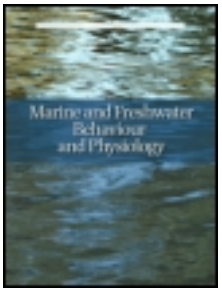

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Vulnerability of microcrustaceans to predation by the invasive filter-feeding mussel *Limnoperna fortunei* (Dunker)

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Limnoperna fortunei is an Asian mussel introduced to South America around 1990. One of the most important impacts of this invader is probably its grazing on the plankton. In this study we evaluate the vulnerability of several planktonic microcrustaceans from the Paraná River floodplain to predation by adult *L. fortunei*. We conducted 2-h laboratory feeding experiments where the bivalves were offered microcrustaceans differing in overall body shape, size, and locomotive abilities. Ingestion and clearance rates for each taxon were estimated. Results suggest that, in addition to detritus and phytoplankton, microcrustaceans may be a very important food item for this invasive mollusc. *Limnoperna fortunei* can prey on larger organisms (up to 1100 µm) than *Dreissena polymorpha*, the European and North American invasive mussel.

Keywords: bivalve; mussel; *Limnoperna fortunei*; filter feeding; microcrustaceans; cladocerans; copepods

Introduction

Freshwater ecosystems worldwide are increasingly impaired by multiple stressors, usually associated with complex interactions between socioeconomic and biophysical factors. River floodplain ecosystems, in particular, are threatened by a range of local, regional, and catchment-wide stressors, among which invasion by exotic species is one of the most detrimental, least controlled, and most difficult to reverse (Tockner et al. 2010). Introduced species can have strong impacts on the biodiversity, biogeochemistry, and economic uses of the ecosystems invaded (Strayer 2010). Molluscs, in turn, represent one of the most important invaders of freshwater systems (Karatayev et al. 2009), due to their ability to form massive populations

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affecting, among others, the abundance and composition of planktonic organisms (Strayer 2010).

The golden mussel, *Limnoperna fortunei* (Dunker), is a freshwater bivalve native to the rivers, lakes, and estuaries of Southeast Asia. In the early 1990s, this species was introduced to South America via the Río de la Plata estuary, probably in the ballast water of ships (Pastorino et al. 1993). The widespread abundance of this bivalve has resulted in it becoming an important ecological concern. For instance, in just 20 years, this species has already colonized most of the Río de la Plata basin and is currently present in Argentina, Bolivia, Paraguay, Uruguay, and Brazil, reaching densities of over 200,000 ind m^{-2} (ind, individuals) (Darrigran 2002; Brugnoli et al. 2005; Muñiz et al. 2005; Boltovskoy et al. 2006; Sylvester et al. 2007; Oliveira et al. 2010). Since its introduction to South America, the golden mussel has caused both ecological and economic problems (Cataldo et al. 2003; Boltovskoy et al. 2006).

One of the most important impacts of this successful invader is probably its plankton grazing activity. Laboratory experiments and field data indicate that *L. fortunei* has high filtration rates that strongly impact phytoplankton densities (Sylvester et al. 2005; Pestana et al. 2009; Cataldo, O'Farrell I et al. 2011; Cataldo D, Vinocur A et al. 2011). Studies performed in secondary channels of the Middle Paraná River (South America) showed significant decreases in the concentration of chlorophyll-*a* (>50%) and zooplankton abundance (>60%) when compared to periods prior to the invasion of *L. fortunei* (Rojas Molina and José de Paggi 2008). While phytoplankton is usually the major source of nutrition for bivalves (Cohen et al. 1984; Bastviken et al. 1998; Prins et al. 1998), several studies have shown that they can also feed on zooplankton (MacIsaac et al. 1995; Wong and Twining 2003; Wong et al. 2003; Wong and Levinton 2005). Field data indicate that zooplankton represent a major food source for *L. fortunei* accounting for up to 70% of the total biomass of the diet with the microcrustaceans of the Chydoridae and Bosminidae being the main components (Rojas Molina et al. 2010). In this study, we evaluate the vulnerability of several microcrustaceans to *L. fortunei* in laboratory experiments. The microcrustaceans studied are frequent in the plankton of the Paraná River floodplain.

Materials and methods

Microcrustaceans and L. fortunei

The microcrustaceans used in this study comprised an assortment of copepodites of three species, *Argyrodiaptomus falcifer* (Daday), *Notodiaptomus conifer* (Sars), and *Mesocyclops* sp., and five species of Cladocera: *Alona glabra* Sars, *Ceriodaphnia dubia* Richard, *Moina micrura* Kurz, *Moina reticulata* (Daday), and *Pseudosida variabilis* (Daday) (Table 1).

Laboratory cultures, started with net-collected zooplankton from various waterbodies of the Middle Paraná floodplain, provided the crustaceans used in the experiments. The cultures were maintained at $20 \pm 2^{\circ}C$, 16 : 8 h (light: dark) photoperiod. Approximately one quarter of the culture medium was renewed with filtered and aerated water every 2 days. Organisms were fed *ad libitum* with *Chlorella vulgaris* Beijerinck. Zooplankters used in the experiments were sorted using different size sieves and manually with Pasteur pipettes under a stereoscopic microscope.

Adult specimens of *L. fortunei* were manually removed from marker buoys located in the Colastiné River (a secondary channel of the Middle Paraná River,

Table 1. Body length (mean and standard deviation - SD) of the microcrustaceans used in the experiments; results of the Mann-Whitney U-tests for the differences between zooplankton density in control and bivalve treatment (significant differences at $p < 0.05$ are denoted in bold); and mean clearance (CR) and ingestion rates (IR) of *Limnoperna fortunei* on microcrustaceans.

	Size (μm) (mean ± SD)	Mann–Whitney *U* test (*p*)	Mean CR (SD) (mL h^{-1} $mussel^{-1}$)	Mean IR (SD) (prey h^{-1} $mussel^{-1}$)
A. glabra (in 10 mL)	389.4 ± 35.0	**6.0 (0.034)**	0.31 (0.4)	0.77 (1.2)
A. glabra (in 50 mL)	389.4 ± 35.0	10.0 (0.098)	0.56 (0.7)	0.28 (0.4)
C. dubia	568.3 ± 121.5	**0.0 (0.004)**	3.05 (2.2)	1.53 (1.1)
M. reticulata	633.7 ± 84.1	**4.0 (0.018)**	1.10 (1.2)	0.55 (0.6)
M. micrura	652.5 ± 121.8	**6.0 (0.033)**	0.59 (0.5)	0.30 (0.3)
Copepodites	1122.3 ± 272.9	**6.0 (0.034)**	3.72 (6.7)	0.74 (1.4)
P. variabilis	1201.5 ± 350.8	12.0 (0.156)	0.58 (1.1)	0.29 (0.5)

31°42′51″S, 60°42′02″W). Mussels were transported to the laboratory and transferred to 30 L aquaria filled with river water. The mussels were maintained for 5 days under the same light: dark and temperature conditions as the zooplankton, with continuous aeration, and were fed *ad libitum* with commercial fish food and the algae *C. vulgaris*. To avoid overfiltration by starved animals (Lee and Chung 2001), food was administered until the onset of the experiments.

Experimental design

Experiments to assess predation of *L. fortunei* on microcrustaceans were carried out in 200 mL glass beakers filled to 50 mL with water from a shallow local lake filtered twice through a 25 μm net. Adult bivalves were selected for the experiments (mean shell length ± SD: 19.9 ± 1.6 mm, range 17–24 mm) and acclimated in test beakers for 2 h prior to each predation experiment. Healthy individuals were selected based on (1) the presence of filtering activity (as evidenced by visible water motion around the mussels) and (2) response to tactile stimuli on their extended siphons.

For each feeding experiment, one mollusc and 25 cladocerans of the same species, or one mollusc and 10 copepodites, were used in 10 replicate beakers plus four controls (i.e., without molluscs). With *A. glabra*, a very small species, an additional set of experiments was conducted using 10 mL beakers. Before placing the microcrustaceans in the experimental beakers, a suspension of algae (*C. vulgaris*) was added at a final concentration of 1240 cells mL^{-1} (which is similar to the usual algal concentrations in the Middle Paraná River floodplain (García de Emiliani 1990; Zalocar de Domitrovic et al. 2007). Experiments were carried out in darkness to avoid the potentially disturbing effects of sudden light changes (Diggins 2001; Sylvester et al. 2005). After 2 h, the mussels were removed from the beakers and their pseudofeces deposited on the bottom (which were amorphous and bound in mucus) were collected with a pipette for analysis under the microscope. Subsequently, formaldehyde with erythrosine was added to each beaker (final concentration: 10%) to preserve and stain the remaining microcrustaceans in order to facilitate counting in a 5 cm^3 Bogorov chamber under a stereoscopic microscope.

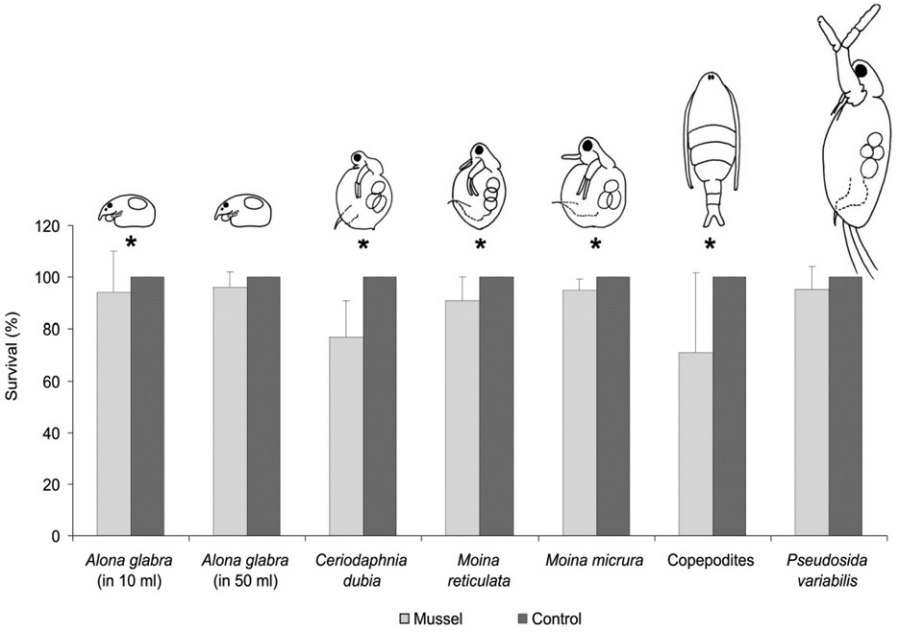

Figure 1. Survival rates of microcrustaceans exposed to predation by *Limnoperna fortunei* (mean of 10 replicates) and the corresponding controls (mean of 4 replicates). Asterisks denote significant differences ($p < 0.05$) (Mann–Whitney U test; see Table 1).

Data analysis

Mann–Whitney tests were used to compare microcrustacean survival rates in experimental and control chambers (transformations of the data failed to improve their normality, for which reason non-parametric tests were required). Species-specific differences in survival were analyzed with Kruskal–Wallis (KW) and Dunn's multiple comparisons tests. Differences were considered significant at $p < 0.05$.

Prey-based clearance rates (CRs, $\mathrm{mL\,h^{-1}\,mussel^{-1}}$) and ingestion rates (IRs, $\mathrm{prey\,h^{-1}\,mussel^{-1}}$) were calculated for each prey as follows (Coughlan 1969):

$$\mathrm{CR} = V \cdot \frac{\log C_0 - \log C_t}{T},$$

$$\mathrm{IR} = CR \cdot C_0,$$

where V is the experimental volume of water (in mL), C_0 and C_t are prey densities before and after filtration ($\mathrm{ind\,mL^{-1}}$), respectively, and T is the experimental time (in hours).

The effects of cladoceran body size on CR and IR were estimated by means of Spearman's correlation coefficients.

Results

Survival of the zooplankton was 100% in all controls, whereas in the experimental containers significant mortality was recorded for the copepodites (30%, on average),

C. dubia (23%), *M. reticulata* (10%), *M. micrura* (5%), and *A. glabra* (in 10 mL) (6%). Levels of *P. variabilis* and *A. glabra* (in 50 mL) were not significantly affected by exposure to *Limnoperna* (Figure 1, Table 1).

Survival rates differed significantly between species (KW 38.070, $p < 0.0001$). The multiple-comparisons *post hoc* test showed significant differences between copepodites and all Cladocera species ($p < 0.01$), and between *P. variabilis* and *C. dubia* ($p < 0.05$). The highest CR values were recorded for copepodites and *C. dubia* (3.72 and 3.05 mL h^{-1} $mussel^{-1}$, respectively), whereas the highest IR figures were those of *C. dubia*, *A. glabra* (in 10 mL) and copepodites (1.53, 0.77, and 0.74 prey h^{-1} $mussel^{-1}$, respectively) (Table 1). At constant densities, with the exception of *A. glabra* (which was not significantly affected by mussel predation), cladoceran body size was significantly (negatively) associated with CR and IR ($r = -0.575$, $p < 0.01$ in both cases). For *A. glabra*, experiments with 25 specimens in 50 mL yielded higher CR and lower IR values than those with 25 specimens in 10 mL.

Neither whole zooplanktonic organisms nor their remains were recorded in the pseudofeces after the 2 h experiments.

Discussion

Our experiments indicate that most of the commonly found microcrustaceans of the middle Paraná River are vulnerable to predation by *L. fortunei in vitro*. The experimental settings used differed, however, from natural conditions. In particular, microcrustacean densities were somewhat higher than those typical of floodplain lakes in this system, where peak values are around 470 ind L^{-1} (for Cladocera) and 70 ind L^{-1} (for Copepoda) (José de Paggi and Paggi 2008; José de Paggi and Paggi unpublished data) (as opposed to 500–2500 Cladocera L^{-1}, and 200 copepodits L^{-1} in our experiments). Nevertheless, while admittedly inadequate for extrapolating these grazing pressure figures to natural conditions, these results support the notion that *L. fortunei* can use large zooplankton as a food source.

Several studies have demonstrated that live zooplankters are able to evade suction-generated currents (Drenner and McComas 1980; Fields and Yen 1997). Our results suggest that several attributes of the preys selected for our experiments, including overall body shape, size (from 389 to 1200 μm) (Figure 1), and locomotive abilities are responsible for their availability to the mussels. For example, under similar conditions, *Limnoperna* consumed more small cladocerans with weak evasive behavior, such as *Ceriodaphnia*, than large and more actively swimming forms, such as *Pseudosida*. Excluding *A. glabra* (see below), lowest survival rates and highest CR and IR were recorded for the small and roundish-oval *Ceriodaphnia*, presumably easier to capture because of its slower swimming (Li and Li 1979; Berner 1986). *Moina* spp., a medium-sized species with a relatively large second swimming antenna showed higher survival rates and lower CR and IR. Finally, *Pseudosida* was the least affected by predation. *Pseudosida* is one of the largest Neotropical Sididae, with a robust general appearance (large head, big and strong swimming appendages; Paggi 1975, 1995), and a remarkable ability to dodge predators performing sudden, quick jumps (Li and Li 1979; Drenner and McComas 1980; Williamson 1983). The results of our study suggest that this species, in particular, and probably the Sididae, in general, are less vulnerable to predation by *L. fortunei* than most other cladocerans.

This conclusion is supported by previous studies in the Paraná River floodplain where the Sididae *Sarsilatona serricaudata* and *Diaphanosoma* spp., present in the plankton, were never recorded in stomachs of *L. fortunei* (Rojas Molina et al. 2010). The fact that *A. glabra*, the smallest of the cladocerans used in our experiments (Table 1), did not follow the above trend, is intriguing (in 50 mL *A. glabra* was the least vulnerable to predation of all cladocerans). It is conceivable that some behavioral traits of this species make it less available to the mussel. *Alona glabra* is a small and compact crustacean with small antennae. As opposed to the other cladocerans used in our experiments, which are rather active swimmers, *A. glabra* usually moves slowly along the bottom or remains stationary while grazing on algae (Paggi 1975; Rojas Molina personal observations). This behavior may keep it away from the area of influence of the mussel's suction for long periods of time, thus reducing its encounter rate with the predator, and consequently the risk of capture. This assumption is supported by the fact that in lower fluid volumes (10 mL), the IR for this species was over twice as high as in 50 mL (Table 1), suggesting that decreasing the space available enhances overlapping of the areas of influence of the mussel's suction and *A. glabra*'s swimming range, resulting in higher capture rates.

As opposed to Cladocera, copepodites have elongated, articulated bodies, more swimming appendages, a highly developed sensory system, and better neuromuscular coordination, which grants them the ability to perform rapid evasive maneuvers (Kerfoot et al. 1980; Dussart and Defaye 2001). However, contrary to expectation, copepodites exhibited the lowest survival rates. With the information at hand, we do not have a clear explanation for this result. It is conceivable that the speed of mussel's suction is below the threshold required by the copepodites to cause an escape reaction (Walton 1988; Fields and Yen 1997). In addition, the small experimental volumes used may have had a stronger effect on the faster-swimming copepods than on the slower cladocerans. Nevertheless, the fact that field-collected *L. fortunei* have copepodites in their guts (Rojas Molina et al. 2010) indicates that our results are not an artifact of the experimental conditions used. Furthermore, these experiments confirm that *Limnoperna* is capable of ingesting particles over 1100 μm in size, which is the mean length of the copepodites used in this study (Table 1) (50% larger than the largest prey so far recorded in the mussels' guts by Rojas Molina et al. 2010). The fact that after filtration no crustaceans were present in the pseudofeces indicates that the animals missing from the water column were effectively ingested, rather than captured, bound in mucus, and rejected.

Feeding on zooplankton by *L. fortunei* may explain its wide distribution in areas where phytoplankton is insufficient for supporting mussel populations. Sylvester et al. (2005) concluded that in the lower Paraná phytoplankton alone can cover as little as 9% of the basal energy requirements of the mussels, the remainder being accounted for by particulate organic matter of a detrital origin. Our results suggest that, in addition to detritus, zooplankton may be a very important food resource. Analyses of the gut contents of field-collected bivalves confirm this assumption: Rojas Molina et al. (2010) found that microcrustaceans constitute about 60% of the biomass of the mussel's diet. Mixed phytoplankton–zooplankton diets yield better growth performance than either of them alone (Wong and Levinton 2004; Safi and Hayden 2010). This may confer some adaptive advantages upon *Limnoperna* such as extended reproduction (Boltovskoy et al. 2006, 2009).

Limnoperna fortunei shares several biological and ecological traits with another invasive bivalve: the zebra mussel *Dreissena polymorpha*, a Ponto-Caspian species

that invaded Europe and North America (Karatayev et al. 2007). There is little doubt that *D. polymorpha* can consume rotifers (Shevtsova et al. 1986; MacIsaac et al. 1991, 1995; Pace et al. 1998; Welker and Walz 1998; Jack and Thorp 2000; Kissman et al. 2010; Bowen and Johannsson 2011), but for microcrustaceans the results are inconclusive. According to Shevtsova et al. (1986), this mussel can feed on small cladocerans (<400 μm). On the other hand, MacIsaac et al. (1991) reported that cladocerans are immune to predation by *Dreissena*. Drops in the numbers of microcrustaceans in association with the presence of zebra mussels are attributed to trophic competition between the bivalves and the zooplankton, rather than to direct grazing (Pace et al. 1998; Strayer et al. 1999; Jack and Thorp 2000).

The fact that *L. fortunei* can consume larger zooplankton than *D. polymorpha* may reflect differences in the functional morphology of these two species. The siphons of *D. polymorpha* have a well-defined margin, formed solely by the fused inner folds of the mantle margins (Morton 1993). When the tentacles that surround the inhalant siphon opening come in contact with a particle too large to ingest, water intake ceases and the siphon is temporarily withdrawn (MacIsaac et al. 1991; Morton 1993). In *Limnoperna*, on the other hand, only the exhalant siphon is formed by fusion of the inner mantle folds, and the inhalant aperture is neither surrounded by tentacles nor separated from the pedal byssal aperture (Morton 1973, 1993). Hence, it is conceivable that structural differences of the siphonal region play a role in the contrasts between the type and size of particles available to the mussels.

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