Impacts of the Invading Golden Mussel *Limnoperna fortunei* on Zooplankton: A Mesocosm Experiment

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Florencia Rojas Molina, Susana José de Paggi, and Diego Frau (2012) Impacts of the invading golden mussel *Limnoperna fortunei* on zooplankton: a mesocosm experiment. *Zoological Studies* **51**(6): 733-744. Invasive filter-feeding mussels and clams are well-known for profoundly impacting the invaded systems. Many studies in South America documented interactions of the Asian mussel *Limnoperna fortunei* with several components of the local biota. However, few experiments have examined in detail the effect of the mussels on zooplankton abundances and the species composition. We conducted a 72-h experiment to assess the impacts of *L. fortunei* on the composition and abundance of Paraná River floodplain zooplankton using experimental mesocosms. Three treatments with 3 replicates each were used in the experiment: control (without mussels) and 2 treatments with mussels at different concentrations. Densities of the most abundant genera of rotifers (*Keratella*) and cladocerans (*Bosmina* and *Diaphanosoma*) significantly declined in mollusc-containing mesocosms compared to the control. Phytoplankton density was significantly lower in the presence of the mollusc. Mesocosms with higher mollusc concentrations had lower zooplankton densities than those with fewer predators. Therefore, our results strongly suggest that *L. fortunei* has negative impacts on this community, affecting the abundance and composition of species, and the size structure. The ability of the mussel to control the zooplankton can be explained by its direct consumption or by competition for trophic resources. http://zoolstud.sinica.edu.tw/Journals/51.6/733.pdf

Key words: Suspension-feeding bivalves, Phytoplankton, Rotifera, Cladocera.

Currently, humans are altering the climate, transforming habitats, connecting previously isolated lands or waters, exterminating species, and transporting organisms worldwide (Brown and Sax 2004). In the midst of these drastic changes in the environment and biodiversity, the magnitude and consequences of intentional or unintentional human-assisted invasions are large and unprecedented (Brown and Sax 2004). Freshwater systems are among the most-often invaded ecosystems, and their biodiversity has declined faster than those of terrestrial and marine systems (Bampfylde et al. 2010, Ricciardi and MacIsaac 2011). Among animals, invasive filter-feeding mussels and clams are well-known for their profound impacts on the systems they invade (Strayer et al. 1999). For example, extensive research demonstrated that *Dreissena polymorpha*, the Ponto-Caspian mussel that invaded North America in the late 1980s, can alter both the structure and function of the invaded ecosystems which affects trophic interactions, mineralization of nutrients, oxygen availability, sedimentation rates, and pollutant dynamics (Karatayev et al. 1997 2007, Strayer et al. 1999).

Limnoperna fortunei, commonly referred to as

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the golden mussel, is a freshwater bivalve native to rivers, lakes, and estuaries of southeastern Asia, including China, Thailand, Korea, Laos, Cambodia, Vietnam, and Indonesia. In 1965, it was unintentionally introduced to Hong Kong, and between 1980 and 1990, it spread to Taiwan, Japan, and Korea (Ricciardi and Rasmussen 1998). In the early 1990s, *L. fortunei* was discovered in the Río de la Plata estuary in Argentina, introduced most probably via water discharged as ballast from Asian ships (Pastorino et al. 1993, Darrigran and Pastorino 1995). Shortly after its introduction, it was recorded in the Middle Paraná River and in different areas of its floodplain in 1996, attached to every natural substrate available (from trunks, rocks, aquatic plants and other organisms to compact silt-sand) and artificial ones (such as piers, tubes, walls, .etc) (Darrigran and Ezcurra de Drago 2000). In South America, the golden mussel has colonized practically the entire Río de la Plata basin extending its distribution to Uruguay, Paraguay, Bolivia, and Brazil in dense colonies of up to 200,000 mussels/m^2 (Boltovskoy et al. 2006).

Since its introduction, the Asian golden mussel has been shown to strongly interact with several components of the local biota (Darrigran et al. 1998, Darrigran 2002, Darrigran and Damborenea 2006, García and Montalto 2006, Paolucci et al. 2007, Sylvester et al. 2007, Sardiña et al. 2008). Investigations indicate that the impacts of the mollusc on the water column involve direct trophic interactions and changes in several water-column properties (water transparency, suspended matter, and nutrients) (Boltovskoy et al. 2009). Trophic relationships with water-column communities have been principally analyzed related to fishes (Montalto et al. 1999, Penchaszadeh et al. 2000, García and Montalto 2006, Paolucci et al. 2007 2010a b) and to a lesser extent, related to plankton (Sylvester et al. 2005, Pestana et al. 2009, Rojas Molina et al. 2010 2011). The main purpose of this work was to analyze the potential impacts of *L. fortunei* on the composition and abundance of Paraná River floodplain zooplankton using experimental mesocosms.

MATERIALS AND METHODS

Experimental set-up, sampling, and analysis

The 72-h experiment was carried out in outdoor mesocosm tanks. The mesocosms con-sisted of 9 randomly assigned opaque plastic cylindrical tanks (57 cm in diameter by 90 cm deep), holding an average volume of about 200 L of water each. The tanks were filled and inoculated with water and phytoplankton and zooplankton from a shallow lake of the Paraná River floodplain. Plankton was collected with a 10-μm net and held in a large container. It was mixed and distributed in several aliquots to stock mesocosms at similar concentrations recorded in floodplain lakes of this system (Iriondo et al. 2007) or pampean shallow lakes (Claps et al. 2011).

Limnoperna fortunei adults were manually removed from marker buoys located in the Middle Paraná River (31°44'30"S; 60°39'50"W). Mussels were brought to the hatchery in plastic containers filled with river water. Groups of mussels were carefully separated and transferred to 80-L aquaria that were filled with river water, on the bottom of which plastic strips (60 cm long by 7 cm wide) had previously been placed for mollusc attachment. Molluscs were homogeneously distributed, allowed to acclimate for 7 d with continuous aeration, and fed ad libitum with fish food and the alga *Chlorella vulgaris*. To avoid overfiltration by starved animals, food was administered until the onset of the experiments.

Three treatments with 3 replicates each were used in the experiment: control without mussels (C), and 2 treatments containing adult mussels (16.1 ± 2.7 mm long, in greatest axial dimension) in different concentrations of M1 with 128 molluscs and M2 with 256 molluscs. Five days after plankton inoculation, the plastic strips with attached mussels were transferred to the mesocosms and suspended vertically at a depth of 20 cm in the center of the tanks. This placement of the molluscs in the water column is similar to that found in shallow lakes of the Middle Paraná River, where *L. fortunei* is associated with the root systems of floating macrophytes such as *Eichhornia crassipes* (Mart.) (Rojas Molina et al. 2010). In areas with a diameter similar to the mesocosms, 90-400 bivalves/m^2 of vegetation cover were recorded (Musín et al. unpubl. data), so the densities of molluscs used in this experiment were similar to concentrations observed in nature.

Water samples were collected from each mesocosm immediately before the mussels were added and 3, 6, 12, 24, 48, and 72 h after their addition. A rigid plastic tube designed for use in mesocosms and shallow lakes (Paggi et al. 2001) equipped with a 50-μm net was used to take integrated zooplankton samples (≈ 5.5 L

per tube). Samples were preserved with 10% formaldehyde, and the analysis was performed under a binocular microscope (rotifers and nauplii were counted in a 1-ml Sedgwick-Rafter chamber, and microcrustaceans in a 5-ml Bogorov chamber, Wetzel and Likens 1979). At least 100 individuals of the 1st dominant species were counted per sample. Phytoplankton samples were taken from the subsurface zone (0.25 m deep) with a 100-ml bottle and fixed with acidified Lugol's solution. Algae were quantified under an inverted microscope in sedimentation chambers, following the method of Utermöhl (1958). At least 200 individuals of the 1st dominant species and 50 fields were counted per sample.

Several physical parameters (pH, temperature, dissolved oxygen (DO), and conductivity) were measured at mid-water using portable meters (HANNA HI 991003, HANNA HI 9143, HANNA HI 9033, Romania). Subsurface water samples were taken from each tank for analysis and measurement of turbidity (in all samples), and nitrate (NO_3), phosphate (PO_4), and ammonium (NH_4) (at 0, 24, and 72 h). Samples were filtered through Whatman GF/F glass-fiber filters (Whatman, England) to analyze nutrients. Nitrate was analyzed with the cadmium-copper reduction method and PO_4 with the ascorbic acid-molibdate method, both using reagent kits of Hach (Loveland, USA), whereas ammonium (NH_4) was analyzed with the indophenol-blue method using a kit of the Wienner Co. (Rosario, Argentine), following the methods of the APHA (1992). Turbidity was spectrophotometrically determined at 450 nm.

Data analysis

Kruskal-Wallis (KW) and Dunn's multiple-comparisons tests were used to compare environmental parameters among treatments (transformation of the data failed to improve their normality, so non-parametric tests were required). All replicate data were included in the test.

Biotic data were normalized with a log(x+1) transformation. Differences in treatment effects were tested with a repeated-measures analysis of variance (RM ANOVA) that allowed evaluation of the effect of mollusc concentrations on plankton densities over time. In this analysis, it was possible to test the effect of each factor in separate forms, times (h), and mollusc concentrations (C, M1, and M2), and their interaction (time × mollusc concentration). Post-hoc tests were used when differences between treatments were significant.

Relationships among phytoplankton and zooplankton densities were analyzed using Pearson parametric correlations. This correlation was performed to determine if the pattern of change of phytoplankton was similar to that of zooplankton. All replicate data were included in the test. The statistical analyses were run using SPSS software (version 18).

RESULTS

Physical and chemical parameters

The average temperature throughout the experiment was about 26°C; the conductivity ranged 237.0-248.7 μs/cm and was similar among treatments. DO and pH variations were very small in the various treatments throughout the experiment. There were no significant differences among mesocosms in NO_3 (KW = 0.615, p = 0.735) or PO_4 (KW = 2.797, p = 0.247), and the variation was low within each treatment (Table 1).

Turbidity was very similar among mesocosms at hour 0. Three hours after the addition of the mussels to the end of the experiment, turbidity values significantly decreased (KW = 6.047, p = 0.0486) in the presence of the molluscs (Dunn's test, C vs. M2 and C vs. M1 p < 0.05 in both cases). Higher average turbidity and lower variability were recorded for C, while M2 showed the lowest turbidity and higher variability (Table 1).

Ammonium did not significantly differ among tanks (KW = 0.425, p = 0.808), but by the end of the experiment in the presence of mussels, this nutrient had increased by 500% over values at the beginning of the experiment (for M1 and M2).

Phytoplankton

In total, 26 taxa of Cyanobacteria, Bacillariophyceae, Chlorophyceae, Chrysophyceae, and Cryptophyceae were recorded, including the dominant genera *Monoraphidium*, *Nitzschia*, *Chlamydomonas*, *Cryptomonas*, and *Goniochloris*. At the beginning of the experiment (hour 0) phytoplankton densities were similar among treatments (RM ANOVA, p = 0.289, F = 1.537, Table 2), but concentrations were severely affected by the time × mollusc concentration interaction. After 6 h to the end of the experiment (at 72 h), M1 and M2 had significantly lower densities than the control (RM ANOVA, F = 2.798, p = 0.008), with important

drops mainly in M2, the final value of which was < 15% of the initial density (Figs. 1, 2, Table 2). Within each treatment, the variability was greater in those with bivalves than in the control (Fig. 2).

Zooplankton

In total, 56 taxa were identified; 41 were Rotifera and 15 were Cladocera. Because the zooplankton assemblages were dominated by very few genera, we restricted the statistical analyses to those genera. Among the Rotifera, *Keratella* and *Polyarthra* were the most abundant (at 53% and 12%, respectively). The Cladocera were numerically dominated by *Bosmina* (48%) and *Diaphanosoma* (20%). Nauplii were dominant (88%) among the Copepoda; the Calanoida was dominant among adults and juveniles.

Table 1. Means (standard deviation) and ranges of physical and chemical parameters recorded in the mesocosms over the 72 h of the experiment. Values represent the mean of replicate treatments. C, control; M1, mussel concentration 1; M2, mussel concentration 2

	C	M1	M2
Temperature (°C)	26.0 (3.1)	25.7 (3.3)	26.2 (3.4)
	22.4-30.8	22.2-30.6	22.5-31.1
Conductivity (µs/cm)	242.4 (3.6)	241.7 (3.4)	244.5 (3.1)
	238.3-247.7	237.0-245.3	240.3-248.7
Turbidity (FTU)	78.5 (6.1)	73.3 (8.5)	72.9 (9.1)
	69.3-85.0	64.3-83.0	63.3-85.0
Dissolved oxygen (ppm)	7.8 (0.4)	7.8 (0.4)	7.5 (0.3)
	7.5-8.4	7.3-8.3	7.1-7.9
pH	8.6 (0.1)	8.5 (0.1)	8.5 (0.2)
	8.5-8.7	8.3-8.7	8.2-8.7
NO_3 (mg/L)	0.8 (0.1)	0.7 (0.2)	0.8 (0.2)
	0.7-0.9	0.5-1.0	0.6-1.1
PO_4 (mg/L)	0.3 (0.2)	0.2 (0.1)	0.3 (0.1)
	0.2-0.6	0.2-0.3	0.2-0.4
NH_4 (mg/L)	0.4 (0.1)	0.5 (0.5)	0.7 (0.6)
	0.3-0.5	0.2-1.1	0.3-1.4

Table 2. Plankton densities in treatments at the beginning (0 h) and end (72 h) of the experiment. PID, percentage of the initial density at the end of the experiment. Phytoplankton is expressed in individuals ind./mL and zooplankton in ind./L. C, control; M1, mussel concentration 1; M2, mussel concentration 2

		0 h	72 h	PID (%)
Phytoplankton	C	9362	5385	58
	M1	4308	2006	47
	M2	8270	1159	14
Zooplankton	C	1133	491	43
	M1	955	343	36
	M2	929	77	8
Rotifera	C	75	6	8
	M1	70	2	3
	M2	72	1	1
Cladocera	C	42	34	81
	M1	62	11	18
	M2	36	3	9
Copepoda	C	1016	451	44
	M1	823	329	40
	M2	822	73	9

Initial concentrations of zooplankton were similar among treatments (RM ANOVA, $F = 0.123$, $p = 0.886$, Table 2). Densities of zooplankton and different genera analyzed were affected by the time factor and the mollusc concentration factor, but the time × mollusc concentration interaction was not significant.

Rotifer concentrations varied in all treatments, with the control being the most variable and with higher densities than in mollusc-containing mesocosms (Fig. 2). The dominant rotifers *Keratella* and *Polyarthra* significantly decreased over time in all treatments (RM ANOVA, $F = 36.723$, $p < 0.001$; $F = 7.33$, $p = 0.004$,
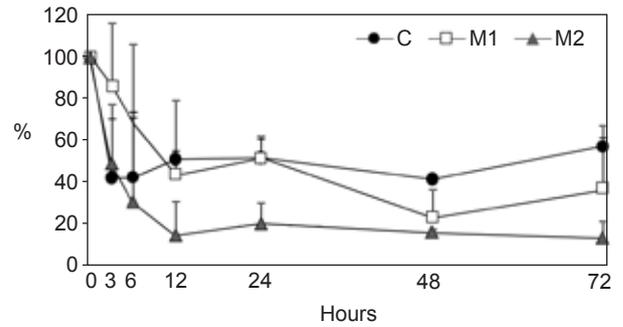
Fig. 1. Variations in percentages of the initial phytoplankton density in experimental mesocosms over the 72 h of the experiment (treatment means + standard deviation). C, control; M1, mussel concentration 1; M2, mussel concentration 2.
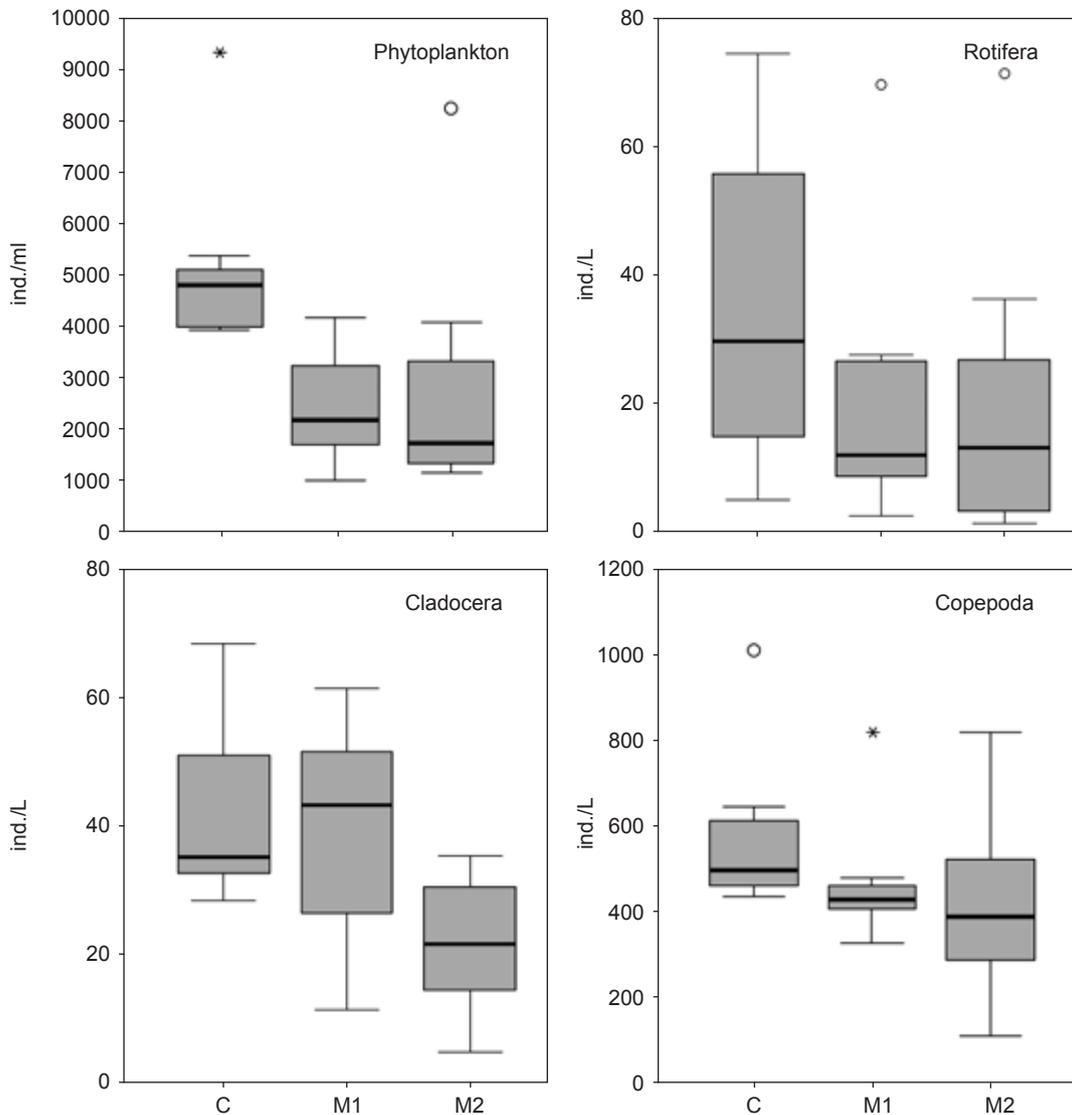

Fig. 2. Cumulative effects of treatments on plankton densities. Outer lines are the 95th percentiles; upper and lower boundaries of the box are the 90th percentiles; and the horizontal line in the box interior is the median value. Circles and asterisks are atypical and extreme values, respectively. C, control; M1, mussel concentration 1; M2, mussel concentration 2.

respectively). However, these drops were faster in the presence of the bivalve, with values < 40% of the initial density during the 1st 6 h of the experiment (Fig. 3). The mean density of *Keratella* in the entire experiment was significantly higher in the control (17.7 individuals (ind.)/L) than in mussel treatments (M1 = 6.22 ind./L and M2 = 5.89 ind./L) (RM ANOVA, $F = 134.242$, $p < 0.001$). In the presence of *L. fortunei*, *Keratella* had decreased by > 90% by 48 h and had disappeared from the mesocosms by the end of the experiment, while *Polyarthra* was not recorded after 24 h in the mesocosm with a higher concentration of mussel (M2) and at 48 h in M1 (Fig. 4).

Cladoceran concentrations varied in the mesocosms, with higher densities in the control (Fig. 2), while in mollusc-containing mesocosms, the final densities (at 72 h) were < 20% of the initial values (Table 2). *Bosmina* varied significantly over time, with higher densities at the beginning of the experiment (RM ANOVA, $F = 6.095$, $p < 0.001$)

(Fig. 3). In the control after 24 h, *Bosmina* had increased > 3-fold with respect to initial values, and by the end of the experiment, these concentrations had dropped but remained slightly higher than at 0 h (Fig. 3). On the other hand, in treatments with molluscs, after a small increase at hour 3, the *Bosmina* abundance markedly declined towards the end of the experiment to < 20% of the initial value. These declines were significant with respect to the control (RM ANOVA, $F = 11.603$, $p = 0.009$).

After 12 h, the density of *Diaphanosoma* had significantly increased in all treatments (up to 400% of the initial values, RM ANOVA, $F = 5.284$, $p = 0.001$). This concentration was similar in the control throughout the experiment; in the mollusc treatments, these values dropped to about 80% of their initial density (Fig. 3). The mean density over the entire experiment was highly significant in the control (12.8 ind./L) compared to mussel treatments (5.1 ind./L for M1 and 4.7 ind./L for M2,
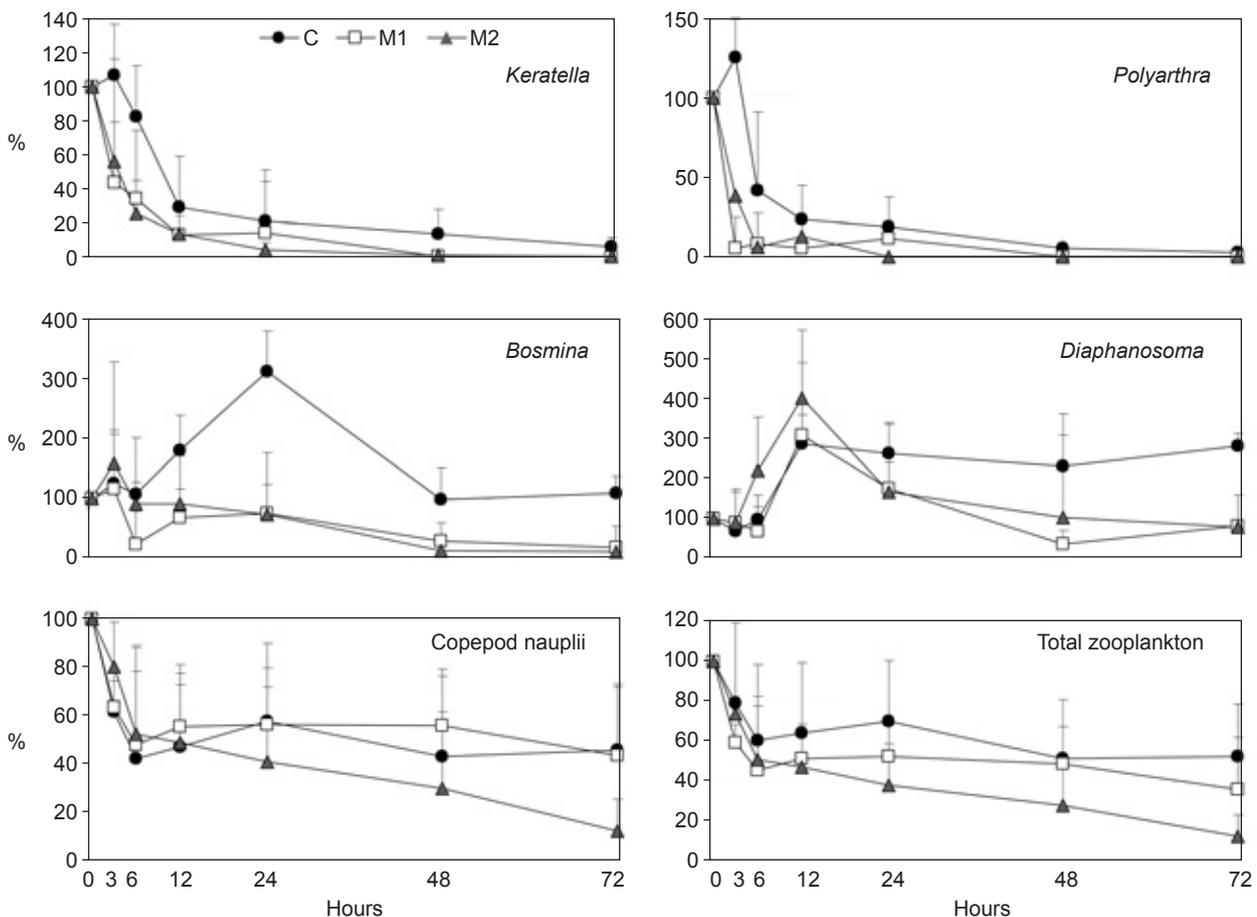

Fig. 3. Variations in percentages of the initial zooplankton density in experimental mesocosms over the 72 h of the experiment (treatment means + standard deviation). C, control; M1, mussel concentration 1; M2, mussel concentration 2.

RM ANOVA: *F* = 14.441, *p* = 0.005).

The greatest variations in copepods density occurred in mesocosms with the highest concentration of bivalves (Fig. 2), the final density of which was < 10% of the initial value (Table 2). In all treatments, naupliar density was significantly lower toward the end of the experiment (RM ANOVA, *F* = 5.868, *p* = 0.031) (Fig. 3), but in turn, differences appeared between treatments as a result of the molluscs' effect (RM ANOVA: *F* = 5.642, *p* = 0.042), with a further decline in M2 (Fig. 3).

In treatments with and without mussels, zooplankton density *in toto* was higher during the 1st 3 h (RM ANOVA *F* = 6.089, *p* = 0.032),

although there was a significant difference due to the mollusc concentration (RM ANOVA *F* = 11.017, *p* = 0.010), with control mesocosms showing significantly higher densities compared to M2 (Table 2). By the end of the experiment, M2 showed < 10% of its initial density (Table 2, Fig. 3).

Zooplankton and phytoplankton abundances had the same patterns of variation in mollusc-containing mesocosms, and the Pearson correlation coefficient showed a significant direct relationship between them (*r* = 0.459, *p* = 0.036 for M1; *r* = 0.4715, *p* = 0.031 for M2), but not in the control (*r* = 0.406, *p* = 0.068).

DISCUSSION

Among the environmental parameters examined, turbidity and ammonia showed clear differences due to the presence of molluscs. While turbidity decreased in all mesocosms, probably due to sedimentation of inorganic particles, at the end of the experiment, it was significantly lower in mesocosms with *Limnoperna fortunei*. This can be explained by the fact that bivalves are capable of filtering organic and inorganic particles from the seston and ingesting some of this particulate material, while a portion is ejected into the environment as pseudofeces (Sprung and Rose 1988, Fanslow et al. 1995). Bivalve invasions are associated with significant decreases in suspended particulate matter (suspended solids and turbidity) and significant increases in water clarity (Secchi depth) in lakes and rivers (Higgins and Vander Zanden 2010).

The effect of mussels on dissolved nitrogen was recorded in the experiment. The strong increase in NH_4 in the mollusc treatments clearly indicated the presence of nitrogenous wastes produced by these molluscs (ammonia excretion) as a result of their metabolic processes. Other enclosure experiments also demonstrated an accumulation of soluble N in the water column in the presence of bivalves (Higgins and Vander Zanden 2010).

Abundances of zooplankton varied over time in mesocosms with and without mussels. The dominant cladocerans, *Bosmina* and *Diaphanosoma*, showed substantial increases in their densities at 12-24 h in all treatments. This could have been due to the fact that at hour 0, numerous ovigerous females were observed (with neonates in an advanced stage of development) perhaps as a result of the high water temperature
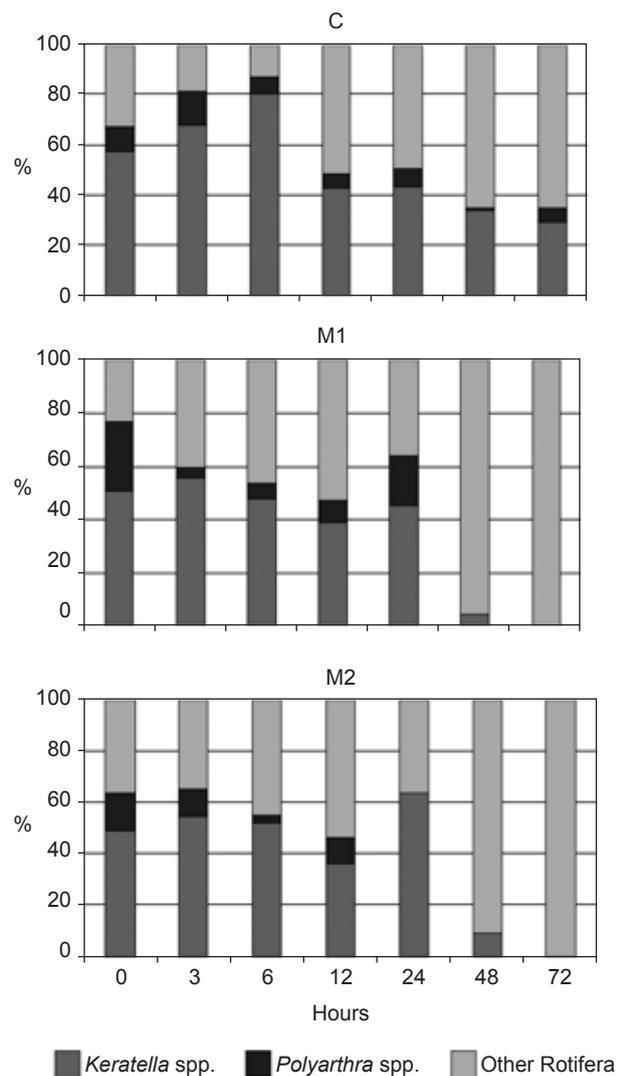

Fig. 4. Relative densities (%) of dominant rotifers in the mesocosms over the 72 h of the experiment. C, control; M1, mussel concentration 1; M2, mussel concentration 2.

at the time of inoculation of the mesocosms, which could have had a favorable impact on the organisms' reproduction processes. It is known that the cladoceran reproductive rate can be reduced to 30-40 h at temperatures of 20-30°C, with development times of eggs of 24-72 h (Melão 1999, Gillooly 2000, Kalff 2002, Rodríguez-Estrada et al. 2003).

Despite these temporal variations in zooplankton, the results of this experiment showed that the golden mussel may have negatively impacted them. In general, the mesocosms with *L. fortunei* presented lower zooplankton densities than the control, and in turn, the mesocosms with the higher mollusc concentration had lower densities than those with fewer predators, as was also the case with phytoplankton; many of these differences were statistically significant. Thus, it is possible to postulate 2 likely mechanisms responsible for these changes: (1) the direct consumption of zooplankton by *L. fortunei*, and (2) starvation of zooplankton due to competition for trophic resources with the molluscs.

The results showed that *Limnoperna* was also capable of rapidly reducing rotifer abundances. The markedly negative effects of this mollusc on the dominant genera, *Keratella* and *Polyarthra*, led to the disappearance of the latter. Larger zooplankton such as *Bosmina* and *Diaphanosoma* cladocerans also showed significant differences in densities between control and treatments with molluscs, exhibiting significant drops in the latter. An analysis of the natural diet of *L. fortunei* (Rojas Molina et al. 2010) indicated that rotifers, mainly the genus *Keratella*, are among the animal organisms with the highest frequency and relative abundance in stomach contents of this mollusc. Small cladocerans, mostly of the Chydoridae and Bosminidae, also represent the greatest biomass in its diet. Large-sized cladocerans, like *Diaphanosoma* and those of the family Sididae, are generally comparatively less vulnerable to predation by *L. fortunei* due to their high escape ability and larger size (Rojas Molina et al. 2010 2011). However, results of our experiment led us to assume that in addition to their smaller size, juveniles of *Diaphanosoma* may be more vulnerable to the suction power of the mollusc. This might explain the decrease in *Diaphanosoma* density observed in our experiment; further experiments are needed to examine this interaction.

Food limitation is another mechanism that could lead to decreased zooplankton densities. It is known that *L. fortunei* has an important ability to reduce phytoplankton through its high filtration rate (350-725 ml/h/mussel; Sylvester et al. 2005, Pestana et al. 2009), which in turn is favored by high temperatures. In mussel treatments, a significant decline occurred in algal abundances that was accentuated throughout the experiment and with the higher concentration of molluscs, falling by 55%-90% by the end of the experiment. Favorable temperature conditions, coupled with the fact that the size of algae (2-40 μm) is well within the range that mussels have been shown to consume (< 250 μm, Rojas Molina et al. 2010), encouraged the consumption of phytoplankton by the bivalve.

Rotifer species respond very differently to starvation; for example at 20°C, *Keratella* has a mean starvation time of 4.9 d, *Synchaeta* 0.4 d, and *Brachionus* 2.2 d (Kirk 1997 2002), and this starvation resistance is reduced by an increase in temperature (Stelzer 2006). There are others factors that could be important; for example, rotifer females emerging from diapausing eggs have a higher tolerance of starvation than females emerging from parthenogenetic eggs (Gilbert 2004, Garcia-Roger et al. 2006). Among cladocerans, *Moina* can survive 4 d at 20°C (Threlkeld 1976), smaller cladocerans have shorter starvation times (Threlkeld 1976, Tessier et al. 1983) than larger species like some *Daphnia* (MacIsaac and Gilbert 1989), and in general, juveniles are more vulnerable to starvation than are adults, but this is not true in all cases (e.g., *Ceriodaphnia*, Matveev and Gabriel 1994). Among copepods, *Diaptomus* nauplii are more vulnerable to starvation than are adults; at 20°C nauplii exhibited 50% mortality under starvation conditions after only 2.4 d, while 50% mortality for adults occurred after 7 d (Williamson et al. 1985). In our mesocosm experiment, zooplankton were exposed to a mean temperature of > 25°C, with a maximum value of 31°C. Therefore, it is assumed that one of the causes of the decline in zooplankton could also be food limitation as a consequence of competition with molluscs which was enhanced at higher temperatures, which reduced starvation tolerance. However, our results did not differentiate as to whether declines in these taxa occurred through direct predation or competition.

In the control, high densities of *Bosmina* and *Diaphanosoma* maintained during the experiment and the absence of zooplanktophagus predators might have led to a reduction in the concentration of rotifers (although slower and less

pronounced than in treatments with molluscs) as the experiment proceeded. This is not surprising, given the competitive efficiency of cladocerans (Hessen 1985, Bogdan and Gilber 1987, DeMott 1989, Brooks and Dodson 1965, Gilbert 1988, Moss 2010).

Other laboratory and limnocorral experiments evaluating the impacts of *L. fortunei*, even with different characteristics from those in our study (duration, tank capacity, and concentrations of molluscs), showed similar results such as a decrease in the density of algae (99%) and higher ammonium and nitrate concentrations by the end of the experiment in the presence of the mollusc (Cataldo et al. 2011). On the other hand, in some lotic and lentic environments of Argentina, some of these ecosystem-wide effects were recorded, which were attributed to invasion by the mollusc. Comparison of data from secondary channels and a shallow lake of the Middle Paraná River floodplain between years before and after invasion by *L. fortunei* showed strong declines in rotifers (mainly the genus *Keratella*) and chlorophyll compared to previous years (Devercelli and Peruchet 2008, Rojas Molina and José de Paggi 2008). In Río Tercero Reservoir, after the introduction of *Limnoperna* in 1998, water transparency increased, while suspended matter, Chl *a*, and primary production significantly decreased (Boltovskoy et al. 2009).

Numerous studies were conducted in outdoor tanks with the invasive mussel *Dreissena polymorpha*. In most cases, this mollusc caused increases in water transparency and ammonia, and reductions in suspended solids and phytoplankton (Richardson and Bartsch 1997, Wilson 2003, Thorp and Casper 2003, Raikow 2004), including changes in the community structure (Jack and Thorp 2000). With respect to the microzooplankton (rotifers and nauplii), the negative effects of *D. polymorpha* were repeatedly noted, especially in species of the genera *Polyarthra* and *Keratella* (Richardson and Bartsch 1997, Jack and Thorp 2000, Thorp and Casper 2002 2003, Raikow 2004), mainly due to their consumption by molluscs and competition for trophic resources. The effects on microcrustaceans; however, differed among experiments and were often less noticeable (Thorp and Casper 2002). Among cladocerans, *Bosmina* was thought to be the most affected because it is directly ingested. In some cases, *Diaphanosoma* showed a decline in its population presumably by competition for trophic resources with the mollusc, and in general, it is not eaten due to its larger size

and better escape ability (Jack and Thorp 2000, Thorp and Casper 2003, Wilson 2003, Raikow 2004).

The results of our study confirm the hypothesis of a negative effect of *L. fortunei* on zooplankton densities. Impacts of the golden mussel are generally comparable to those previously reported for *D. polymorpha*. Thus, our findings of a significant and positive relationship between zooplankton and phytoplankton densities in mussel treatments, and the significant plankton difference between treatments with and without mussels suggest that *L. fortunei* causes declines in the densities of animals and algae, affecting the composition of species and the size structure. This suggests that impacts on native populations of zooplankton can be important. The finding of higher densities of *L. fortunei* on macrophytes in shallow lakes of the Paraná River floodplain (Musín et al. unpubl. data) suggests that the effects on zooplankton may be higher in small lakes with high densities of floating macrophytes. *Limnoperna fortunei* represents a new element in these ecosystems, that undoubtedly contributes to increasing the complexity of predator-prey relationships and animal-macrophyte relationships that occur in these highly biodiverse Neotropical systems (Agostinho et al. 2007, Gómez and Kehr 2011).

Suppression of plankton and the channeling of nutrients and energy from the water column to the benthos by invasive mussels represent a restructuring of freshwater ecosystems. Several studies indicated that invasive bivalve-induced changes in the resource base of freshwater ecosystems can lead to significant and ecologically relevant impacts on higher trophic levels (Higging and Vander Zanden 2010). Therefore, our study stresses the importance of the ecological role of filter-feeding bivalve populations, particularly *L. fortunei*, in linking pelagic and benthic communities, not only for transferring primary production to the benthic compartment, but also secondary production, thus making matter and energy flows more complex in the food web structure. This new benthic-plankton trophic link is a top-down control of biomass (filter feeding) and a bottom-up nutrient supply within these webs that could alter our understanding of plankton-cascade trophic interactions in our systems. It is known that the coupling of benthic and pelagic habitats by native bivalves performs similar ecological functions; however, invasive mussels are capable of achieving filtration pressures several orders

of magnitude higher than most native freshwater mussel communities (Strayer et al. 1999).

Not many studies have been carried out so far on the interactions within these webs since the introduction of *L. fortunei* (cascading effects). Therefore, further research is needed to explain and model the effects of this new planktivore invertebrate on food webs of invaded aquatic systems of South America.

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