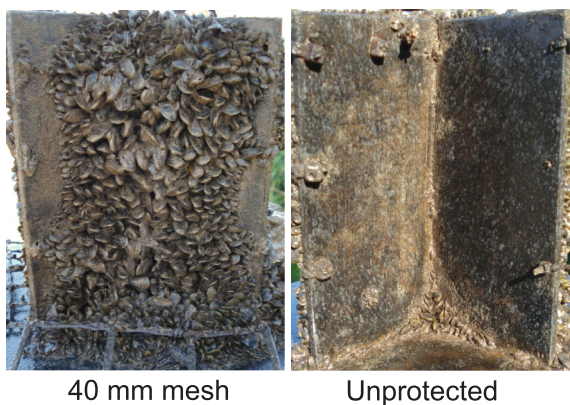


**Fig. 4** Typical appearance of a protected (left; mesh removed in the photograph) and an unprotected (right) cage partially colonized by *L. fortunei* (cages retrieved on 17 July 2013)

time-averaged differences in biomass between cages were even more marked than those based on densities, with figures 19 (40 mm) and 32 (15 mm) times higher than in the unprotected cages (Table 1, Fig. 3C).

### Temporal changes and predation of accompanying invertebrates

The invertebrates recorded in association with *L. fortunei* comprised a wide array of groups including Oligochaeta, Nematoda, Hirudinea Rotifera, Tardigrada, Copepoda, Cladocera, Chironomidae, Gastropoda, Hydracarina, Amphipoda, and nauplii, yet only the first three were common and abundant enough across sampling dates and cages to allow analyses of their abundance as a function of protection against predators and the presence of mussels (see Supplementary material).

Oligochaeta and Nematoda shared the following conspicuous trends: (1) abundances of both groups exhibited a marked seasonal pattern, dropping during the summer and peaking in late winter-spring (Fig. 5); (2) protected cages hosted significantly higher abundances and biomass than unprotected cages (Table 1, Fig. 6); and (3) cages protected by 15-mm meshes yielded significantly more animals than those protected by 40-mm meshes (Table 1, Fig. 7).

Hirudinea were much scarcer than Oligochaeta and Nematoda, their seasonal behavior was less consistent, and their densities were more closely associated with those of large mussels and the concomitant gradual increase in mussel biomass (Fig. 5C), than with reproductive cycles, presumably responsible for the seasonal pattern of Oligochaeta and Nematoda (Fig. 5A, B) (see below). Unprotected cages yielded much lower (yet not statistically significant) densities and biomass of Hirudinea than cages protected against predation, and differences between the latter (15- and 40-mm meshes) were smaller and less consistent than for Oligochaeta and Nematoda (Fig. 7C).

### Effects of large *L. fortunei* on young recruits and associated invertebrates

Within each cage, time-averaged densities of young ($< 1$ mm) mussels and of the other invertebrates assessed were invariably higher in areas colonized by large mussels than in those barren of them (Table 2, Fig. 5E–H). Enhancement of the densities of

**Table 1** Statistical tests (Generalized Linear Models, Poisson/quasi-Poisson distribution) of the differences between the density and biomass of mussels and other common invertebrates in protected and unprotected cages

| | Mean 15-mm mesh | Mean 40-mm mesh | Mean unprotected | $F$ | $P$ | LSD fisher contrasts |
|---|---|---|---|---|---|---|
| **Abundance (ind. m$^{-2}$)** | | | | | | |
| All mussels | 109,405 | 43,344 | 7,344 | 5.960 | 0.006 | 15 mm $\neq$ 40 mm $\neq$ unprot |
| Mussels < 1 mm | 78,102 | 24,609 | 4,728 | 4.390 | 0.020 | 15 mm $\neq$ 40 mm $\neq$ unprot |
| Mussels > 1 mm | 31,303 | 18,736 | 2,616 | 11.050 | 0.000 | 15 mm $\neq$ 40 mm $\neq$ unprot |
| Oligochaeta | 65,111 | 35,299 | 2,152 | 5.660 | 0.008 | 15 mm $\neq$ 40 mm $\neq$ unprot |
| Nematoda | 70,926 | 27,397 | 1,430 | 8.780 | 0.001 | 15 mm $\neq$ 40 mm $\neq$ unprot |
| Hirudinea | 990 | 1390 | 39 | 1.600 | 0.218 | 15 mm = 40 mm = unprot. |
| **Biomass (mg dry weight m$^{-2}$)** | | | | | | |
| All mussels | 650,495 | 400,245 | 20,611 | 5.100 | 0.012 | 15 mm $\neq$ 40 mm $\neq$ unprot |
| Mussels < 1 mm | 373 | 118 | 23 | 4.390 | 0.020 | 15 mm $\neq$ 40 mm $\neq$ unprot |
| Mussels > 1 mm | 650,121 | 400,128 | 20,589 | 5.410 | 0.009 | 15 mm $\neq$ 40 mm $\neq$ unprot |
| Oligochaeta | 685 | 372 | 23 | 5.660 | 0.008 | 15 mm $\neq$ 40 mm $\neq$ unprot |
| Nematoda | 22 | 9 | 0 | 8.780 | 0.001 | 15 mm $\neq$ 40 mm $\neq$ unprot |
| Hirudinea | 206 | 289 | 8 | 1.600 | 0.218 | 15 mm = 40 mm = unprot |

The means shown are average values for the entire experimental period ($N = 12$)

Oligochaeta and Nematoda in areas with large mussels (as compared with those without them) were much stronger when the communities were exposed to predation (unprotected cages), than when they were protected (40-mm cages). Thus, while in the protected cages areas with large *L. fortunei* hosted $\sim$ 5–6 times more Oligochaeta and Nematoda than areas without them, in those exposed to predation Oligochaeta and Nematoda were 22–31 times (respectively) more abundant in areas with large mussels than in those without them (Fig. 6A, B). Differences in biomass followed a same pattern (Fig. 6C, D).

The effects of beds of large mussels, but apparently less so those of mesh protection in the presence of large mussels, were also reflected by the abundances of small (< 1 mm) recently settled *L. fortunei*. In areas with large musses, not only protected (40 mm), but also unprotected cages, hosted very high densities of juveniles ($\sim$ 66,000 and 68,000 ind. m$^{-2}$, respectively, overall means). Thus, facilitation of small mussels by large conspecifics was even higher than facilitation of other invertebrate groups: while in protected cages areas with large mussels hosted 4 times more small mussels, in unprotected cages the same figure was up to 41 times (Fig. 5H; Table 2). In areas with large mussels, temporal profiles for these

recruits were also generally similar in protected and unprotected cages (Fig. 5D).

Hirudinea were only common in areas colonized by large *L. fortunei*, especially in the protected (40 mm) cages (Fig. 5C, G), but these densities did not differ significantly from those recorded in areas barren of large mussels and in unprotected cages (Tables 1, 2).

## Discussion

### Facilitation effects

This work is the first survey to assess the facilitation of benthic invertebrates by *L. fortunei* at different levels of predation pressure. Previous investigations on the effects of the golden mussel on benthic invertebrates reported both negative (e.g., Darrigran, 2002; Mansur et al., 2003; Rojas Molina & Williner, 2013; Linares et al., 2017) and positive impacts (Botts et al., 1996; Sylvester et al., 2007b; Karatayev et al., 2010; Sylvester & Sardiña, 2015), as well as neutral effects (Marçal et al., 2015), but none of them investigated the combined effects of mussel beds and exposure to predation on the invertebrates surveyed. Our results suggest that *L. fortunei* is a strong facilitator, and that
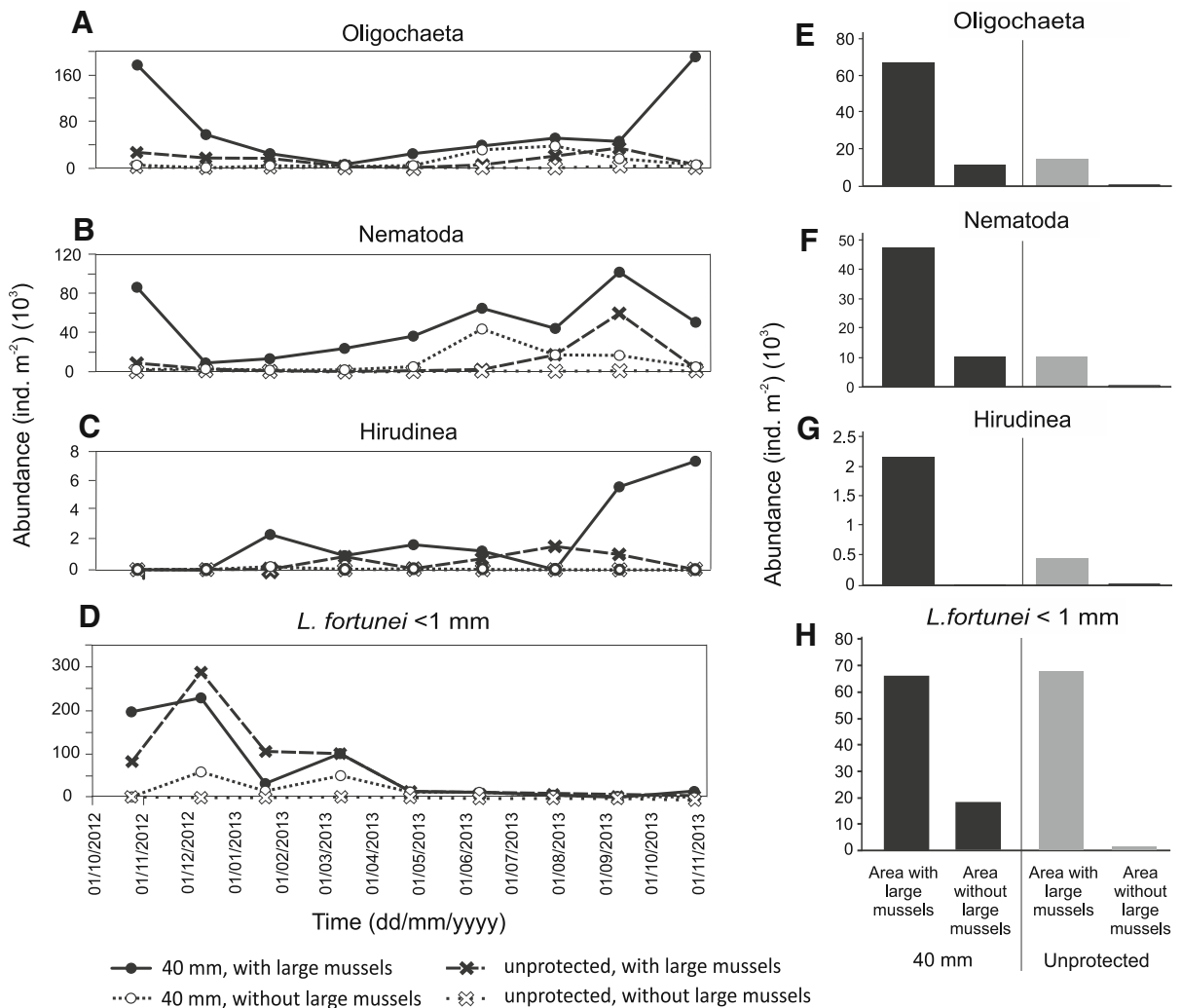
**Fig. 5** Temporal profiles (**A–D**) and average (**E–H**) abundance of dominant invertebrate groups in areas colonized by *L. fortunei* (with *L. f.*) and areas barren of them (without *L. f.*). First three retrieval dates are not shown because no large mussels were still present on the substrates

its facilitation effect increases with increasing exposure to predation.

It should be stressed that most publications reporting negative effects have either focused on a single taxon or extrapolated the putative effects of *L. fortunei* from the literature on *Dreissena* spp. in North America and Europe. A recent review of the information available on the effects of *L. fortunei* on benthic invertebrates in invaded South American water bodies concluded that evidences are mixed, but positive effects prevail (Sylvester & Sardiña, 2015).

Facilitation of benthic fauna by invasive bivalves is typically associated with the provision of substrate,

shelter, and food from the enrichment of sediments with organic matter from the bivalve's feces and pseudofeces (Botts et al., 1996; Stewart et al., 1998; Sardiña et al., 2008; Boltovskoy & Correa, 2015), but the impacts are not alike across taxa. Our results suggest that facilitation is highest for leeches, which are virtually absent from areas barren of mussels (Fig. 5C, G; Sylvester et al., 2007b). In addition to the protection conveyed by the mussels, this pattern can respond to the fact that predatory leeches thrive where their prey is more abundant (i.e., within mussel beds), whereas deposit-feeding leeches benefit from the enhanced food availability provided by the mussel's
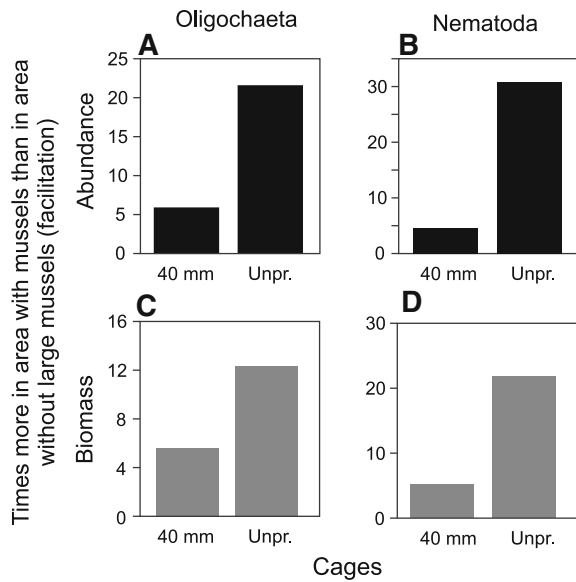
Fig. 6 Ratios between the abundance (**A**, **B**) and the biomass (**C**, **D**) of Oligochaeta and Nematoda for areas with and without *L. fortunei* in cages protected by the 40-mm mesh and in the unprotected cages. Notice that in all cases abundance and biomass were higher in areas colonized by large mussels than in those barren of them, but increases in the mussel beds (with respect to values outside of the beds) were much higher in cages open to predation (unprotected), than in those protected from predators (40-mm mesh)

feces and pseudofeces (Sylvester et al., 2007b). Similar to leeches, nematodes include species with different feeding habits, and thus facilitation of this group is also likely the result of a combination of mechanisms (Sardiña et al., 2008). Oligochaeta, by contrast, are chiefly deposit-feeders, and as such are expected to mainly respond to the increased food supply (Sardiña et al., 2008). This benefit may chiefly affect epifaunal detritivorous oligochaetes, whereas for infaunal animals the sign of the effect is less clear, due to the detrimental effects of oxygen depletion associated with high levels of organic matter within the mussel colonies (Karatayev et al., 2010).

Although the other invertebrate groups recorded in our samples (rotifers, copepods, chironomids, tardigrades, gastropods, cladocerans, and amphipods) were too scarce to allow reliable comparisons between treatments (see Materials and methods and Supplementary material), it is noteworthy that, in the unprotected cages, their abundances were invariably higher (3–95-fold) in areas with large mussels than in
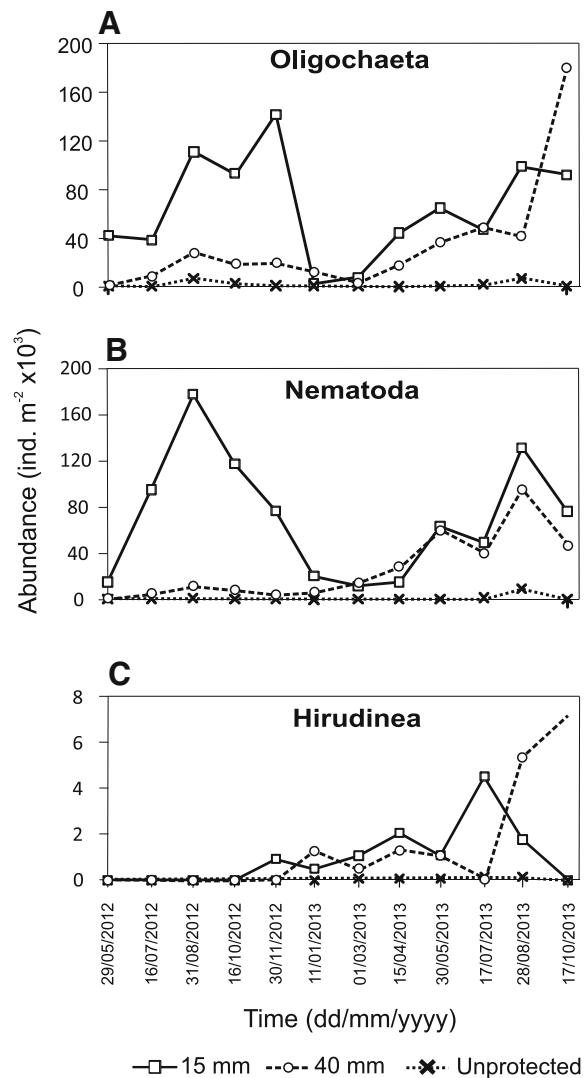


Fig. 7 Temporal changes in the abundance of associated invertebrates in protected and unprotected cages (areas with and without *L. fortunei* pooled) (**A–C**)

those barren of them (Tables 3, 4, and Supplementary material).

Judging from differences in mussel colonization as a function of the size of the protective mesh (Fig. 3), predators that consume *L. fortunei* span a wide range of sizes. Comparison of the yields of the cages protected by the 15-mm mesh (considered as a base-level representative of predation-free conditions) indicated that, on average, 60% and 93% of the mussels (in terms of numbers; 38% and 97% in biomass) were eliminated from the cages protected by 40-mm-mesh nets and from the unprotected cages,

**Table 2** Statistical tests (Generalized Linear Models, Poisson/quasi-Poisson distribution) of the differences in the density and biomass of small (< 1 mm) mussels and common invertebrates recorded in areas with and without large (> 1 mm) mussels

| | Abundance (ind. m$^{-2}$) | | Biomass (mg dry weight m$^{-2}$) | | | |
| --- | --- | --- | --- | --- | --- | --- |
| | Mean for areas without large (> 1 mm) mussels | Mean for areas with large (> 1 mm) mussels | Mean for areas without large (> 1 mm) mussels | Mean for areas with large (> 1 mm) mussels | $F$ | $P$ |
| 40 mm mesh | | | | | | |
| Mussels < 1 mm | 17,660 | 66,034 | 84 | 316 | 2.950 | 0.105 |
| Oligochaeta | 11,435 | 67,580 | 120 | 711 | 6.560 | 0.021 |
| Nematoda | 10,256 | 47,605 | 3 | 15 | 8.820 | 0.009 |
| Hirudinea | 14 | 2178 | 3 | 453 | 1.790 | 0.199 |
| Unprotected | | | | | | |
| Mussels < 1 mm | 1644 | 67,701 | 8 | 324 | 3.050 | 0.100 |
| Oligochaeta | 708 | 15,329 | 7 | 161 | 11.200 | 0.004 |
| Nematoda | 364 | 11,259 | 0.1 | 3 | 2.300 | 0.149 |
| Hirudinea | 8 | 469 | 2 | 97 | 2.860 | 0.110 |

The means shown are average values for the nine retrieval dates when areas with and without mussels were clearly distinguishable

respectively (Table 1, Fig. 3). Not surprisingly, the invertebrates facilitated by *L. fortunei* followed a very similar trend: ∼ 46–97% of the abundance and biomass of the oligochaetes, and 61–98% of the nematodes were eliminated from the same cages when compared with those protected with the 15-mm mesh (Table 1, Fig. 7). These two meiofaunal groups are largely dominant in the communities associated with freshwater mussel beds (Sylvester et al., 2007b; our results), and have been observed to be intensively predated upon by fish in similar experimental settings (Weber & Traunspurger, 2014, 2015). The Paraná River basin hosts a rich fish fauna including several hundred species, ca. 50 of which have been reported to consume golden mussels (Cataldo, 2015). Predation

on *L. fortunei* is most probably not restricted to fishes. Crabs, reptiles, waterfowl, and mammals have been suggested or observed to consume mussels as well (Bujes et al., 2007; Sylvester et al., 2007a; Boltovskoy et al., 2009; Torres et al., 2012; Carvalho et al., 2013). Fishes and other predators may impact populations of the invertebrates associated with mussel beds as well, either by actively selecting them or by ingesting them along with the mussels, in which case the mussel bed itself might represent an important attractor for these predators. However, our data suggest that these potential effects do not override those of the mussels as a facilitator.

Contrasts in the numbers of oligochaetes and nematodes in areas with and without large mussels

**Table 3** Average density and biomass of the rare invertebrates retrieved from the experimental substrates (areas with and without *L. fortunei* pooled; $N = 12$)

| | Abundance (ind. m$^{-2}$) | | | Biomass (mg dry weight m$^{-2}$) | | |
| --- | --- | --- | --- | --- | --- | --- |
| | 15 mm | 40 mm | Unprotected | 15 mm | 40 mm | Unprotected |
| Rotifera | 2,052 | 4,127 | 565 | 0.87 | 1.75 | 0.24 |
| Copepoda | 567 | 556 | 80 | 1.38 | 1.36 | 0.20 |
| Chironomidae | 438 | 309 | 177 | 56.91 | 40.13 | 23.00 |
| Tardigrada | 824 | 153 | 36 | 0.32 | 0.06 | 0.01 |
| Gastropoda | 0 | 108 | 16 | 0.00 | 19.81 | 3.02 |
| Cladocera | 162 | 141 | 44 | 0.12 | 0.10 | 0.03 |
| Amphipoda | 299 | 22 | 17 | 1.51 | 0.11 | 0.08 |
| Nauplii | 0 | 47 | 6 | 0.00 | 0.00 | 0.00 |
| Hydracarina | 6 | 6 | 0 | 0.01 | 0.01 | 0.00 |

**Table 4** Average densities (ind. m$^{-2}$) of the rare invertebrates retrieved from the unprotected experimental substrates, and substrates protected with a 40-mm mesh, in areas colonized by large mussels and areas barren of them

|  | 40 mm | | Unprotected | |
|---|---|---|---|---|
|  | Mean for areas with large (> 1 mm) mussels | Mean for areas without large (> 1 mm) mussels | Mean for areas with large (> 1 mm) mussels | Mean for areas without large (> 1 mm) mussels |
| Rotifera | 1,088 | 1,885 | 1,526 | 264 |
| Copepoda | 845 | 372 | 1075 | 8 |
| Chironomidae | 521 | 179 | 1968 | 70 |
| Tardigrada | 142 | 238 | 161 | 25 |
| Gastropoda | 130 | 115 | 158 | 8 |
| Cladocera | 187 | 57 | 549 | 0 |
| Amphipoda | 31 | 0 | 114 | 9 |
| Nauplii | 62 | 57 | 57 | 0 |
| Hydracarina | 0 | 45 | 0 | 0 |

Data are based on the nine retrieval dates when areas with and without mussels were clearly distinguishable

were substantially lower when the substrates were protected from predation (40-mm mesh), than under the more stressful ("natural") conditions of the unprotected cages, where predators had access (Fig. 6). In other words, facilitation by the mussels was particularly strong when the communities were exposed to predation, but less so when mussels and accompanying fauna were artificially protected from them. Facilitators (typically ecosystem engineers) alleviate harsh conditions to a large number of organisms, which would otherwise wane or disappear altogether. Our results provide support to the notion that the harder the conditions, the larger the gap between the population densities supported with and without the facilitator. The mechanisms by which the facilitator can improve otherwise unsuitable living conditions for other organisms are numerous, including the provision of food and shelter, substrate, protection against disturbances, such as current and wave action, enhanced retention of propagules, etc. (Bruno & Bertness, 2001; Bruno et al., 2003; Sardiña et al., 2008).

The predation values observed in our experiment are likely underestimated because our "no predation" reference, the 15-mm mesh-protected cages, has most probably suffered at least some predation pressure, both from larval and juvenile fishes, and by invertebrate predators (e.g., leeches, nematodes) within the cages (Sylvester et al., 2007a; see below).

Decadal comparisons

For the assessment of decadal changes of the impact of *L. fortunei*, we compared the results of the present work (2012–2013) with those of a similar survey conducted in the same area 10 years earlier (2002–2004, Sylvester et al., 2007a, b). A potential caveat of this exercise is the fact that the two experiments were started at different times of the year (in spring in 2002–2004, and in autumn in 2012–2013), for which reason the contrasts discussed below are limited to the most clear trends only.

The most striking difference between the two surveys is that consumption of *L. fortunei* in the unprotected cages and in those protected by the 40-mm mesh increased substantially in the time elapsed. On average, the amount of mussels eliminated from these cages (with respect to the ones protected by the 15-mm mesh) increased from 2–4 to 6–15 times in terms of abundance, and from 4–5 to 19–32 times in biomass (Fig. 8). Interestingly, while in cages open to predators yearly average mussel abundances decreased by ∼ 50% between 2002–2004 and 2012–2013, densities in those protected by the 40-mm mesh increased ∼ 50%, and in the 15-mm cages ∼ 140% (Fig. 8). These figures suggest that the relentless geographic spread of the golden mussel since its introduction in South America around 1990 (Oliveira et al., 2015) has been accompanied by enhanced reproductive potential, but resident predators have responded to this presence,

such that they currently exert a more intensive control on mussel populations than during earlier stages of the invasion.

In Lake Ohshio (Japan), 32–89% of the mussels present on substrates protected with a 25-mm mesh were eliminated by predators from simultaneously deployed unprotected substrates (Nakano et al., 2010). The golden mussel was first detected in this lake only 2 years earlier; thus, if the introduction had effectively occurred so recently, the highest predation values (89%, at 6 m depth) leave little room for further increase with time. On the other hand, predation at 18 and 12 m was much lower (45 and 32%, respectively), and could conceivably increase with time. Methodological and environmental differences, including depth and dissolved oxygen concentrations, as well as mesh pore size of predator exclosures, complicate interpretation of the dissimilarities between mussel

consumption rates in Japan and in Argentina, where *L. fortunei* was introduced at about the same time (Ito, 2015; Oliveira et al., 2015). Yet these dissimilarities may also point at the fact that ecosystem responses are context dependent, whereby the same invader may engender quite dissimilar responses depending on the ecosystem invaded (Boltovskoy & Correa, 2015).

Close comparisons between the facilitation effects recorded in this study and those of the one conducted 10 years earlier (Sylvester et al., 2007a, b) are hindered by the fact that the two experiments were started in different seasons (see above). Further, Sylvester et al. (2007b) analyzed temporal changes in the invertebrates recorded in areas with and without colonies of large mussels on substrates protected by a 5-mm mesh (in contrast with the present results, where these cages had to be discarded due to extensive siltation shortly after deployment, see Materials and methods; in Sylvester's study siltation and clogging were much lower). Nevertheless, some broad conclusions on the effects on the mussel beds on other invertebrates can be drawn. First, both studies clearly indicate that *L. fortunei* strongly facilitates oligochaetes and nematodes: abundances of these groups are consistently higher in areas with mussels than in those without them (Fig. 5E, F, cf. Figure 3 in Sylvester et al., 2007b). Second, facilitation seems to be extensive to practically all invertebrates recorded in the two studies (Supplementary material, Fig. 4 in Sylvester et al., 2007b). Third, Hirudinea depict the highest dependency on the mussels, as they occur exclusively (Fig. 4 in Sylvester et al., 2007b) or almost exclusively (Fig. 5C, G) in association with beds of large *L. fortunei*, which may respond to the fact that they feed on other invertebrates (Nematoda, Oligochaeta), and their numbers increase after these prey become abundant (Fig. 7). Fourth, the two studies coincide in that facilitation is greatest in "natural" conditions (i.e., unprotected cages), and drops as protection from predators increases (40- and 5-mm-mesh cages). While differences in the experimental periods and treatments involved constrain these comparisons, they seem to confirm the tenet that facilitation is highest under more stressful conditions (Bruno & Bertness, 2001; Bruno et al., 2003).
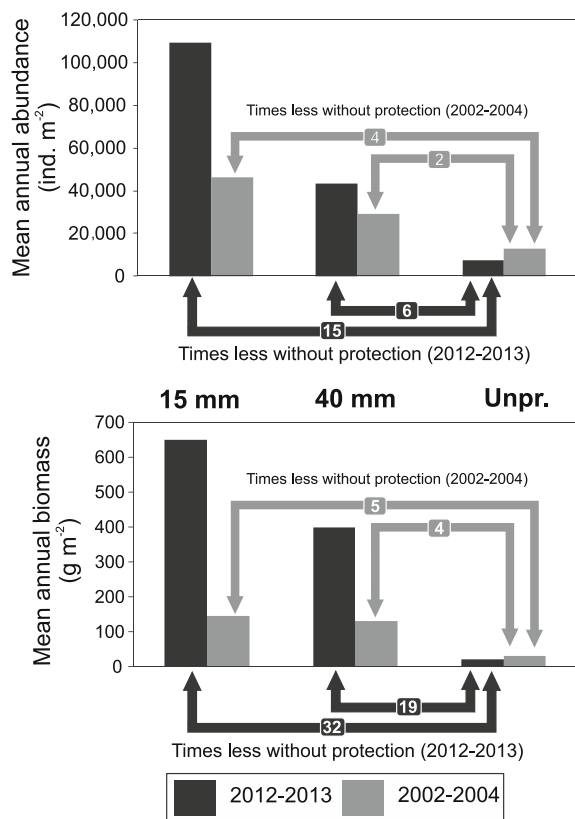


**Fig. 8** Mean annual abundance and biomass of *L. fortunei* in cages protected by 15- and 40-mm meshes, and in unprotected cages, as recorded in the present survey (2012–2013) and 10 years earlier (2002–2004; data from Sylvester et al., 2007a, b)

## Concluding remarks

Invasive species are often seen only as competitive dominants that threaten native biodiversity (Pimentel, 2002; Simberloff, 2003). Our findings challenge this standpoint insofar as, judging from their densities, aquatic invertebrates thrive better in association with the invader's colonies, where habitat heterogeneity, shelter, and food are higher than elsewhere. Further species-specific studies are necessary to assess whether facilitation by the mussel enhances species diversity as well, or if facilitation affects only a few species that end up reducing a pre-invasional more diverse taxocoenosis. Our results also seem to disagree with the hypothesis that, in the areas invaded, introduced species fare better than indigenous ones because they have fewer predators and competitors (Colautti et al., 2004). Our results show that, in its invasive range (South America, Japan), golden mussels endure a tremendous predation pressure albeit, admittedly, we do not know whether this pressure is indeed higher than that on native prey, or if it is higher in South America and Japan than in their native range. These conclusions by no means imply that the overall impacts of *L. fortunei* in the areas invaded are negligible or positive. Rather, we contend that its effects on the ecosystem are large and significant, but while some are clearly undesirable (e.g., promotion of cyanobacterial blooms, introduction of fish parasites; Cataldo et al., 2012; Baba & Urabe, 2015), others suggest that this bivalve plays the role of a foundation species, by virtue of which in some ecosystem compartments facilitation effects may have a comparable importance or even prevail over the negative ones (Bertness & Callaway, 1994; Bruno et al., 2003).

## References

Baba, T. & M. Urabe, 2015. Parasites of *Limnoperna fortunei*. In Boltovskoy, D. (ed.), *Limnoperna fortunei*: The Ecology, Distribution and Control of a Swiftly Spreading Invasive Fouling Mussel. Springer International Publishing, Cham: 55–65.

Barbosa, N. P. U., F. A. Silva, M. D. de Oliveira, M. A. dos Santos Neto, M. D. de Carvalho & A. V. Cardoso, 2016. *Limnoperna fortunei* (Dunker, 1857) (Mollusca, Bivalvia, Mytilidae): first record in the São Francisco River basin, Brazil. Check List 12: 1846.

Benke, A. C., A. D. Huryn, L. A. Smock & J. B. Wallace, 1999. Length–mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society 18: 308–343.

Bertness, M. D. & R. Callaway, 1994. Positive interactions in communities. Trends in Ecology and Evolution 9: 191–193.

Boltovskoy, D., 2015. Ecology and environmental impact of *Limnoperna fortunei*: introduction. In Boltovskoy, D. (ed), *Limnoperna fortunei*: The Ecology, Distribution and Control of a Swiftly Spreading Invasive Fouling Mussel. Springer International Publishing, Cham: 147–151.

Boltovskoy, D. & N. Correa, 2015. Ecosystem impacts of the invasive bivalve *Limnoperna fortunei* (golden mussel) in South America. Hydrobiologia 746: 81–95.

Boltovskoy, D., A. Y. Karatayev, L. E. Burlakova, D. Cataldo, V. Karatayev, F. Sylvester & A. Mariñelarena, 2009. Significant ecosystem-wide effects of the swiftly spreading invasive freshwater bivalve *Limnoperna fortunei*. Hydrobiologia 636: 271–284.

Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygierek, A. Herzig, A. Hillbricht-Ilkowska, H. Kurasawa, P. Larsson & T. Weglenska, 1976. A review o some problems in zooplankton production studies. Norwegian Journal of Zoology 24: 419–456.

Botts, P. S., B. A. Patterson & D. W. Schloesser, 1996. Zebra Mussel effects on benthic invertebrates: physical or biotic? Journal of the North American Benthological Society 15: 179–184.

Bruno, J. F. & M. D. Bertness, 2001. Habitat modification and facilitation in benthic marine communities. In Bertness, M. D., S. D. Gaines & M. E. Hay (eds), Marine Community Ecology. Sinauer Associates, Sunderland: 201–218.

Bruno, J. F., J. J. Stachowicz & M. D. Bertness, 2003. Inclusion of facilitation into ecological theory. Trends in Ecology & Evolution 18: 119–125.

Bujes, C. S., I. Ely & L. Verrastro, 2007. *Trachemys dorbigni* (Brazilian Slider) diet. Herpetological Review 38: 335.

Burlakova, L. E., A. Y. Karatayev & D. K. Padilla, 2006. Changes in the distribution and abundance of *Dreissena polymorpha* within lakes through time. Hydrobiologia 571: 133–146.

Carvalho, D. A., P. A. Collins & C. J. De Bonis, 2013. Predation ability of freshwater crabs: age and prey-specific differences in *Trichodactylus borellianus* (Brachyura: Trichodactylidae). Journal of Freshwater Ecology 28: 573–584.

Cataldo, D., 2015. Trophic relationships of *Limnoperna fortunei* with adult fishes. In Boltovskoy, D. (ed), *Limnoperna fortunei*: The Ecology, Distribution and Control of a Swiftly Spreading Invasive Fouling Mussel. Springer International Publishing, Cham: 231–248.

Cataldo, D., I. Ó. Farrell, E. M. Paolucci, F. Sylvester & D. Boltovskoy, 2012. Impact of the invasive golden mussel (*Limnoperna fortunei*) on phytoplankton and nutrient cycling. Aquatic Invasions 7: 91–100.

Colautti, R. I., A. Ricciardi, I. A. Grigorovich & H. J. MacIsaac, 2004. Is invasion success explained by the enemy release hypothesis? Ecology Letters 7: 721–733.

Correa, N., P. Sardiña, P. Perepelizin & D. Boltovskoy, 2015. *Limnoperna fortunei* colonies: structure, distribution and dynamics. In Boltovskoy, D. (ed), *Limnoperna fortunei*: The Ecology, Distribution and Control of a Swiftly Spreading Invasive Fouling Mussel. Springer International Publishing, Cham: 119–143.

Darrigran, G., 2002. Potential impact of filter-feeding invaders on temperate inland freshwater environments. Biological Invasions 4: 145–156.

Feller, R. J. & R. M. Warwick, 1988. Energetics. In Higgins, H. P. & H. Thiel (eds), Introduction to the study of meiofauna. Smithsonian Institution Press, Columbia: 181–196.

Ito, K., 2015. Colonization and spread of *Limnoperna fortunei* in Japan. In Boltovskoy, D. (ed), *Limnoperna fortunei*: The Ecology, Distribution and Control of a Swiftly Spreading Invasive Fouling Mussel. Springer International Publishing, Cham: 321–332.

Karatayev, A. Y., L. E. Burlakova, V. A. Karatayev & D. Boltovskoy, 2010. *Limnoperna fortunei* versus *Dreissena polymorpha*: population densities and benthic community impacts of two invasive freshwater bivalves. Journal of Shellfish Research 29: 975–984.

Karatayev, A. Y., D. Boltovskoy, L. E. Burlakova & D. K. Padilla, 2015. Parallels and contrasts between *Limnoperna fortunei* and *Dreissena* species. In Boltovskoy, D. (ed.), *Limnoperna fortunei*: The Ecology, Distribution and Control of a Swiftly Spreading Invasive Fouling Mussel. Springer International Publishing, Cham: 261–297.

Kluza, D. A. & K. M. McNyset, 2005. Ecological niche modeling of aquatic invasive species. Aquatic Invaders 16: 1–7.

Linares, M. S., M. Callisto & J. C. Marques, 2017. Invasive bivalves increase benthic communities complexity in neotropical reservoirs. Ecological Indicators 75: 279–285.

Mansur, M. C. D., C. P. Santos, G. Darrigran, I. Heydrich, C. T. Callil & F. R. Cardoso, 2003. Primeiros dados quali-quantitativos do mexilhão-dourado, *Limnoperna fortunei* (Dunker), no Delta do Jacuí, no Lago Guaíba e na Laguna dos Patos, Rio Grande do Sul, Brasil e alguns aspectos de sua invasão no novo ambiente. Revista Brasileira de Zoologia 20: 75–84.

Marçal, S. F., C. T. Callil & R. C. D. Santos, 2015. Trichoptera (Insecta) in water hyacinth roots: evaluation of the influence of exotic mussel and environmental factors. Acta Limnologica Brasiliensia 27: 341–355.

McCullagh, P. & J. A. Nelder, 1983. Generalized Linear Models. Chapman and Hall, London.

McEwen, G. F., M. W. Johnson & T. R. Folsom, 1954. A statistical analysis of the performance of the Folsom plankton sample splitter, based upon test observations. Archiv für Meteorologie, Geophysyk und Klimatologie A7: 502–527.

Nakano, D., T. Kobayashi & I. Sakaguchi, 2010. Predation and depth effects on abundance and size distribution of an invasive bivalve, the golden mussel *Limnoperna fortunei*, in a dam reservoir. Limnology 11: 259–266.

Nalepa, T. F. & D. W. Schloesser (eds), 2014. Quagga and Zebra Mussels: Biology, Impacts, and Control, 2nd ed. CRC Press, Boca Raton.

Oliveira, M. D., S. K. Hamilton, D. F. Calheiros, C. M. Jacobi & R. O. Latini, 2010. Modeling the potential distribution of the invasive golden mussel *Limnoperna fortunei* in the Upper Paraguay River system using limnological variables. Brazilian Journal of Biology 70: 831–840.

Oliveira, M. D., M. C. S. Campos, E. M. Paolucci, M. C. D. Mansur & S. K. Hamilton, 2015. Colonization and spread of *Limnoperna fortunei* in South America. In Boltovskoy, D. (ed), *Limnoperna fortunei*: The Ecology, Distribution and Control of a Swiftly Spreading Invasive Fouling Mussel. Springer International Publishing, Cham: 333–355.

Pastorino, G., G. Darrigran, S. M. Martín & L. Lunaschi, 1993. *Limnoperna fortunei* (Dunker, 1857) (Mytilidae), nuevo bivalvo invasor en aguas del Río de la Plata. Neotropica 39: 101–102.

Pimentel, D. (ed) 2002. Biological invasions. In Economic and Environmental Costs of Alien Plant, Animal, and Microbe Species. CRC Press, Boca Raton.

Rojas Molina, F. & V. Williner, 2013. First record of the non-indigenous mussel *Limnoperna fortunei* (Bivalvia, Mytilidae) as an epibiont of the crab *Trichodactylus borellianus* (Decapoda, Trichodactylidae). Crustaceana 86: 682–692.

Sardiña, P., D. Cataldo & D. Boltovskoy, 2008. The effects of the invasive mussel, *Limnoperna fortunei*, on associated fauna in South American freshwaters: importance of physical structure and food supply. Fundamental and Applied Limnology/Archiv für Hydrobiologie 173: 135–144.

Sardiña, P., E. Chaves & M. Marchese, 2011. Benthic community responses to invasion by the golden mussel, *Limnoperna fortunei* Dunker: biotic homogenization vs environmental driving forces. Journal of the North American Benthological Society 30: 1009–1023.

Simberloff, D., 2003. Confronting introduced species: a form of xenophobia? Biological Invasions 5: 179–192.

Smock, L. A., 1980. Relationships between body size and biomass of aquatic insects. Freshwater Biology 10: 375–383.

Spaccesi, F. G. & A. R. Capitulo, 2012. Benthic communities on hard substrates covered by *Limnoperna fortunei* Dunker (Bivalvia, Mytilidae) at an estuarine beach (Río de la Plata, Argentina). Journal of Limnology 71: 144–153.

Stanczykowska, A., 1977. Ecology of *Dreissena polymorpha* (Pall.) (Bivalvia) in lakes. Polskie Archiwum Hydrobiologii 24: 461–530.

Stewart, T. W., J. G. Miner & R. L. Lowe, 1998. Quantifying mechanisms for zebra mussel effects on benthic macroinvertebrates: organic matter production and shell-generated habitat. Journal of the North American Benthological Society 17: 81–94.

Strayer, D. L. & H. M. Malcom, 2006. Long-term demography of a zebra mussel (*Dreissena polymorpha*) population. Freshwater Biology 51: 117–130.

Strayer, D. L. & H. M. Malcom, 2014. Long-term change in the Hudson River´s bivalve populations. In Nalepa, T. F. & D. W. Schloesser (eds), Quagga and Zebra Mussels: Biology, Impacts, and Control, 2nd ed. CRC Press, Boca Raton: 71–81.

Sylvester, F., 2006. Biología alimentaria y ecología del molusco invasor *Limnoperna fortunei* (Mytilidae) en el Paraná inferior y Río de la Plata. PhD thesis, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina. 160 p. https://www.opac.bl.fcen.uba.ar. Accessed 5 Mar 2018.

Sylvester, F. & P. Sardiña, 2015. Relationships of *Limnoperna fortunei* with benthic animals. In Boltovskoy, D. (ed), *Limnoperna fortunei*: The Ecology, Distribution and Control of a Swiftly Spreading Invasive Fouling Mussel. Springer International Publishing, Cham: 191–210.

Sylvester, F., D. Boltovskoy & D. Cataldo, 2007a. Fast response of freshwater consumers to a new trophic resource: predation on the recently introduced Asian bivalve *Limnoperna fortunei* in the lower Paraná River, South America. Austral Ecology 32: 403–415.

Sylvester, F., D. Boltovskoy & D. Cataldo, 2007b. The invasive bivalve *Limnoperna fortunei* enhances benthic invertebrate densities in South American floodplain rivers. Hydrobiologia 589: 15–27.

Torres, M. V., V. Williner & F. Giri, 2012. Size selective predation on an invasive bivalve, *Limnoperna fortunei* (Mytilidae), by a freshwater crab, *Zilchiopsis collastinensis* (Trichodactylidae). Journal of Crustacean Biology 32: 698–710.

Weber, S. & W. Traunspurger, 2014. Top-down control of a meiobenthic community by two juvenile freshwater fish species. Aquatic Ecology 48: 465–480.

Weber, S. & W. Traunspurger, 2015. The effects of predation by juvenile fish on the meiobenthic community structure in a natural pond. Freshwater Biology 60: 2392–2409.