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Research Article

Impact of the invasive golden mussel (*Limnoperna fortunei*) on phytoplankton and nutrient cycling

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Abstract

In order to evaluate the effects of the golden mussel *Limnoperna fortunei* on phytoplankton density and composition and nutrient recycling we conducted a 24 h filtration experiment in Río Tercero Reservoir (Argentina) using four 400 L mesocosms, two of them stocked with 1700-1800 adult mussels each, and two controls (without mussels). Nutrient concentrations and phytoplankton composition and density were evaluated at 0, 3, 6, 12, and 24 h. Estimated filtration rates were 1.48-3.14 mL mg DW^{-1} h^{-1}. Grazing pressure by the mussel was not associated with algal taxonomy or cell size. After 24 h, *L. fortunei* removed 84% of the particulate nitrogen, and 49% of the particulate phosphorus. Nutrient regeneration was very significant as well: ammonium was produced at a rate of 3 µM NH_3g DW^{-1} h^{-1}, whereas production of phosphates was 0.42 µM PO_4g DW^{-1} h^{-1}. It is concluded that the impact of *L. fortunei* on phytoplankton and nutrient cycling can be as significant as that reported for another invasive bivalve - the zebra mussel *Dreissena polymorpha* in Europe and North America, but the overall effect of this impact on the biota may differ strongly under different environmental settings.

Key words: Barrow, Nore, alien, non-native, introductions, Scuba diving

Introduction

Between 1965 and 1990, the invasive bivalve *Limnoperna fortunei* (Dunker, 1857), the golden mussel, native to mainland China, was unintentionally introduced in Hong Kong, Taiwan, Japan, and Argentina (Pastorino et al. 1993; Ricciardi 1998). In South America, ca. 15 years after entry, *L. fortunei* had colonized practically all the Río de la Plata basin extending as far north as the Pantanal and the States of Paraná, São Paulo, and Minas Gerais (Brazil). At present, beds of *L. fortunei* are widespread on hard substrates throughout the entire Río de la Plata watershed (Boltovskoy et al. 2006).

In many biological and ecological aspects *L. fortunei* resembles the European and North American invasive pest mussel *Dreissena polymorpha* (Pallas, 1771). Both are dioecious and have similar sizes, grow rapidly, attach to hard substrata by means of a strong byssus, and are rapidly dispersed by their planktonic larvae (Karatayev et al. 2007). These similarities suggest that some of their impacts may be comparable as well. Extensive research has demonstrated that zebra mussels change existing habitat and provide new habitat for other organisms; they affect trophic interactions and the availability of food for both pelagic and benthic species, and they influence the rates of other processes including mineralization of nutrients, oxygen availability, sedimentation rates, and dynamics of pollutants (Karatayev et al. 1997). Of particular importance are the very high grazing rates of these bivalves (Berg et al. 1996; Sylvester et al. 2005), responsible for a significant impact on phytoplankton abundance and composition and nutrient turnover (Karatayev et al. 1997; Boltovskoy et al. 2009). It is therefore highly probable that ecological

shifts as important as those that took place in the European and North American areas colonized by the zebra mussel are underway in Río de la Plata basin rivers, lakes and reservoirs.

In this survey we addressed the question whether *L. fortunei´s* grazing affects phytoplankton composition and density and nutrient concentrations. Our results provide information for forecasting the effects of this invasive mussel on other freshwater bodies, thus aiding to the decision-making processes involved in the allocation of research and management funds associated with the control of this freshwater invasive species.

Methods

Filtration experiments were carried out on 16-17 March 2005 in a shallow (bottom depth ca. 0.9 m) coastal area of Río Tercero Reservoir (see below). We used four PET (polyethylene terephthalate) cylindrical 400 L mesocosms 75 cm in diameter and 105 cm high, with their bottoms sealed off with a polyethylene liner, filled with reservoir water to about 15 cm from the rim. On the bottom of each of two of the mesocosms several clusters totaling 1688 and 1741 mussels 14-35 mm in length, collected nearby, were placed before starting the experiment. The other two were used as controls. Experimental data reported in this work are averages between these two pairs of replicates. During the experiment, water in the mesocosms was permanently gently stirred by the movement of the flexible walls of the enclosures induced by the natural water motion outside of the mesocosms.

Samples from the experimental and control units were retrieved from mid-depth at 0, 3, 6, 12, and 24 h in order to analyze nutrient concentrations and phytoplankton density and composition.

The dissolved fraction was analyzed after sample filtration through fiberglass filters (Whatman GF/F) (APHA 1992). Reactive phosphorus was assessed according to the stannous chloride method. Nitrates using cadmium reduction with Hach reactives. Ammonia: phenate (APHA 1992). Total phosphorus and nitrogen using simultaneous oxidation of nitrogen and phosphorus compounds by persulfate (Koroleff 1983). Excretion rates of ammonia and soluble reactive phosphorus are expressed as µM excreted per gram dry weight of soft tissue per hour.

Phytoplankton counts and identifications were carried out on unfiltered, Lugol-preserved samples under an inverted microscope in 5, 10, 25 or 100 mL settling chambers (depending on phytoplankton concentrations; Utermöhl 1958). Samples were left to settle for 24-48 h, depending on chamber volume. Counting error was estimated at ±20% for the most abundant species (Venrick 1978). Algal concentrations refer to individuals, where multi-celled colonies were counted as one individual (the term “cells” in subsequent references to phytoplankton densities designates isolated cells and multi-celled colonies). Phytoplankton biomass values were estimated calculating species biovolumes following the criteria and formulae of Hillebrand et al. (1999).

After the experiments mussels were recovered and randomly selected samples with 400 specimens were isolated, the individuals were measured to the nearest 0.01 mm with a digital caliper, and their soft tissue extracted and dried at 60°C to constant weight.

Filtration (F) and Grazing (G) rates were estimated following the expressions (Quayle 1948):

$$k = \left[\ln(C'_f/C'_i)\right] / T$$

$$r = (F \bullet N)/V$$

$$F = \frac{V.\left[\ln(C_i/C_f) - \ln(C'_i/C'_f)\right]}{N.T}$$

$$G = (V \bullet r/N) \bullet \left\{(C_f - C_i)/\left[(k - r) \bullet T\right]\right\}$$

Where F is the filtration rate (mL ind^{-1} h^{-1}), V is the volume of the experimental enclosure (in mL), C_i, C_f and C'_i, C'_f are the algal concentrations (in cells mL^{-1}) before and after filtration for each time offset in the enclosures with mussels, and in the controls, respectively, N is the number of experimental mussels used, T is the filtration time (in hours), G is the grazing rate (cells ind^{-1} h^{-1}), r is the feeding coefficient, and k is the algal growth rate. The results of experimental vs. control treatments were compared with a repeated-measures ANOVA on logarithmically transformed (algal concentrations, nitrates and ammonia) or raw data (total and particulate N and P) using the software package Statistica (Statsoft, Inc., Tulsa).

Río Tercero Reservoir is located in central Argentina (32ºS; 64ºW). It was originally dammed in 1936, chiefly for energy production, and since 1983 its main purpose is furnishing cooling water for a nuclear power plant. This medium-sized (47 km^2) meso- to eutrophic water body (mean yearly chlorophyll a concentrations around 17 µg L^{-1}; Mariazzi et al. 1992) has relatively clear water (Secchi disk depths up to 6-8 m), and moderate nutrient levels (NO_3: 0-30 µg L^{-1}; PO_4: 0-10 µg L^{-1}; inorganic N: 80 µg L^{-1}; Mariazzi et al. 1988, 1992; Boltovskoy et al. 2009).

Results

Initial concentrations of total N (mostly in particulate form, 96%) were around 290±16 µg L^{-1}. Total N remained stable in both experimental and control mesocosms until the end of the experiment (around 302±22 and 294±27 µg L^{-1}, respectively, at 24 h; p=0.698, repeated measures ANOVA; Figure 1). In contrast, particulate N remained stable in the control but dropped almost 8-fold after 24 h in the mesocosms with mussels (p=0.011, repeated measures ANOVA, Figure 1). Nitrates and ammonia also differed significantly in experimental and control units (p=0.004 and 0.033, respectively, repeated measures ANOVA). In the control their levels remained stable, whereas in the experimental unit they increased from 10±0 to 40±0 µg L^{-1} (nitrates), and from 0 to 220±14 µg L^{-1} (ammonium) (Figure 1).

No changes in total P were recorded in either treatment throughout the experiment (p=0.069, repeated measures ANOVA), but particulate P dropped noticeably in the mesocosms with *Limnoperna* (from 27.7±5 to 12.6±3 µg L^{-1}; p=0.009, repeated measures ANOVA), while phosphates increased (from 0.9±0.1 to 13.1±1.4 µg L^{-1}; p=0.001, repeated measures ANOVA; Figure 2).

Ammonium excretion rates, calculated on the basis of variations in their concentration in the experimental chambers, were 3 µM g DW^{-1} h^{-1}; whereas for phosphates they were 0.42 µM g DW^{-1} h^{-1}.

In total, 67 phytoplanktonic taxa were identified (see Appendix), yet over 90% of the individuals were represented by only ten species, both in terms of numbers and of biovolume. In total, 15 species ranked among the first 10 in terms of abundance and/or summed biovolume

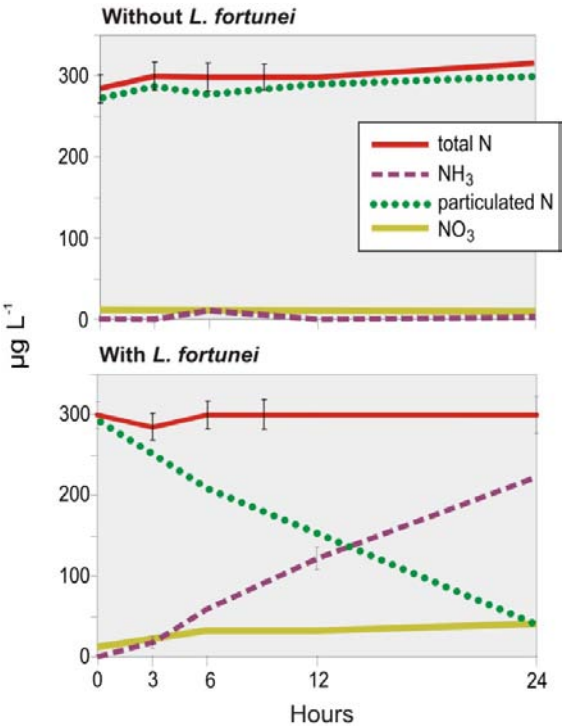

Figure 1. Changes in the concentrations of nitrogen with and without *Limnoperna fortunei* throughout the experimental period (bars denote SE).

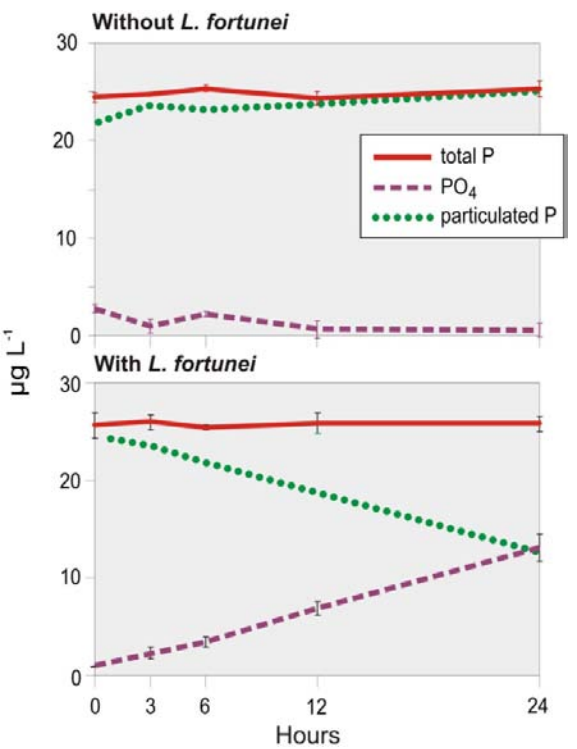

Figure 2. Changes in the concentrations of phosphorus with and without *Limnoperna fortunei* throughout the experimental period (bars denote SE).

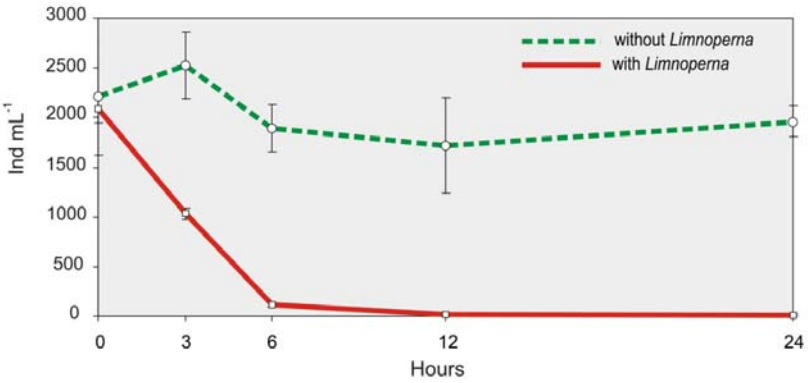

Figure 3. Changes in algal densities throughout the experimental period (bars denote SE).

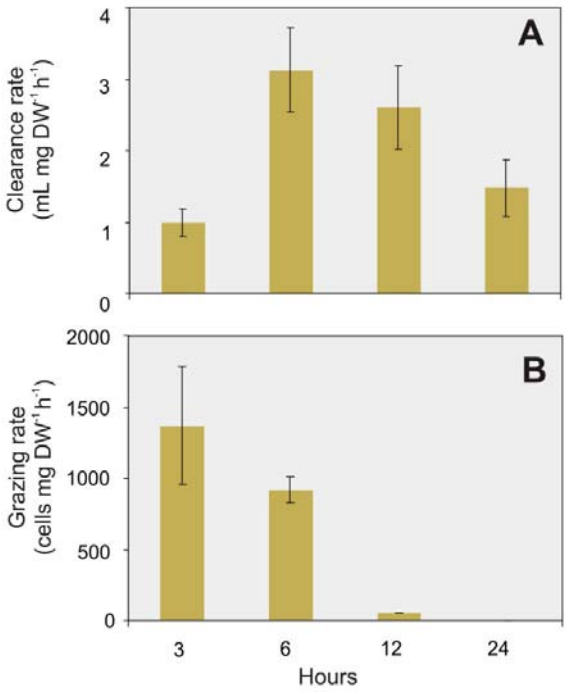

Figure 4. Clearance (A) and grazing rates (B) of *Limnoperna fortunei* (bars denote SE).

(as indicated by averaged values across all samples counted) (Table 1).

Changes in algal concentrations throughout the experiment differed strongly between the control and the experimental chambers ($p = 0.0045$, repeated measures ANOVA). During the 24 h grazing experiment mean (±SE) algal densities decreased slightly (and non-significantly) in the control (from 2215±420 to 1959±110 cells mL^{-1}), whereas in the experimental mesocosms (with *Limnoperna*) after 24 h their densities dropped to 1% of initial values (Figure 3). Clearance rates were moderate at the start, peaking at 6 h (3.14±0.59 mL mg DW^{-1} h^{-1}), and decreasing thereafter to 1.48±0.40 mL mg DW^{-1} h^{-1} at 24 h (Figure 4A). Grazing rates were highest at 3 h (1370±415 cells mg DW^{-1} h^{-1}), decreasing thereafter to only 2±0.36 cellsmg DW^{-1} h^{-1} at 24 h (Figure 4B).

The relationship between the volumes of the algal cells fed to *Limnoperna* (range: 8 to 280,596 μm^3; see Appendix) and their corresponding drops in relative abundance after 24 h, suggests that grazing impact was not associated with cell size ($r = -0.014$; Figure 5).

Discussion

After 24 h, *Limnoperna* removed 89% of the particulate N and 49% of the particulate P from the water column. Drops in these particulates were accompanied by strong increases in phosphates and NH_3, as a result of the metabolism of the mussels. Comparison of the mineralization rates measured in this work with those reported for several marine and freshwater bivalves shows ample variations, which to a great extent are due to dissimilar experimental and environmental settings (Table 2). Indeed, water temperature, food availability, mollusc age, size and physiological state have been shown to affect these measurements significantly (Aldridge et al. 1995; James et al. 1997; Kuenzler 1961; Mellina et al. 1995). Nevertheless, for both nutrients the rates measured are among the highest reported (Table 2).

Filtration activity was uneven throughout the 24 h experimental period: rates were low at the beginning (0-3 h), peaking at 3-6 h, and dropping steadily thereafter (Figure 4). Low rates at the

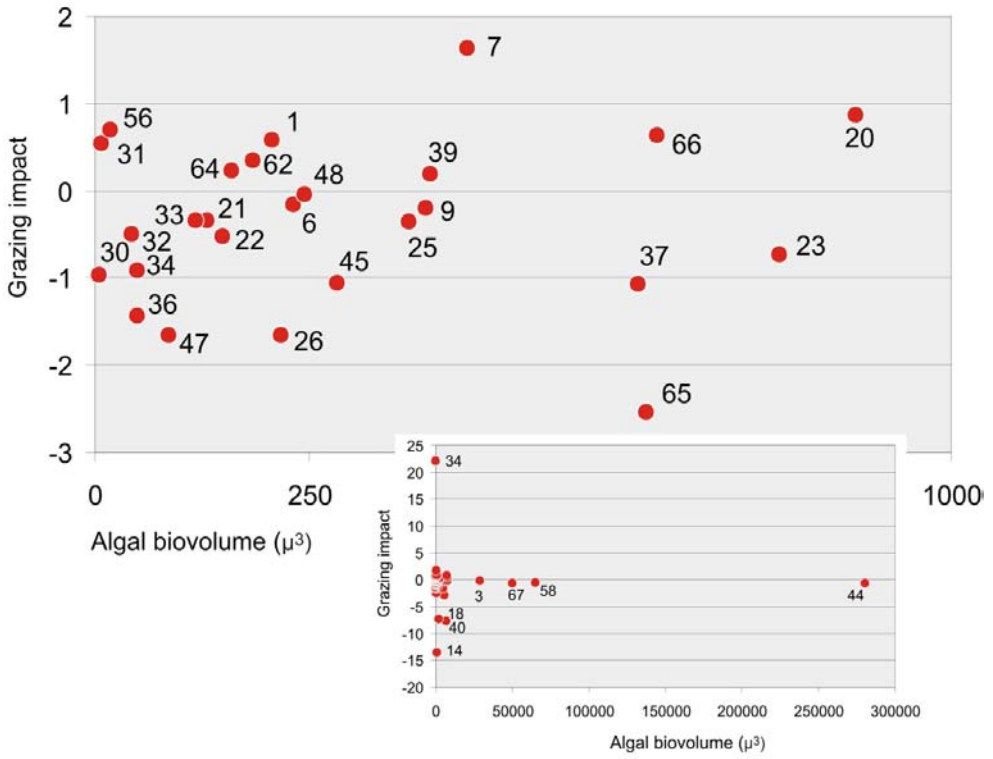

Figure 5. Relationship between algal biovolume and grazing impact by *Limnoperna fortunei*. Grazing impact for each algal taxon is defined as initial % of the species (with respect to all algae) minus % of the same species in the latest subsequent sample where the species was still present (i.e., at 3, 6, 12 or 24 h), or minus zero (if the species disappeared from the mesocosms altogether after 3 h). Positive values along the Y-axis indicate positive selection by the mussel. Main graph encompasses the ranges for the majority of the species recorded (grazing impacts between -3 and 2, biovolumes of up to 1000 μ^3). Inset (smaller) graph depicts all the datapoints included in the analysis (28 species; the remaining 39 algae were absent in both experimental mesocosms at time 0). Numbers next to each datapoint identify the algal species as listed in the Appendix. All data are based on averages for the two experimental mesocosms.

start may be attributed to the stress induced by initial manipulation, while declining trends toward the end of the experiment are probably the result of satiety, and/or of declining food concentration (as shown for other bivalves, like *Dreissena polymorpha*: Horgan and Mills 1997). Mean clearance rates throughout the 24 h experimental period (1.6 mL mg DW^{-1} h^{-1}) are lower than the ones reported for *Limnoperna* by Rückert et al. (2004) (17-25 mL mg $DW^{-1} \cdot h^{-1}$), and by Sylvester et al. (2005) (10 to 30 mL mg DW^{-1} h^{-1}). While filtration activity may be affected by a wide variety of physiological and environmental factors (Morton 1971; Sprung 1995; Berg et al. 1996; Diggins 2001), differences between our results and those reported earlier are most probably due to (1) the fact that previous studies used monospecific cultures in their experiments (*Chlorella* sp., *Selenastrum capricornutum*, *Microcystis viridis*, *Pseudoanabaena sp.*), rather than natural plankton, and especially (2) the fact that experimental periods used by other authors were restricted to 30-60 min and the animals were visually monitored subtracting from total times the intervals when no filtering activity was observed (Sylvester et al. 2005). Our own (unpublished) observations indicate that *Limnoperna* spends ca. 51% (range: 35-64%) of the time actively filtering, while during the other half it keeps its valves closed (these values are generally similar to those reported for other freshwater, byssate mussels: Morton 1979; Horgan and Mills 1997). However, even doubling the clearance rates found in our experiments (in order to account for the mussel's inactivity), the resulting values are still lower than those reported by Rückert et al. (2004) and

Table 1. Comparison of the feeding and excretion rates found in this work for *Limnoperna fortunei* with those reported in the literature for several freshwater and marine bivalves.

Species	Filtration rate (mL ind^{-1} h^{-1})	Filtration rate (mL mg DW^{-1} h^{-1})	N excr. rate (µmol g DW^{-1} h^{-1})	P excr. rate (µmol g DW^{-1} h^{-1})	Dry weight (mg) [Size (mm)]	Temp. (°C)	Source
Limnoperna fortunei	100-214	1.50-3.10	3	0,42	75 [28.03]	24-25	This work
	125-350	9.90-29.50	-	-	8.1-22.2 [15-23]	15-25	Sylvester et al. (2005)
	92,45	17,2	-	-	5.4 [18.97]	22-24	Rückert et al. (2004)
	133,75	24,52	-	-	5.5 [18.57]	22-24	Rückert et al. (2004)
	89,19	11,91	-	-	7.79 [18.64]	22-24	Rückert et al. (2004)
Dreissena polymorpha	-	-	5,26	1,02	40-100	18-25	Arnott and Vanni (1996)
	-	-	3,18	-	40-100	6-21	Quigley et al. (1993)
	40	4,12	-	-	4.9-17.1 [10-15]	22	Berg et al. (1996)
	125	2,1	-	-	41.4-82.3 [20-25]	22	Berg et al. (1996)
	110-225	3.08-6.94	-	-	32.4 [20]	-	Diggins (2001)
	60-170	3.77-10.69	-	-	15.9 [15]	8-22	Diggins (2001)
	78-170	1.62-3.53	-	-	41.4-55.5 [20-22]	13-17	Reeders et al. (1989)
	125-223	4.64-9.06	-	-	13.8-48.1 [14-21]	17	Horgan and Mills (1997)
	375	9,06	-	-	41.4 [20]	24	Sprung (1995)
	-	-	-	0,048	[5-20]	17	Mellina et al. (1995)
	-	-	-	0,109	[5-20]	22	Mellina et al. (1995)
	-	-	2,29	-	10.89 [13-17]	20	Aldridge et al. (1995)
	-	-	2,65	-	10.45 [13-17]	24	Aldridge et al. (1995)
	-	-	7,94	-	10.24 [13-17]	28	Aldridge et al. (1995)
	-	-	11,24	-	9.59 [13-17]	32	Aldridge et al. (1995)
	-	-	-	0,042	[21 average]	18	James et al. (1997)
Dreissena bugensis	40-200	2.16-10.81	-	-	18.5 [15]	8-22	Diggins (2001)
	120-310	2.72-7.04	-	-	44 [20]	8-22	Diggins (2001)
Mytilus edulis	-	-	1,87	-	50-5000	11-21	Bayne and Scullard (1977)
Mytilus californianus	-	-	1,7	-	550-4100	13	Bayne et al. (1976)
Modiolus demissus	-	-	-	0,087	10-1000	6-24	Kuenzler (1961)
Lampsilis radiata siliquoidea	-	-	1,16	0,042	2300-8000	10-23	Nalepa et al (1991)
Geukensia demissa	-	-	1,41	-	100-1000	not given	Jordan and Valiela (1982)
Hydridella menziensi	-	-	0,42	-	690 (average)	18	James (1997)
Corbicula fluminea	490	2,2	-	-	222.5 [29.4]	22	Silverman et al. (1997)
	567	1,89	-	-	300 [32.8]	15	Way et al. (1990)
	347	20,5	-	-	-	21-24	Buttner and Heidinger (1981)

by Sylvester et al. (2005), which may indicate that the type of food offered to the animals (wild plankton vs. monospecific cultures) plays a major role in the rates obtained. It is suggested that the values reported by Rückert et al. (2004) and Sylvester et al. (2005) are "physiological maxima" that can be attained by starved animals under optimum conditions, whereas our present results are more indicative of realistic long-term clearance rates in the field.

On the other hand, the clearance and grazing rates found in this work are very similar to the ones reported for other invasive, freshwater bivalves, like *Dreissena polymorpha* (1.63-4.12 mL mg DW^{-1} h^{-1}: Diggins 2001; Berg et al. 1996; Reeders et al. 1989), *Dreissena bugensis* (2.16-10.81 mL mg DW^{-1} h^{-1}: Diggins, 2001), and *Corbicula fluminea* (Müller, 1774) (1.89-2.2 mL mg DW^{-1} h^{-1}: Way et al. 1990; Silverman et al. 1997) (Table 2) .

Algal species consumption rates did not seem to be influenced by cell-size. Figure 5 shows that grazing pressure, as measured by the difference in the proportions of each algal taxon before and after filtration, was not associated with the biovolume of the cells (range: 5 to 280,596 μm^3). A similar analysis based on the largest phytoplanktonic cell dimension (rather than on biovolume) yielded a similar result (not shown). Although the abundances of most of the algae counted were too low to allow precise estimates of selective grazing pressure, the high number of species involved in the counts suggests that had there been an even marginally clear trend, we would have detected some pattern. In addition, the same analysis using the 11 most abundant species only (those accounting for >90-95% of all phytoplankton at 0 h; biovolumes: 50 to 1226 μm^3) showed no trend either. It should be stressed that our results reflect grazing by individuals >14 mm in length; it is conceivable that younger animals, which at times dominate the population, may behave differently.

Comparison of these results with reported filtration selectivity by the zebra mussel is complicated by disagreements in the data reported by different authors. While some surveys concluded that the grazing impact of *Dreissena* is similar for a wide range of phytoplankton size classes (e.g., Nicholls and Hopkins 1993; Horgan and Mills 1997), others noticed enhanced consumption of some size fractions and taxa over others. Furthermore, suggested feeding preferences of the zebra mussel vary between studies. For example, Heath et al. (1995) found that diatoms and chlorophytes are eliminated at higher rates than cyanobacteria and chrysophytes, whereas Bastviken et al. (1998) concluded that invasion of *Dreissena* is associated with the virtual elimination of cyanobacteria and an increase in the relative abundance of diatoms (in our data no trend in association with algal classes was found). These disagreements may respond to several causes, including different environmental settings, differences in the toxicity of the cyanobacteria involved (*Dreissena* has been observed to avoid microcystin-producing strains, e.g.; Raikow et al. 2004), etc.

The impact of suspension-feeding organisms depends chiefly on their clearance rates and population densities. As opposed to indigenous bivalves, whose densities are usually moderate, invasive species can reach extremely high numbers and dominate the dynamics of lentic and lotic systems (Karatayev et al. 1997). In Europe and North America the zebra mussel can reach high densities (MacIssac et al. 1991), and the feeding activity of these populations has been observed to impact severely both the abundance and the composition of plankton (Leach 1993; MacIsaac et al. 1992). Our experimental results suggest that the impact of *Limnoperna* is comparable to that of *Dreissena*.

Río Tercero Reservoir has a residence time of 227 days (Boltovskoy et al. 1983). The bottom is dominated by coarse gravel and boulders, and although most deep areas are covered with soft sediment (the reservoir was flooded in 1936), much of the littoral belt down to approximately 10 m is free of silt and therefore fit for colonization by the mussel. Particulate organic matter is chiefly represented by autochthonous plankton. A detailed recent survey indicates that the mean density of *L. fortunei* in this water body is 959 ind m^{-2} (Boltovskoy et al. 2009). With a maximum reservoir volume of 0.48 km^3 (at spillway level), and a mussel filtration rate of 1.6 mL mg DW^{-1} h^{-1} (this work), a volume equivalent to that of the reservoir can theoretically be filtered by the bivalves every 7-8 days. While water mixing processes impose limitations on the availability of suspended particles to the mussels, these figures and the results of our experiments suggest that the impact on the water column must be considerable. Indeed, in Río Tercero (where *L. fortunei* was first detected in 1998) some changes seem to have started occurring between 2002 and 2004. The results of a water-quality monitoring program started here in 1996 indicate that after 2003-2004 concentration of seston dropped up to 40%, and primary production decreased 49% (Boltovskoy et al. 2009). In 1998 Secchi disk depths typically ranged from 0.25-3 m (Mariazzi et al. 1989, 1992), whereas after 2000 they increased to 6-9 m (Mariñelarena 2003). Submerged aquatic plants (*Elodea* spp.) have also spread extensively along the shore in recent years, supporting a large population of coots (*Fulica leucoptera* Vieillot, 1817 and *F. armillata* Vieillot, 1817). These changes are consistent with the enhanced plankton depletion-water transparency and nutrient regeneration processes characteristic of the grazing impact by filtering bivalves (Griffiths 1993; MacIsaac 1996; Karatayev et al. 1997).

Much research is needed before we can adequately understand the impacts of *Limnoperna* in South American water bodies. As

new results are produced it is becoming increasingly clear that this invader is strongly affecting both the structure and the dynamics of the habitats colonized. Aside from the impacts on the water-column, previous studies reported enhancement of invertebrate diversity, numbers and biomass, trophic interactions with invertebrates and fishes, modification of the substrate, etc. (Boltovskoy et al. 2006; Sylvester et al. 2007a, b; Paolucci et al. 2007, 2010; Sardiña et al. 2008; Darrigran and Damborenea 2011). However, since the impact of non-indigenous species is as much a function of the invader as it is of the ecological settings of the area invaded, the same invader can have dissimilar effects in different environments (Zaiko et al. 2007). The most important freshwater system invaded by *L. fortunei* in South America is the Río de la Plata-Paraná-Uruguay watershed (Darrigran 2002; Boltovskoy et al. 2006), but the impact of the mussel on its water-column properties is most probably much lower than that described here for a lentic water body. As opposed to Río Tercero Reservoir, the Paraná is a lotic environment with very high concentrations of particulate organic carbon (POC), often over 3 mg L^{-1} (Depetris and Kempe 1993), over 90% of which is of detrital origin (Boltovskoy et al. 1995). Because phytoplankton is scarce in this system, it supplies but a small fraction of the energetic requirements of *L. fortunei*, the bulk being covered by detrital organic matter (Sylvester et al. 2005) and, probably, zooplankton (Molina et al. 2010). A very rough estimate of *Limnoperna* densities in the Paraná River suggests that the rate volume of water: number of mussels is between 20 and 200 times higher here than in Río Tercero Reservoir. In other words, there is much more water for each mussel to retrieve organic particles from in the Paraná River than in the reservoir. Furthermore, Paraná-Río de la Plata waters host at least twice as much POC as Río Tercero Reservoir waters (Depetris and Kempe 1993; Mariñelarena 2003), and typical nutrient concentrations (P around 50 µg P L^{-1}, N around 200 µg N L^{-1}; Gómez and Bauer 1998; O'Farrell et al. 1998; Mercado and Gómez 2000) are above values that limit phytoplankton growth (3 µg P L^{-1}, 100 µg N L^{-1}; Reynolds 2006). Under these conditions it is unlikely that in the Paraná basin *Limnoperna*'s filtration has a strong impact on nutrient recycling, phytoplankton or aquatic plant growth, and water transparency.

These results stress the need to evaluate each invasion event independently, within its regional context, and particularly to be cautious when using the impacts of the zebra mussel on European and U.S. inland waters as a proxy of *Limnoperna*'s impact in subtropical South America.

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Supplementary material

The following supplementary material is available for this article.

Appendix 1. Densities and biovolumes of dominant algal taxa in grazing experiments at 0 and 24 h.

Appendix 2. Phytoplankton biovolumes and counts.

This material is available as part of online article from:
http://www.aquaticinvasions.net/2012/Supplements/AI_2012_1_Cataldo_etal_Supplement.pdf