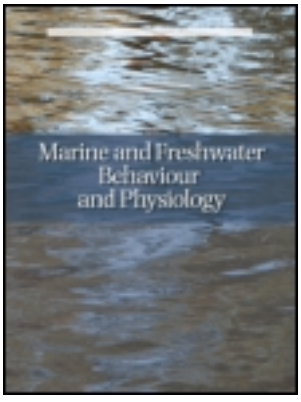

Marine and Freshwater Behaviour and Physiology
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/gmfw20

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Published online: 31 Oct 2012.

Marine and Freshwater Behaviour and Physiology, 2013
Vol. 45, No. 5, 303–316, http://dx.doi.org/10.1080/10236244.2012.735419

The effect of an invading filter-feeding bivalve on a phytoplankton assemblage from the Paraná system: a mesocosm experiment

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(*Received 9 August 2012; final version received 27 September 2012*)

The effect of different concentrations of the bivalve *Limnoperna fortunei* on the algal density and structure and its filtration rate was estimated in a mesocosm experiment. The experiment was carried out using containers of 200 L and three treatments: Control (without bivalves), C1 (with 128 individual bivalves), and C2 (with 256 individual bivalves). Decrease in phytoplankton density was detected in bivalve treatments after 6 h. A decrease of 52% and 86% of the initial density was measured in C1 and C2, respectively, after 48 h. All algae groups showed substantial decrease in densities (>60%) and the composition of the algae assemblages changed in the presence of the bivalve. In particular, there was an increase in the density of Flagellates. The maximum estimated bivalve filtration rate was 357 mL ind^{-1} h^{-1} at 28°C. Our results suggest that the invading bivalves could significantly affect both the plankton density and assemblage structure in natural systems.

Keywords: mussel; invasive; *Limnoperna fortunei*; phytoplankton; species selectivity; filtration rate; mesocosm

Introduction

Intercontinental trade and travel have increased considerably in recent decades, and with this trend has come the intentional or accidental transport of non-native organisms. This has already led to certain major economic impacts and could eventually affect the structure and functioning of entire ecosystems through changes in baseline abiotic conditions and in resident biota (Pimm et al. 1995; Sala et al. 2000; Grosholz 2002). One recurrent phenomenon is the development of dense populations of invasive bivalves by means of human introduction via marine transport, recreational navigation, and channelization (Carlton 1992; Gutiérrez et al. 2003; Strayer 2010). Several bivalve species have invaded aquatic ecosystems worldwide. Of these, *Dreissena polymorpha* (Pallas) is the most aggressive in the freshwater ecosystems of Europe and North America, and its presence has had significant ecological and economic consequences (Katatayev et al. 2007). Given the high

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densities and broad spatial distributions that are characteristic of *D. polymorpha*, the filtering activity can significantly alter natural ecosystems, causing a major decline in the abundance of zooplankton and in chlorophyll-a concentration levels, thus affecting nutrient recycling and increasing the concentration (Grigorovich and Shevtsova 1995; Pace et al. 1998; Welker and Walz 1998; Jack and Thorp 2000; Wilson 2003).

In South America by the early 1990s, the Asiatic mollusc *Limnoperna fortunei* (Dunker) had entered Del Plata Basin through the ballast water discharged from transoceanic vessels (Pastorino et al. 1993). This species has since invaded several water bodies in Argentina, Bolivia, Paraguay, Uruguay, and Brazil (Boltovskoy et al. 2006; Oliveira et al. 2010), reaching maximum densities of 5000–250,000 ind m^2 on rigid substrates (Boltovskoy et al. 2006; Oliveira et al. 2006; Sylvester et al. 2007; Darrigran and Damborenea 2011). It has also proven capable of colonizing less rigid substrates such as macrophytes in lower densities (90–2000 ind m^2, Marçal and Callil 2008; Musín et al. unpublished). Several studies have shown that the abundance and spatial distribution of the bivalve populations change habitat complexity with notable effects on the composition of benthonic fauna (Darrigran et al. 1998; Darrigran 2002; Sardiña et al. 2008; Darrigran and Damborenea 2011; Spaccesi and Rodrígues Capítulo 2012).

Two decades after its introduction, *L. fortunei* is an important component in the complex food web of the Paraná River system, forming part of the diet of native fishes and crustaceans (García and Protogino 2005; Collins et al. 2007; Paolucci et al. 2007; Sylvester et al. 2007). As in the cases of other non-indigenous bivalves (MacIsaac 1996; Karatayev 2007), field studies carried out in reservoirs, rivers and lakes have shown that the filtering activity of *L. fortunei* can modify the characteristics of the water column. Reductions in suspended matter, water transparency and in phytoplankton and zooplankton densities were observed (Rojas Molina and José de Paggi 2008; Boltovskoy et al. 2009; Rojas Molina et al. 2010). Enclosure experiments conducted in reservoirs demonstrate that *L. fortunei* is capable of removing more than 95% of the phytoplankton in just 24 h (Cataldo et al. 2011). Changes in the structure of algal assemblage were also observed favoring the development of the cyanobacteria *Microcystis,* as well as reducing other algal group densities (Cataldo et al. 2012). Thus, higher filtration rates, as calculated by these and other authors, were observed in laboratory experiments (between 130 and 725 mL ind^{-1} h^{-1}) when compared with other invader molluscs (Von Rückert et al. 2004; Sylvester et al. 2005; Pestana et al. 2009). These values were calculated on the basis of communities in modified environments (reservoirs) or by feeding *Limnoperna* with algal monocultures.

The most important freshwater system invaded by *L. fortunei* in South America is the Río de la Plata-Paraná watershed (Darrigran 2002; Boltovskoy et al. 2006). But neither survey carried out has focussed on the potential changes that mollusc filtration activity could generate on the phytoplankton structure in the Paraná water bodies.

The work described here assesses the effect of *L. fortunei* on phytoplankton found in the Paraná River floodplain. The experiment was carried out using mesocosms that simulated environmental conditions found in the lentic water bodies associated with the Paraná River. We did this by examining the effect of different concentrations of the mollusc on algal density and structure, and also estimated the algal filtration rates.

Materials and methods

The experimental system

The experiment was carried out in early spring, using opaque plastic containers with a capacity of about 200 L. Five days prior to initiating the experiment, the mesocosms were filled with water and inoculated with planktonic organisms (collected with 10 μm mesh net), both obtained from a floodplain lake pertaining to the Middle Paraná River.

Organisms

Specimens of *L. fortunei* were manually removed from marker buoys located in the Colastiné River (Santa Fe, Argentina). The experimental mussels used were 16.2 ± 2.7 mm long (maximum length valvar). In preparation for the experiment, individuals were placed on rectangular plastic substrata located at the bottom of the aquaria. This was to ensure their adherence to these substrata through the formation of the byssus. For seven days, molluscs were maintained with constant oxygen and were fed daily (with fish food and *Chlorella vulgaris* algae).

The experiments

One experimental substratum with attached mussels was hung vertically in the center of each container to permit the molluscs to filter the column of water, thus simulating the usual position of these organisms when they attach themselves to the roots of floating vegetation. Three treatments were developed in this way: one without mussels (Control), another with 128 mussels per mesocosm (C1) and the last with 256 bivalve individuals per mesocosm (C2). The number of individuals employed in each treatment was adjusted for the effects recorded in preliminary experiments and corresponding to density levels for molluscs attached to floating vegetation in the waters of the Middle Paraná between 90 and 400 bivalves per m^2 of vegetation cover (Musín et al. unpublished). All treatments were replicated thrice (Figure 1). For further details on the mesocosm design, see Rojas Molina et al. (2012).

Samples were collected from each mesocosm at 9 a.m., before mussels were added to them, and again 3, 6, 12, 24, 48, and 72 hours later the mussels were added. HANNA portable meters were used to measure temperature, pH, and dissolved oxygen, each time and turbidity was spectrophotometrically determined at 450 nm absorbency. Nutrient concentrations were measured following APHA (1995) indications. Nitrate ($N–NO_3^-$) levels were analyzed applying the cadmium–copper reduction method, and phosphate (PO_4^{3-}) levels were taken using the ascorbic acid–molibdate method (both using HACH Company reagent kits). Ammonium (NH_4^+) levels were analyzed using the indophenol-blue method, and employing kits from the Wienner Company.

Phytoplankton samples were taken with a 100 mL bottle and were fixed with 1% acidified lugol solution. Sample counts were taken in accordance with the Utermöhl method (1958) and densities were expressed as ind mL^{-1}. Phytoplankton organisms were grouped into four categories according to morphological and taxonomic characteristics: single cells, flagellates, diatoms, and colonies.

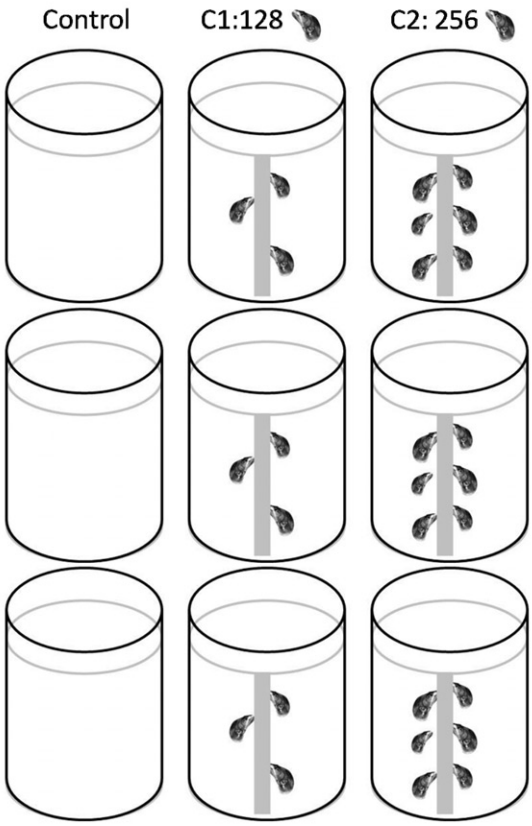

Figure 1. Experimental design used in the experiment. Control: without *L. fortunei*, C1 and C2: low and high concentration of mussels, respectively.

The mollusc filtration rate was estimated for time lapses of 0–3, 24–48, and 48–72 h from the beginning of the experiment, in accordance with the equation proposed by Jørgensen (1990):

$$F = V \cdot \left[\frac{\ln(C_i/C_f) - \ln(C'_i/C'_f)}{NT} \right]$$

where F is the filtration rate (mL ind^{-1} h^{-1}), V is the volume of water in the experimental mesocosm (mL), N is the number of mussels per mesocosm, T is the total filtration time (hours), C_i and C_f are plankton concentrations in the mesocosm with molluscs at the beginning and end of the time lapse and C'_i and C'_f are the plankton concentrations in the control mesocosm for the beginning and final time lapse.

Statistical analysis

Differences in phytoplankton concentrations from one treatment to another were tested with a two-way ANOVA analysis with repeated measurements for one factor.

Table 1. Mean and standard deviation of physical and chemical parameters recorded in the treatments (control, C1, and C2) over the 72 h that the experiment lasted.

	Control	C1	C2
pH	8.59 ± 0.10	8.51 ± 0.12	8.51 ± 0.19
Dissolved oxygen (mg L^{-1})	7.75 ± 0.51	7.80 ± 0.37	7.54 ± 0.29
Turbidity (FTU)	78.14 ± 6.69	73.29 ± 7.76	73 ± 9.13
Temperature (°C)	26.15 ± 3.34	25.71 ± 3.10	26.14 ± 3.29
Nitrates (mg L^{-1})	0.82 ± 0.12	0.7 ± 0.23	0.78 ± 0.24
Orthophosphates (mg L^{-1})	0.34 ± 0.21	0.25 ± 0.07	0.29 ± 0.10
Ammonium (mg L^{-1})	0.37 ± 0.11	0.53 ± 0.46	0.69 ± 0.59

Notes: These values represent the mean for replicate treatments. Control without *L. fortunei*, C1 and C2: low and high concentration of mussels, respectively.

In this analysis it is possible to test the effect of each factor in separate form, mollusc concentration (Control, C1, C2), and time (hours), and their interaction (mollusc concentration*time). The concentration of molluscs was considered as a simple factor (between-subjects factor) and the time as a factor for repeated measurements (within-subjects factor). Data were $\log_{10} x + 1$ transformed and normal distribution (Kolmogorov–Smirnov test), homoscedasticity (Levene test), and sphericity (Mauchly test) were verified. The analysis was applied to the total phytoplankton density and abundances of each algal group. When ANOVA results were significant, Tukey's test was performed to analyze the effect of the between-subjects factor and a multiple comparison test was carried out to analyze the effect of the within-subjects factor. For each treatment, Student's *t*-test was used to compare the relative density of each algal group at the beginning and at the end of the experiment.

Results

All treatments registered similar environmental conditions during the experiment. The mean temperature was 26 ± 3.34°C. Dissolved oxygen and pH ranged between 6.63–8.40 mg L^{-1} and 8.23–8.64, respectively. Turbidity showed the highest variation. It was lower in the treatments with molluscs (73.3 ± 8.5 FTU in C1 and 72.9 ± 9.1 FTU in C2) than in the control treatment (78.5 ± 6.1 FTU). Nitrate and orthophosphate concentrations were slightly higher in the control mesocosm. By contrast, ammonium levels were highest in the treatments with molluscs (Table 1).

Phytoplankton

A list of 29 taxa was recorded, dominated by single cells (11 spp.) and Flagellated algae (8 spp.). The most frequent were individuals belonging to the *Monoraphidium, Nitszchia*, *Chlamydomonas, Cryptomonas* and *Goniochloris* genera. The most abundant algae were those of the single cell group.

The mean phytoplankton density was 7272 ind mL^{-1} at the beginning of the experiment and there were no statistically significant differences among treatments (Table 2). Phytoplankton density decreased after 3 h in all treatments and tended to

Table 2. Multiple comparison results for effects of treatments (control, C1, and C2) on phytoplankton densities at different sampling times (0, 3, 6, 12, 24, 48, and 72 h).

Time (h)	Treatment (a)	Treatment (b)	Mean differences (a–b)	Signification
0	Control	C1	0.34	0.130
		C2	0.10	0.620
3	Control	C1	0.03	0.800
		C2	0.01	0.910
6	Control	C1	0.14	0.040
		C2	0.18	0.010
12	Control	C1	0.40	0.020
		C2	0.55	0.006
24	Control	C1	0.28	0.150
		C2	0.48	0.032
48	Control	C1	0.65	0.026
		C2	0.50	0.065
72	Control	C1	0.38	0.045
		C2	0.66	0.005

Note: Control without *L. fortunei*, C1 and C2: low and high concentration of mussels, respectively.

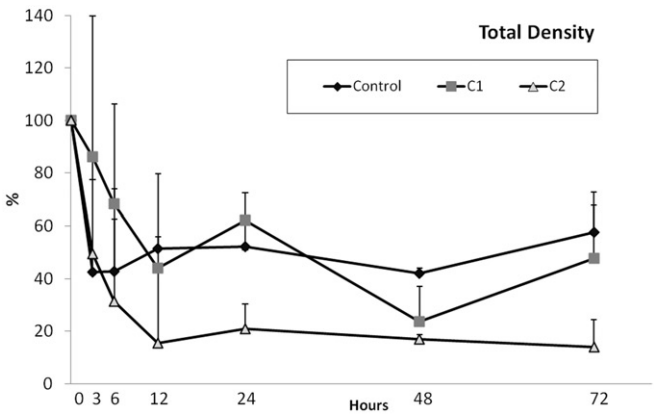

Figure 2. Variations in the percentage of initial phytoplankton density in experimental mesocosms (Control, C1 and C2) over the 72 h time lapse of the experiment (treatment means + standard deviation). Control: without *L. fortunei*, C1 and C2: low and high concentration of mussels, respectively.

stabilize in the control treatment at densities between 60% and 40% of initial values (Figure 2).

The ANOVA repeated measurements showed significant differences related to time effect ($\rho < 0.01$), mollusc presence effect ($\rho = 0.03$) and to the interaction of these two factors ($\rho = 0.008$). The Tukey post test demonstrated differences between control and C1 ($\rho = 0.001$) and between control and C2 ($\rho < 0.01$) from 6 h until the end of the experiment (Table 2). At 72 h the mean densities were 2006 ind mL^{-1} in C1 and 1159 ind mL^{-1} in C2 (a reduction of 52% and 86% of the initial density, respectively), while in the control mesocosm the density was 5385 ind mL^{-1}.

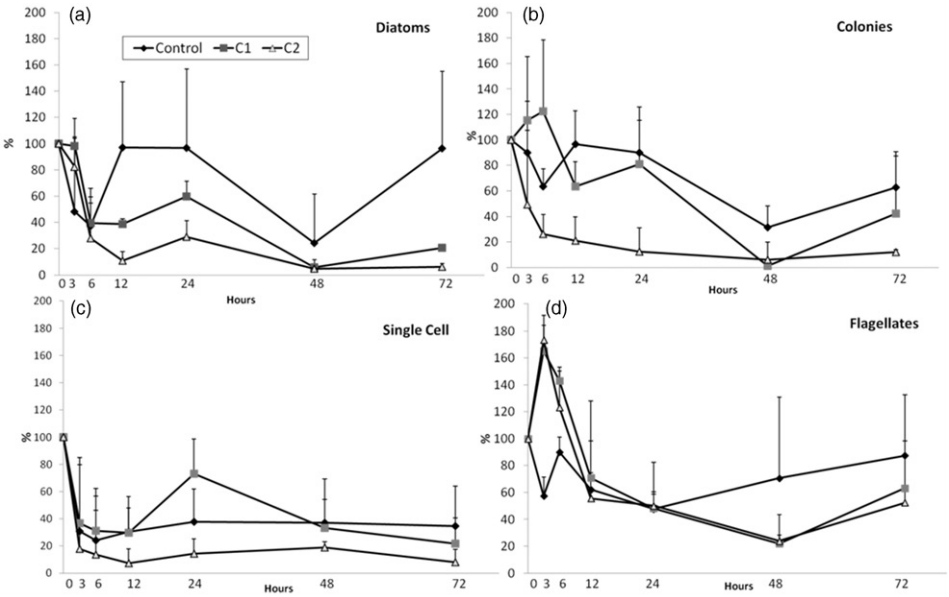

Figure 3. Variations in the percentage of each algal groups density (diatoms, colonies, single cells, and flagellates) in the different treatments (control, C1, and C2) over the 72 h of the experiment (means of treatment + standard deviation). Control: without *L. fortunei*, C1 and C2: low and high concentration of mussels, respectively.

The abundance of the different phytoplankton groups changed over time, demonstrating greater abundance at the beginning of the experiment (diatoms: $\rho = 0.003$ and $\rho < 0.01$ for colonies, single cells, and flagellated algae). In the treatments with molluscs the densities of these groups were lower than for the control (Tukey's test, diatoms: $\rho = 0.038$, colonial algae: $\rho = 0.015$, single cells: $\rho = 0.038$, flagellated algae: $\rho = 0.026$). Multiple comparisons testing for control *versus* C1 and C2 showed that, at least for the 72 h time lapse, this density difference was significant.

In the control mesocosm, the abundance of diatoms at the beginning and at the end of the experiment was similar, despite variations in between. In the mollusc treatments, on the other hand, density decreased significantly towards the end of the experiment (72 h) to less than 21% from the initial density level (Figure 3a). These differences between the other two treatments and the control mesocosm were statistically significant (Tukey's test, control *vs.* C1: $\rho = 0.046$; control *vs.* C2: $\rho = 0.002$), mainly at 72 h (control *vs.* C1: $\rho = 0.032$ and control *vs.* C2: $\rho = 0.007$).

The group of colonial algae varied in control and C1 throughout the experiment (between 115% and 1% of the initial density), while in C2 the decrease in abundance was continuous throughout the time lapse for the entire experiment (Figure 3b). Tukey's test showed differences between control and C1 ($\rho = 0.02$) and control and C2 ($\rho = 0.017$). The differences were observed at 12 h between control and C1 ($\rho = 0.019$) and control and C2 ($\rho = 0.015$); at 48 h between control and C1 ($\rho = 0.016$); and at 72 h between control and C2 ($\rho = 0.019$).

Single cells demonstrated a clear tendency toward decreasing density in all treatments. This trend was more significant in the mollusc treatment. The greatest

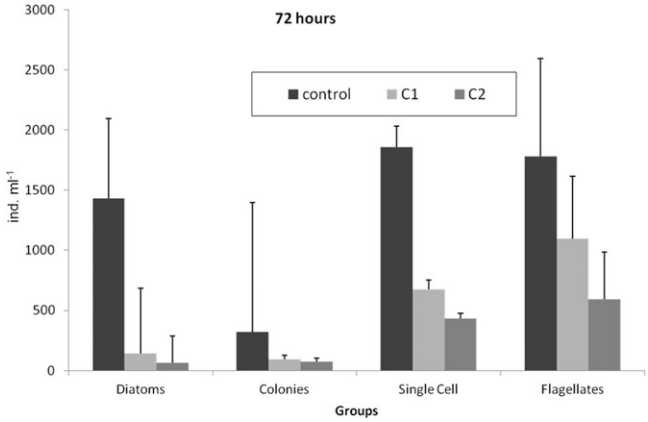

Figure 4. Density (means + standard deviation) of each algal group (diatoms, colonies, single cells, and flagellates) in the treatments (control, C1, and C2) at the end of the experiment (72 h). Control: without *L. fortunei*, C1 and C2: low and high concentration of mussels, respectively.

declines occurred in the mesocosms with the highest concentration of bivalves, whose final density was less than 20% of the initial value (Tukey's test: control *vs.* C1, $\rho = 0.01$ and control *vs.* C2, $\rho = 0.03$) (Figure 3c). These differences were recorded principally at the end of the experiment (72 h), control vs. C1 ($\rho = 0.034$) and control vs. C2 ($\rho = 0.008$).

The abundance of flagellates declined from 12 h until the end of the experiment (Figure 3d). This decreasing trend was more significant in C2 compared to the control (Tukey's test, $\rho = 0.005$), mainly at 72 h ($\rho = 0.024$).

With the exception of the flagellate algae in C1, by the end of the experiment, in mollusc treatments compared to control, all algae groups showed substantial decrease in their densities (>60%). These declines were always higher in C2 (Figure 4).

At the end of the experiment, the structure of algae assemblages in mollusc treatments changed due to the increase in the relative abundance of the flagellated group (*t*-test, $\rho = 0.042$), while no significant changes were observed in the control treatment. Meanwhile, the proportion of diatoms decreased significantly in the presence of molluscs (*t*-test, $\rho = 0.002$). No statistical differences were recorded between 0 and 72 h for the other considered groups (Figure 5).

Filtration rate

The highest filtration rate was for the C1 treatment (357 mL ind^{-1} h^{-1}) was recorded during the first time period (0–3 h). In both mollusc treatments, the filtration rate decreased over time (Figure 6).

Discussion

The feeding behavior of invasive bivalves can cause several changes in both phytoplankton and water transparency (MacIsaac et al. 1992; Leach 1993; Strayer 2010).

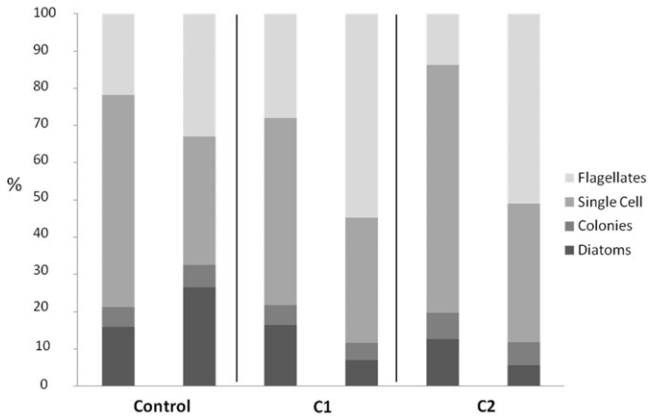

Figure 5. Relative density (%) of each algal group (diatoms, colonies, single cells, and flagellates) in the different treatments (control, C1, and C2) at the beginning and end of the experiment. Control: without *L. fortunei*, C1 and C2: low and high concentration of mussels, respectively.

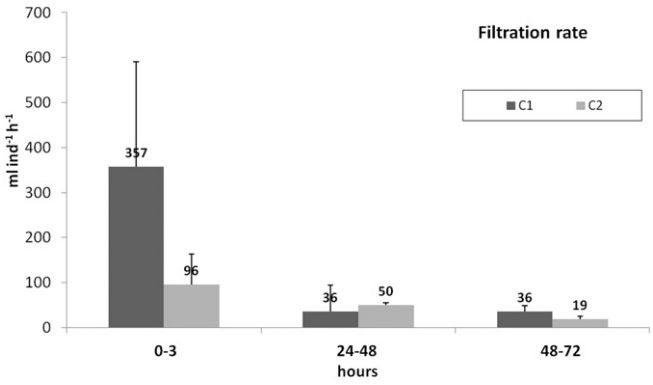

Figure 6. Mean filtration rate of *L. fortunei* in the treatments (C1 and C2) at different time lapses (0–3, 24–48, and 48–72 h). C1 and C2: low and high concentration of mussels, respectively.

Our results showed that *L. fortunei* is capable of exerting strong pressure on phytoplankton density and structure, which is in agreement with the previous finding. In addition, suspended organic and inorganic material in the mesocosms was reduced over time in the presence of bivalves, a phenomenon witnessed by a corresponding reduction in turbidity. Part of this material is probably ingested, yet another part is rejected as pseudofeces (Sprung and Rose 1988; Jørgensen 1996). In the Río Tercero Reservoir (Argentina), where *L. fortunei* has been present since 1998, the capacity of bivalves to remove suspended particles, combined with its high population densities, has caused increases in water clarity and significant decrease in suspended matter, chlorophyll-a, and primary production (Boltovskoy et al. 2009).

Ammonium concentration was higher in bivalve treatments, a phenomenon to be expected, as a result of feces production following digestive activity. This phenomenon had already been observed in other experiments involving *L. fortunei* (Cataldo et al. 2011) and other bivalves, such as *D. polymorpha* (Wilson 2003).

Changes in turbidity and ammonium concentration, and in the density and structure of phytoplankton were more evident in the treatment with high mollusc concentrations, which is consistent with results obtained by other authors (Prins et al. 1995; Cataldo et al. 2012). In a similar mesocosm experiment carried out at the Río Tercero Reservoir, Cataldo et al. (2011) found that 4 mollusc L^{-1} (of between 14–35 mm in length) can reduce the phytoplankton density by 99% in 24 h. In our experiment, a single mollusc L^{-1} (of 16 mm in length) reduced the phytoplankton density by 80% in the same time period.

Bastviken et al. (1998) determined that bivalves can affect the phytoplankton composition directly, by means of selective ingestion or through differential digestion, as well as through indirect effects that generate changes in light penetration and nutrient concentration. Studies carried out with *D. polymorpha* have shown that this bivalve can discriminate between food items or even display selective feeding behavior, in accordance with seasonal phytoplankton changes or available food sources (Wearly 2004; Nadaffi et al. 2007). In our study, all the observed phytoplankton groups showed significant statistical reductions within the time of the observations. The flagellate group (dominated by *Chlamydomonas* and *Chriptomonas* genera) was, however, the least affected (Figure 4) despite its palatability (Gladyshev et al. 1999) and the preferences demonstrated by other bivalves (Ten Winkel and Davids 1982; Naddafi et al. 2007). The relative density of this group was higher in comparison with the other groups, a phenomenon which could be attributed to its high reproductive rate (Reynolds 2006) and availability of nutrients re-mineralized by the molluscs that could favor its reproduction (Cataldo et al. 2012). The diatom group, on the other hand, was the most affected (Figure 4), growing in the control mesocosm but reducing its density in treatments with molluscs. These changes could be attributed to the palatability of the frustule organic layer, which could stimulate positive selection, as was found in the cases of other bivalves (Beninger and Decottignies 2005). It has been shown, furthermore, that diatoms may also be expelled in large quantities as pseudofeces without being ingested after filtration by the golden mussel (Gazulha et al. 2012b). The colonies, mainly represented by *Aphanocapsa delicatissima* ($>80\%$ density in all treatments), formed another group that was severely affected during the experiment. This principal algae is found in smaller colonies than *Microcystis* cyanobacteria, which had already been reported as a food item for the mollusc (Gazulha et al. 2012a, 2012b).

Zooplankton density was also affected during experimentation (Rojas Molina et al. 2012). Results showed a reduction in the abundance of zooplankton in treatments C1 and C2, a tendency that proved very similar to the trend for phytoplankton. Mesocosm experiments and field studies involving *D. polymorpha* and *Corbicula leana* have documented severe reductions in density through the effects of filtration by these bivalves; e.g. Jack and Thorp (2000), Wilson (2003) and Hwang et al. (2004, 2011) have documented a reduction in the abundance of zooplankton through the effects of these two invasive bivalves. Zooplankton reduction in the presence of *L. fortunei* has also been observed by Rojas Molina and

José de Paggi (2008) and by Rojas Molina et al. (2011) in the field and in laboratory experiments, respectively.

We are dealing with mussels feeding on a complex community of planktonic organisms. *Limnoperna fortunei* is able to ingest large organisms such as copepodites, nematodes, and ostracods (Rojas Molina et al. 2010, 2011), however several authors indicate that the golden mussel has a preference for smaller organisms (Pestana et al. 2009; Gazulha et al. 2012a, 2012b). In this study, the presence of the molluscs resulted in observed changes in the structure of the phytoplankton assemblage. In a natural environment there could be additional factors such as interactions with other trophic levels (e.g. omnivorous fishes, macrocrustaceans, and zooplankton) as well as changes in nutrient availability and concentration. These could result in changes to the phytoplankton assemblage upon which the molluscs are feeding consequently changing the dynamics within this community.

The mollusc filtration activity was high at the beginning of the experiment (0–3 h), but a decreasing trend was observed thereafter and up to the end of the experiment, a factor probably related to a reduction in food concentration levels. The maximum filtration rate obtained during the experiment was 357 mL ind^{-1} h^{-1} at 28°C. This rate was consistent with feeding rates estimated in other reports (133.75 and 725 mL ind^{-1} h^{-1}, Von Rückert et al. 2004; Sylvester et al. 2005; Pestana et al. 2009). Many factors such as food concentration and quality (monospecific cultures or wild plankton), algae size, and several environmental factors like temperature and pH can affect the filtration rate (Sprung and Rose 1988; Widdows 2001).

Laboratory experiments carried out with monospecific cultures or in small receptacles with only one organism (e.g. Sylvester et al. 2005; Pestana et al. 2009) provided information regarding the maximum filtration capacity of *L. fortunei*. This article provides information as to a filtration rate representative of a natural environment, considering that food items and mollusc concentration are representative of those found in the Paraná River floodplain. Reduction levels after 48 h for all algae groups considered in this experiment indicate that the mollusc does not discriminate among groups, but is able to generate changes in algal assemblage.

Conclusions

The results obtained in our experiment indicate that densities of 256 individuals of *L. fortunei* are capable of producing a major effect on water quality, in terms of modification of turbidity, ammonium concentration, and phytoplankton density and structure. Considering that densities registered in alluvial water systems of the Paraná River are of between 90 and 400 ind m^{-2} and that the molluscs are capable of a high filtration rate, we can predict a strong potential for predation in natural systems within short periods of time.

Limnoperna fortunei has been established as a key element in modifying matter and energy fluxes at an ecosystemic level. Its presence could have consequences on the productivity and diversity of the water systems invaded. For this reason, studies that further evaluate the intensity of these changes are required for developing suitable management strategies.

Acknowledgments

Our special thanks to Juan César Paggi for his cooperation in the planning stage of the experiment, to Cristian De Bonis for his help in the assembly of the mesocosms, and to the Municipality of Santo Tomé (Santa Fe, Argentina) for the assistance it provided during our fieldwork. This study was funded by the *Universidad Nacional del Litoral* (Projects CAI+D PI6-44, I+D PJ14082 and CAI+D 14-78).

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