Benthic community responses to invasion by the golden mussel, *Limnoperna fortunei* Dunker: biotic homogenization vs environmental driving forces

Author(s) :Paula SardiñaEliseo ChavesMercedes Marchese

Source: Journal of the North American Benthological Society, 30(4):1009-1023. 2011.

Published By: North American Benthological Society

DOI: 10.1899/10-170.1

URL: http://www.bioone.org/doi/full/10.1899/10-170.1

J. N. Am. Benthol. Soc., 2011, 30(4):1009–1023

DOI: 10.1899/10-170.1

Benthic community responses to invasion by the golden mussel, *Limnoperna fortunei* Dunker: biotic homogenization vs environmental driving forces

---

Paula Sardiña[1]

Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" and Consejo Nacional de Investigaciones
Científicas y Técnicas (CONICET), Av. Angel Gallardo 470, C1405DJR, Buenos Aires, Argentina

Eliseo Chaves[2]

Instituto Nacional de Tecnología Agropecuaria (INTA)-Estación Experimental Agropecuaria,
7620 Balcarce, Argentina

Mercedes Marchese[3]

Facultad de Humanidades y Ciencias and Instituto Nacional de Limnología (INALI-CONICET-UNL),
Universidad Nacional del Litoral (UNL), Ciudad Universitaria 3000, Santa Fe, Argentina

Abstract. The goal of our study was to investigate the interaction between the invasive mussel *Limnoperna fortunei* and benthic invertebrate communities at different spatial scales and under different environmental conditions. We analyzed the effects of *L. fortunei* on benthic invertebrate communities at different downstream distances (meters) from mussel beds and compared these trends in 2 rivers characterized by dissimilar chemical disturbance levels. In areas distant from *L. fortunei* beds, invertebrate composition at the 2 rivers differed strongly, probably in response to different levels of environmental pollution. In areas near *L. fortunei* beds, invertebrate composition at the 2 rivers was similar, suggesting that golden mussels have strong homogenizing effects on faunal makeup. We also found that facilitation was species specific and, in contrast to the general paradigm, weaker (rather than stronger) under more stressful conditions. Our results show that understanding the effects of *L. fortunei* requires accounting for scale- and species-specific effects.

Key words: *Limnoperna fortunei*, golden mussel, invasive species, benthic community, invertebrates, facilitation, biotic homogenization.

The spread of invasive nonindigenous species can be one of the most harmful and least reversible disturbances in ecosystems (Strayer 1999, Ricciardi and MacIsaac 2000, Rahel 2002). Proliferation of invasive species is a major component of global environmental change (Vitousek et al. 1996, Sala et al. 2000), but the specific effects of invasive species on native biota are often unpredictable and depend on the properties of the invading species and the invaded ecosystem (Parker et al. 1999, Sakai et al. 2001, Crooks 2002). In freshwaters, invasive species have had large effects on community structure and ecosystem function (Lodge et al. 1998, Strayer 1999, Ricciardi 2003). Some of these changes arise from biotic interactions between invasive and native species, including competition (Kerans et al. 2005, Riley et al. 2008), facilitation (Sylvester et al. 2007, Ward and Ricciardi 2007, Sardiña et al. 2008), and predation (Grosholz et al. 2000, Nyström et al. 2001).

The invasive golden mussel, *Limnoperna fortunei*, was introduced in South America around 1990 through the Río de la Plata (Pastorino et al. 1993). This mussel is unique among the Río de la Plata watershed freshwater bivalves in possessing free-swimming larval stages and byssate adults. These characteristics have facilitated rapid dispersal and allowed the species to become the dominant macroinvertebrate on hard substrates along a >3000 km

---

[1] E-mail addresses: psardina@macn.gov.ar

[2] eliseo_chaves@yahoo.com.gr

[3] mmarchese@inali.unl.edu.ar

stretch of the Paraguay–Paraná–Río de la Plata system. During the reproductive period (September–April) when recently settled juveniles are abundant, densities can be ≥200,000 mussels/m^2, but density of adults and subadults (7–10 mm in length) usually ranges from 5000 to 10,000/m^2 (Darrigran 2002, Boltovskoy et al. 2006, Sylvester et al. 2007). High initial abundance is often a characteristic of invaders that have profound ecosystem-level effects (Simon and Townsend 2003). The full ecological effects of *L. fortunei* on aquatic communities are still poorly known, but this ecosystem engineer has direct and indirect effects on the several physical, chemical, and biological properties of the environment. For example, colonization of *L. fortunei* has been associated with significant reductions in zooplankton abundance and chlorophyll *a* concentration (Rojas Molina and José de Paggi 2008, Boltovskoy et al. 2009), an increase in water transparency (Boltovskoy et al. 2009), and changes in trophic interactions (Paolucci et al. 2010). Positive interactions between *L. fortunei* and associated invertebrates also have been documented (Sylvester et al. 2007, Sardiña et al. 2008). However, the strength of these interactions at different spatial scales and under different environmental conditions has not yet been studied.

Positive interactions between ecosystem-engineer species and associated invertebrates are common in ecological communities (Norkko et al. 2006). These species often modify habitats both physically and biologically and facilitate conditions for associated organisms by reducing stress or by increasing the flow of resources (Karatayev et al. 2007, Ward and Ricciardi 2007, 2010, Sardiña et al. 2008). The balance between positive and negative interactions can shift along environmental gradients, with facilitation being more important in harsh environments where ecosystem-engineer species alleviate conditions and act as an environmental buffer for associated organisms (Bertness and Callaway 1994, Greenlee and Callaway 1996, Bertness and Leonard 1997, Bruno and Bertness 2001, Bruno et al. 2003).

We investigated the interaction between *L. fortunei* and benthic invertebrate communities (exclusive of *L. fortunei*) at different spatial scales and under different environmental conditions. We analyzed the effects of *L. fortunei* on associated invertebrates in and at different distances (meters) from mussel beds and compared these trends across 2 sites several kilometers apart characterized by dissimilar environmental conditions (i.e., different pollution levels). Our study was designed to test the following hypotheses: 1) effects of *L. fortunei* on benthic communities are stronger near the mussel beds, chiefly because of enhancement of deposit feeders that benefit from *L. fortunei* feces and pseudofeces, and 2) positive interactions between *L. fortunei* and the associated invertebrates are stronger in Río Luján, where environmental conditions are harsher than in Canal del Este.

Methods

Study site

The Río Paraná has the 2^{nd}-largest drainage basin in South America (2.6×10^6 km^2), stretching from lat ~15°S to the Río de la Plata estuary at lat 34°S, where it discharges >470 km^3 water/y (Depetris and Kempe 1993). Upon receiving the Río Paraguay (at lat ~27°S), the Paraná develops a large floodplain composed of streams, oxbow lakes, and ponds, which stretches all the way to its mouth. The southern part of this floodplain forms the Paraná delta, which is 60 km wide, extending between the Río Uruguay in the north to the Río Luján in the south (Fig. 1). In this region, the Paraná branches into several major streams and hundreds of minor waterways (Fig. 1).

The Río Paraná receives considerable loads of polluted wastes from several heavily industrialized and populated cities, but its high discharge has a strong cleansing power. As a result, pollution levels in most of the Paraná delta, including the Canal del Este, where we had a sampling site (lat 34°20′41″S, long 58°31′13″W; Fig. 1), are generally moderate (Boltovskoy et al. 1997). The other sampling site was in the Río Luján (lat 34°25′43″S, long 58°32′56″W; Fig. 1), which receives extremely high loads of industrial and sewage contaminants directly and through its tributaries, in particular the Río Reconquista (Loez and Salibian 1990, Cataldo et al. 2001) (Fig. 1). Suspended particulate matter (49.7 mg/L) and dissolved organic C (8.2 mg/L) are higher at Río Luján and decrease gradually towards Canal del Este (31.6 and 6.8 mg/L, respectively). Sediment-associated contaminants (chlorinated pesticides, polychlorinated biphenyls [PCBs], aliphatic hydrocarbons, aromatic hydrocarbons, and metals) also decrease from Río Luján to Canal del Este and Río Paraná de las Palmas (Fig. 1). This decrease reflects the major input sources: industrial plants along the upper Río Reconquista and Río Luján and port-related activities in the lower Río Luján (Cataldo et al. 2001). Despite these differences, mean temperature (27.9°C at both rivers), conductivity (261 μS/cm at both rivers), and dissolved O_2 (7.23 mg/L at Río Luján, 7.3 mg/L at Canal del Este) were identical or very similar across sites and in the 2 rivers during our study.

Physical conditions were similar at the Río Luján and Canal del Este sites. Mussel beds occurred on

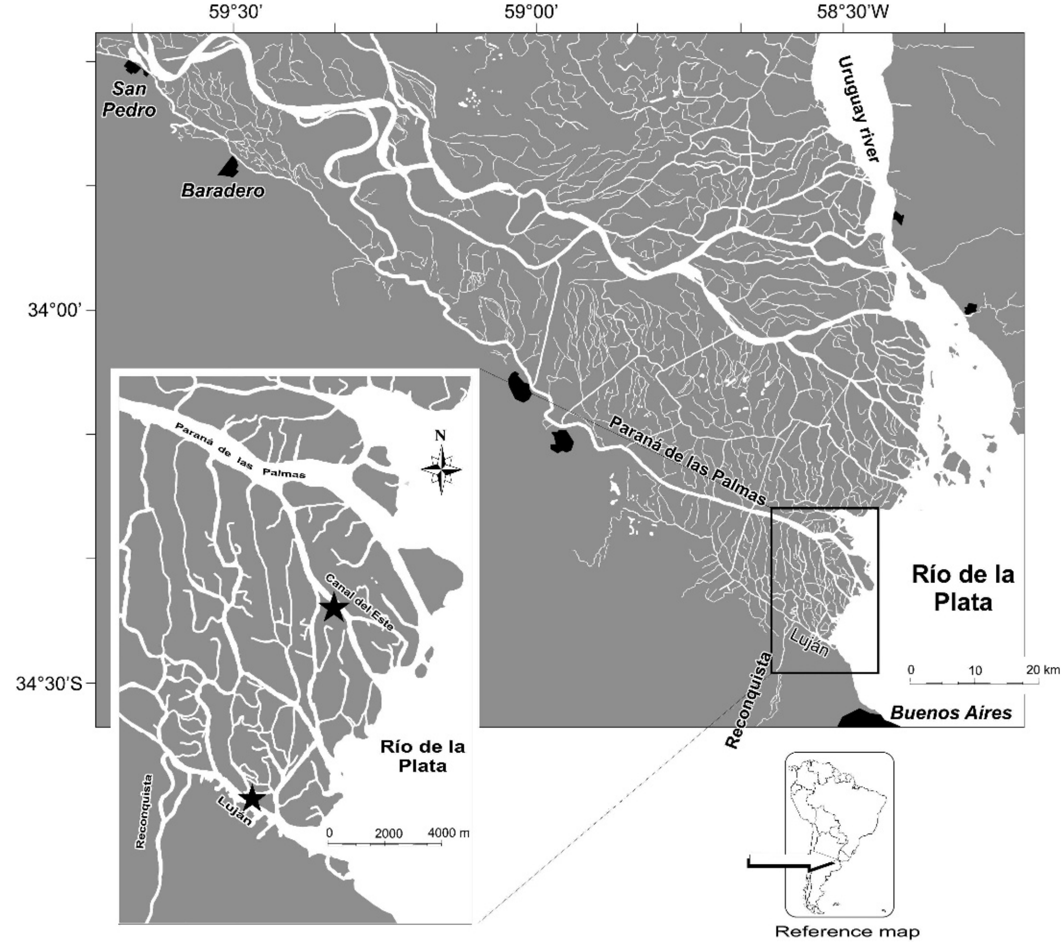

FIG. 1. Locations of the sampling sites in the Paraná River delta (stars).

concrete revetments that had only a small amount of overlying sediment composed of silt (mean = 68%) and clay (32%). Downstream of mussel beds, sediments were dominated by silt (66%) and clay (17%). Immediately downstream of mussel beds (0 m), the proportion of sand was low (<5%) but sand increased further from the beds (5–15 m, 17–29%). Depth in mussel beds was ~0 m (i.e., water surface) in both Río Luján and Canal del Este. Bottom depths at downstream sites increased with increasing distances from the beds. Direction and intensity of flow in each site vary with tide and wind conditions, but predominant water motion is toward the Río de la Plata estuary. Maximum estimated flow speeds at the surface are ~0.5 to 0.8 m/s.

Sample collection and processing

Samples were collected from Río Luján (L) and Canal del Este (CE) in December 2008. At each river, benthic samples were obtained from mussel beds on concrete revetments (LBED and CEBED) and sediments at different distances downstream from the mussel beds: 1) immediately downstream (0 m; L0 and CE0), 2) 5 m downstream (L5 and CE5), and 3) 15 m downstream (L15 and CE15). Samples in mussel beds were collected from 10 × 10-cm frames. Mussels and associated invertebrates were carefully scraped into plastic containers, and care was taken not to lose fine sediment and mobile invertebrates. Samples downstream of beds were collected with a Peterson grab. Mean density and shell length of *L. fortunei* in the beds did not differ between rivers (L: density = 18,000 ± 1291 mussels/m^2 [mean ± SE], L: length = 16.97 ± 0.27 mm, CE: density = 18,400 ± 2400, CE: length = 16.29 ± 0.29 mm; *t*-tests, $p > 0.05$).

Four replicates were obtained at each sampling site. Three were used for faunal analyses and 1 for sediment analysis, except at site L0 where only 1 sample was available because of high amounts of waste in the bottom (i.e., plastic bags and bottles), which made it difficult to collect more sediment samples with the grab. This single sample was divided into 2 halves: one half was used for faunal analysis, and the other was used for sediment analysis.

In the laboratory, sediments of each of the 3 faunal replicates were sieved through a 300-μm mesh. All invertebrates were identified to the lowest taxonomic category possible (Appendix), counted, and measured, and their mass was estimated. Nematodes, oligochaetes, and chironomids were identified to species, but their abundance and mass were summed within each group. Mass of Nematoda, Ostracoda, Hydracarina, Turbellaria, Oligochaeta, and Tanaidacea was estimated volumetrically according to methods published by Feller and Warwick (1988). Wet to dry mass conversions for Oligochaeta were based on a factor of 0.15 (Sylvester et al. 2007). Mass was estimated from size–mass relationships for all other groups including Copepoda and Cladocera (Dumont et al. 1975), *Corbicula fluminea* (Stites et al. 1995), Amphipoda, Gastropoda, Ephemeroptera (Smock 1980), Coleoptera (Meyer 1989), Odonata (Pavlov and Zubina 1990), Trichoptera, Chironomidae, and other Diptera (Benke et al. 1999). Density and mass values were standardized to numbers of individuals (ind.)/m^2 and g/m^2, respectively, and are reported as mean ±1 standard error (SE).

Sediment samples were analyzed for median grain size, sorting and composition (proportions of sand, silt, and clay), and organic matter content. Organic matter (ash-free dry mass [AFDM]; g/m^2]) was assessed as the difference between dry and ash mass (ignition at 500°C for 3 h). Organic matter exclusive of invertebrates >300 μm (see previous) was estimated by subtracting mean invertebrate biomass in the 3 faunal samples from the total organic matter mass in the sediment sample.

Data analysis

Limnoperna fortunei was absent from sites 5 m and 15 m downstream from mussel beds in both rivers. At 0-m-downstream sites, small juveniles (4.8 ± 0.17, mean total shell length ± SE) were present at very low abundances (116 ± 39 ind./m^2) in Río Luján but not at Canal del Este. These individuals were not included in estimates of richness, abundance, or biomass. For each site Chao-2 richness was calculated, and estimated values within each river were compared by means of 95% confidence intervals. Chao-2 estimates and confidence intervals were computed using EstimateS (version 8.2; R. K. Colwell, http://purl.oclc.org/estimates). In addition, differences in abundance and biomass were evaluated among sites within each river with single-factor analysis of variance (ANOVA) and Tukey multiple comparisons (STAT, version 7.0; StatSoft, Tulsa, Oklahoma).

To compare the strength of the interactions between *L. fortunei* and associated organisms under different environmental conditions, the average ratio of total invertebrate abundance and total biomass (excluding *L. fortunei*) were calculated between mussel beds (BED) and sites 5 m and 15 m downstream (e.g., abundance at LBED vs abundance at L5) for each river. We compared these ratios (dependent variable) between rivers and sites (independent variables) with a 2-way ANOVA. Data were log(x)-transformed to homogenize variances. Sites at 0 m were excluded from this analysis because they showed a clear influence of the mussel beds above them (see nonmetric multidimensional analysis [NMDS] below). Comparisons of individual taxa between the mussel beds and each downstream site were evaluated with t-tests or Mann–Whitney U tests (when homogeneity of variances was not reached after transformation of the data) to identify those taxa that contributed most to differences in abundance and biomass among sites in each river.

Invertebrate community structure was described using PRIMER v.6 (Clarke and Gorley 2006). Classification (group average sorting of Bray–Curtis similarity measures based on $\sqrt[4]{(x)}$-transformed abundance data) and ordination (NMDS on the above similarity matrices) were used to group sampling sites based on their faunal content (Field et al. 1982, Clarke and Warwick 2001). The adequacy of the NMDS representation obtained was measured using the stress coefficient (Clarke and Warwick 2001). Low stress (<0.1) gives confidence that the 2-dimensional plot is an accurate representation of the sample relationships. For values >0.1, the combination of NMDS and cluster analysis is suggested (Clarke and Warwick 2001). The statistical significance of the defined groups was analyzed using the SIMPROF routine. This similarity profile permutation test identifies statistically significant clusters in a set of samples (Clarke and Warwick 2001). The similarity percentage procedure (SIMPER) was used to examine the relative contribution of individual taxa to the separation between sample groups, and % contribution of individual species was listed in decreasing order (Clarke and Warwick 2001). The BIO-ENV procedure was used to identify the environmental variables (similarity calculated with the Euclidean distance coefficient on log[x]-transformed data) that best explained the biological structuring (Clark and Warwick 2001). Before this analysis, the intercorrelation among variables was evaluated. Proportions of

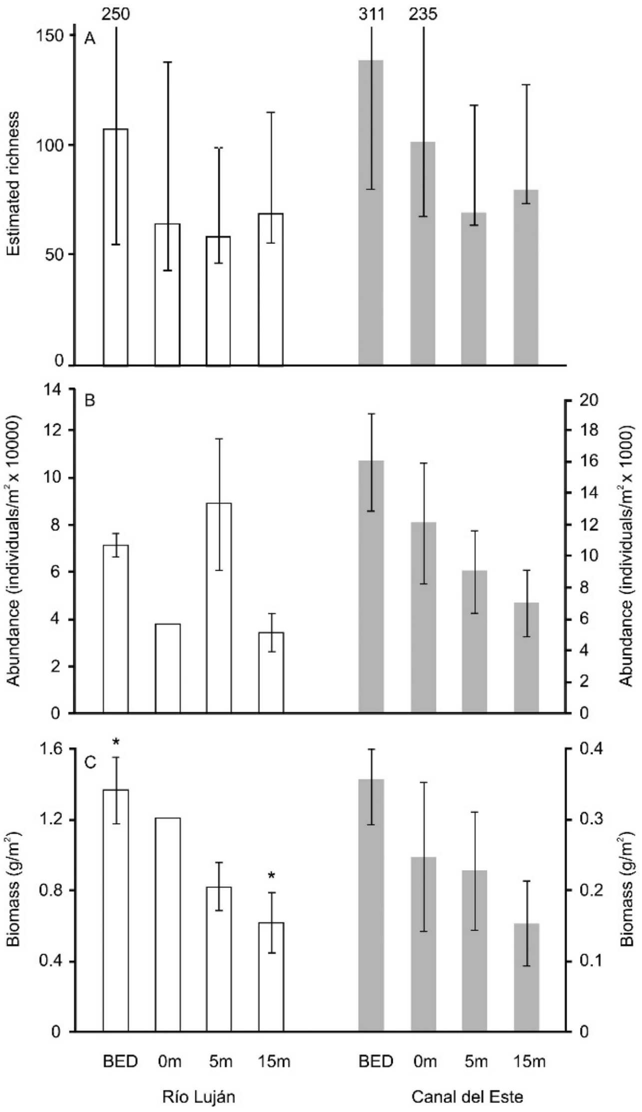

FIG. 2. Mean Chao-2 estimated richness (95% CI) (A), invertebrate abundance (±1 SE) (B), and biomass (±1 SE) (C) in *Limnoperna fortunei* beds (BED) and from sites 0 m, 5 m, and 15 m downstream of the beds at Río Luján and Canal del Este (note different scales for abundance and biomass). * indicates significant differences ($p < 0.05$) among sites within rivers. The site at 0 m in Río Luján could not be tested because no replicates were collected.

clay and sand were omitted from the BIO-ENV analysis because of their high correlation with mean grain size (Spearman's correlation coefficient: clay, $\rho_W = -0.933$; sand, $\rho_W = 0.971$). Differences in environmental characteristics associated with the sample groups defined in the NMDS were assessed by a Kruskal–Wallis test followed by a Dunn test. Only variables that were best correlated with the NMDS were tested.

Results

In both Río Luján and Canal del Este, Chao-2 richness was, on average, 1.7× higher in the mussel beds than at all downstream sites, but no significant differences were found among sites in either river (Fig. 2A). In Canal del Este, mean total invertebrate abundance and biomass appeared to decline with increasing distance from mussel beds (Fig. 2B, C). In Río Luján, this trend was observed only for biomass. However, only biomass at Río Luján differed significantly among sites (between LBED and L15; Fig. 2C).

The river × site interaction did not affect abundance or biomass ratios (Table 1). The magnitude of increase in invertebrate abundance in mussel beds relative to at downstream sites (i.e., the degree of facilitation by *L. fortunei*) was higher in Canal del Este than in Río Luján, and at 15-m than at 5-m downstream sites. No differences were found in invertebrate biomass ratios between rivers or sites (Table 1).

Snails (*Heleobia piscium*), tanaidaceans (*Sinelobus*, probably *S. stanfordi*), amphipods (*Hyalella* spp.), and harpacticoid copepods were significantly more abundant and had significantly higher biomass in mussel beds than at downstream sites in both rivers (Appendix, Table 2). Oligochaetes, isopods, caddisflies (Trichoptera), and flatworms (Turbellaria) followed the same pattern at Canal del Este. At Río Luján, the abundance and biomass of other snails (*Potamolithus* sp.), ostracods (*Cyprideis hartmanni*), nematodes, and chironomids were significantly lower in mussel beds than at downstream sites. In Canal del Este, only chironomids were less represented in the mussel bed than in downstream sites (Appendix, Table 2).

Invertebrate communities were similar among rivers in *L. fortunei* beds and at sites immediately downstream (0 m), but communities differed widely between beds and downstream sites (Fig. 3; results were identical for NMDS and cluster analysis, so only results of the NMDS are presented). Farther away from the mussel beds, faunal dissimilarity between rivers was strong, yielding a sharp separation between Canal del Este and Río Luján (Fig. 3).

Oligochaeta and Nematoda were generally the most important contributors to intragroup similarity, although their relative contribution varied among sample groups (Table 3). Oligochaetes were the most abundant organisms in *L. fortunei* beds and immediately downstream of the beds (0 m), where they accounted for 54% of all invertebrates (Fig. 4A). In terms of biomass, oligochaetes were of lesser importance (<25% of the biomass) at these sites, and faunal

Table 1. River and site mean (± SE) abundance and biomass of invertebrates and results of 2-way analysis of variance comparing the ratios of total invertebrate abundance and biomass between mussel beds (BED) and sites 5 and 15 m downstream from the beds (BED/5 m vs BED/15 m) between Río Luján and Canal del Este. * = $p < 0.05$; ** = $p < 0.01$.

	Abundance				Biomass			
Effect	Mean	*p*	*F*	df	Mean	*p*	*F*	df
River × site		0.11	2.68	1		0.83	0.04	1
River		_0.02_*	5.62	1		0.82	0.05	1
Río Luján	1.65 ± 0.21*				2.06 ± 0.20			
Canal del Este	2.69 ± 0.45*				3.10 ± 0.64			
Site		_0.004_**	9.57	1		0.10	2.92	1
5 m	1.65 ± 0.30**				2.17 ± 0.43			
15 m	2.69 ± 0.39**				3.00 ± 0.53			

composition differed more widely (Fig. 4B). In *L. fortunei* beds, oligochaetes, tanaidaceans (*Sinelobus* sp.), snails (*H. piscium*), and amphipods (*Hyalella* sp.) each composed roughly equal percentages of biomass. Immediately downstream of beds, assemblages were dominated by *H. piscium* (50% of biomass), with smaller and roughly equal representation of oligochaetes, limpets (Ancylidae), and other snails (Planorbidae). Communities at 5 m and 15 m downstream of beds in both rivers were dominated numerically by oligochaetes and nematodes. However, patterns of biomass differed widely between rivers at these sites. Biomass was dominated by oligochaetes at Río Luján sites but by the snail *Heleobia parchappei* in Canal del Este. Subdominant taxa overlapped between rivers at these sites, but did not overlap between *L. fortunei* beds or 0-m beds in both rivers (Fig. 4B).

Organic matter content, mean grain size, and depth were most strongly correlated with community differences among sites ($\rho_w = 0.661$). Organic matter was significantly higher in mussel beds than in all downstream sites (Table 4). It also was significantly higher at 0-m sites (downstream *L. fortunei* [0 m] in Fig. 3) and at 5- and 15-m sites in Río Luján than in Canal del Este. However, the magnitude of these differences was small compared to the much higher organic matter content in mussel beds. Mean grain size and depth tended to be greater at increasing distances from the mussel colonies, but these variables did not differ significantly between groups ($p > 0.05$; Table 4).

Discussion

Invertebrate composition differed strongly between rivers at sites 5 m and 15 m downstream of *L. fortunei* beds. This result suggests that differences in water quality or other habitat variables largely determined faunal composition, and effects of mussels did not extend far beyond the beds. However, we do not know the composition of these communities before invasion or at sites without upstream mussel beds. Within and immediately downstream of mussel beds, the mussels had a strong homogenizing effect that forced a convergence in faunal makeup. However,

Table 2. Comparisons of taxon abundance and biomass among samples from *Limnoperna fortunei* beds (BED) and sites 5 m and 15 m downstream from the mussel beds in Río Luján and Canal del Este. Unless specified, *p* values are for both rivers and for both downstream sites. * = $p < 0.05$, ** = $p < 0.01$.

Taxa with higher abundance and biomass in the mussel beds	Taxa with higher abundance and biomass in downstream sites
Heleobia piscium*[a]	*Potamolithus* sp.: Río Luján: 5 m > BED**[b]
Sinelobus sp.*[a]	*Cyprideis hartmanni*: Río Luján: 15 m > BED*[a]
Hyalella sp.*[a]	Nematoda: Río Luján: 15 m > BED**[b]
Harpacticoidea*[a]	Chironomidae: Río Luján: 15 m > BED *[a], Canal del Este: 5 and 15 m > BED*[a]
Oligochaeta: Canal del Este*[b]	
Isopoda: Canal del Este*[a]	
Trichoptera: Canal del Este*[a]	
Turbellaria: Canal del Este*[a]	

[a] Mann–Whitney test

[b] *t*-test

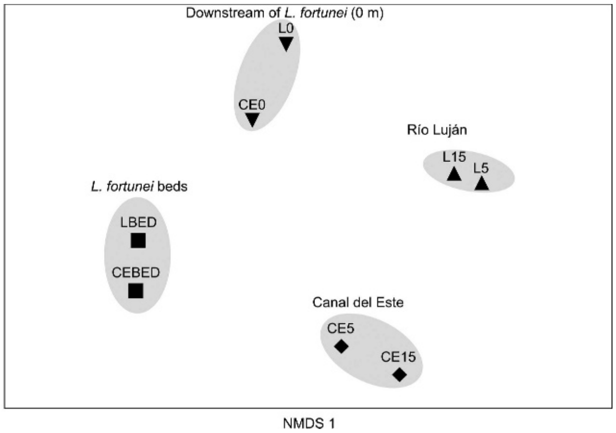

FIG. 3. Nonmetric multidimensional scaling (NMDS) plot of invertebrate communities in *Limnoperna fortunei* beds (LBED, CEBED), and from sites 0 m (L0, CE0), 5 m (L5, CE5), and 15 m (L15, CE15) downstream of the beds at Río Luján (L) and Canal del Este (CE). Final stress = 0.12, separation is supported at $p < 0.05$.

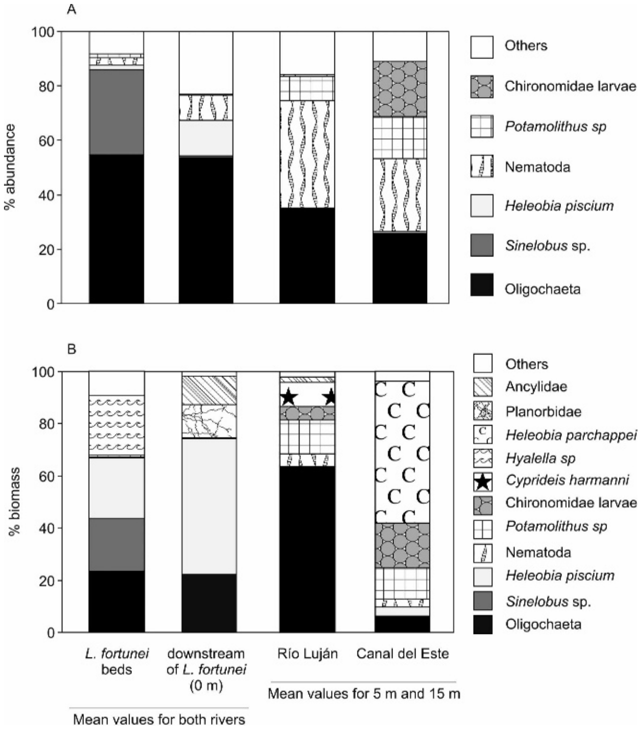

FIG. 4. Percent abundance (A) and % biomass (B) of invertebrates for groups defined by nonmetric multidimensional scaling (NMDS) and cluster analyses. *L. fortunei* beds = *Limnoperna* mussel bed samples from Río Luján and Canal del Este, downstream of *L. fortunei* = samples from sites 0 m downstream of the beds in both rivers, Río Luján = samples from sites 5 and 15 m downstream of the beds in Río Luján, Canal del Este = samples from sites 5 and 15 m downstream of the beds in Canal del Este.

communities differed strongly between mussel beds and sites immediately downstream, suggesting that effects of mussels differ even at this small scale.

Differences in benthic communities between hard substrates in mussel beds and soft substrates at downstream sites could largely reflect vastly different habitat characteristics. In the Río Paraná delta, *L. fortunei* is the most abundant macroinvertebrate, both in abundance and biomass, on hard substrates. This mussel has occupied an essentially vacant niche and has spread rapidly and colonized hard substrata throughout the area and provides a continuous microenvironment to the associated organisms (Boltovskoy et al. 2006). The recent and widespread

TABLE 3. Similarity analysis (SIMPER) for groups defined by nonmetric multidimensional scaling (NMDS) and cluster analyses. *L. fortunei* beds = *Limnoperna* mussel bed samples from Río Luján and Canal del Este, downstream of *L. fortunei* = samples from sites 0 m downstream of the beds in both rivers, Río Luján = samples from sites 5 and 15 m downstream from the beds in Río Luján, Canal del Este = samples from sites 5 and 15 m downstream from the beds in Canal del Este. Values indicate % contribution of each taxon to the groups' similarity (only the most important taxa are presented for each group).

Taxa	*L. fortunei* beds	Downstream of *L. fortunei* (0 m)	Río Luján	Canal del Este
Oligochaeta	76.5	85.18	48.00	25.00
Nematoda	3.01	8.27	33.19	32.24
Sinelobus sp.	4.83	0.00	0.00	0.00
Heleobia piscium	4.54	3.79	0.00	0.00
Harpacticoidea	4.36	0.00	0.00	0.00
Hyalella sp.	2.49	0.00	0.00	0.00
Potamolithus sp.	1.32	0.00	10.22	10.52
Chironomidae	0.00	0.00	0.44	23.68
Culicoides sp.	0.00	0.00	0.00	4.60
Heleobia parchappei	0.00	0.00	0.00	3.29
Total	97.05	97.24	91.85	99.34

TABLE 4. Mean (SE) values of environmental variables for groups of sites defined by nonmetric multidimensional scaling and cluster analyses. *L. fortunei* beds = *Limnoperna* mussel bed samples from Río Luján and Canal del Este, downstream of *L. fortunei* = samples from sites 0 m downstream of the beds in both rivers, Río Luján = samples from sites 5 and 15 m downstream from the beds in Río Luján, Canal del Este = samples from sites 5 and 15 m downstream from the beds in Canal del Este. Only variables that best correlated with the nonmetric multidimensional scaling ordination (BEST, PRIMER v.6) were tested for statistical differences between groups (organic matter [OM], mean grain size [MGS], and depth). MGS and depth did not differ among groups. Means with the same letters are not significantly different.

Group	OM (g OM/g dry sediment)	% clay	% silt	% sand	MGS (μm)	Depth (m)
L. fortunei beds	0.38^a (0.001)	32.1 (1.6)	67.7 (1.9)	0.2 (0.3)	12.2 (0.0)	0.0 (0.0)
Downstream of *L. fortunei* (0 m)	0.033^b (0.002)	23.3 (2.1)	74.3 (0.2)	2.4 (2.0)	19.3 (3.0)	1.5 (0.0)
Río Luján	0.032^b (0.001)	11.5 (1.5)	63.4 (3.3)	25.1 (4.8)	45.4 (8.0)	2.0 (0.0)
Canal del Este	0.019^c (0.001)	16.7 (5.3)	60.7 (0.1)	22.6 (5.2)	44.2 (13.4)	6.0 (0.0)

availability of this microenvironment appears to have facilitated higher abundances of several other invertebrate taxa.

In both rivers, *L. fortunei* had positive effects on epibenthic crustaceans, large scrapers (*H. piscium*), and deposit-feeding taxa. Some predatory invertebrates, such as isopods and flatworms, also were positively affected by *L. fortunei* in Canal del Este, probably because of increased prey availability. On the other hand, density and biomass of small scrapers (*Potamolithus*), chironomidae larvae, nematodes, and ostracods were lower in the presence of *L. fortunei*, although the latter 2 groups may have been underestimated because of the sieve aperture size used. Invertebrate communities associated with *L. fortunei* largely reflect assemblages typical of rocky substrata. These organisms probably were restricted in occurrence before the invasion of *L. fortunei* because they are unable to occupy soft sediments, which dominate the Paraná delta. Mobility also may affect faunal composition in different habitats. Highly mobile epifauna may colonize mussel beds quickly (Mörtl and Rothhaupt 2003), but infaunal species, such as nematodes, are less mobile (Merritt and Cummins 1984). This lack of mobility may limit the ability of infauna to colonize and persist in *L. fortunei* beds (Ward and Ricciardi 2007). The distribution of small scrapers, such as *Potamolithus*, could result from intra- or interspecific competitive displacement by larger individuals (e.g., *H. piscium*), a behavior previously observed elsewhere (Stewart et al. 1999, Sylvester et al. 2007).

In accordance with its high filtration rates (Sylvester et al. 2005), *L. fortunei* removes large amounts of suspended organic matter from the water column and shunts C to the benthos in the form of feces and pseudofeces. Field experiments carried out in Río Luján demonstrated that sedimentation rates are increased by 3.4 to 9.6× and sediment organic content by 1.3 to 7× in the presence of *L. fortunei* than in their absence (i.e., passive physical sedimentation alone; D. Cataldo, Universidad de Buenos Aires, and PS, unpublished data). This pattern is corroborated in our study, where samples from *L. fortunei* beds had higher organic matter content and lower mean grain size, characteristic of biodeposits, than all other sites (Norkko et al. 2006).

Biodeposits are normally rich in C and N (Kautsky and Evans 1987), both of which enrich the sediments, stimulate algal and microbial growth (Grenz et al. 1990, Stoeck and Albers 2000), and thereby provide an important food resource for the surrounding benthos (Norkko et al. 2006), especially large scrapers and deposit-feeders which dominate mussel beds. The increase of these functional feeding guilds on substrates colonized by *L. fortunei* has been reported previously (Sylvester et al. 2007, Sardiña et al. 2008) and is concordant with observations from *Dreissena polymorpha* (Ward and Ricciardi 2007, Nalepa et al. 2009).

As expected, transport of organic material caused increases in abundance of deposit-feeders and scrapers at sites immediately downstream of mussel beds (0 m). However, communities differed strongly between mussel beds and sites immediately downstream. At immediately downstream sites, communities were dominated by oligochaetes and snails (*H. piscium*, limpets, and other snails), and epibenthic crustaceans were absent or scarce. These differences may be the result of lack of protection outside the mussel beds. Protection from predation via reduction of foraging efficiency of fishes and crabs in mussel beds probably plays a significant role in modulating the distribution and abundance of epibenthic fauna (Reise 1978, Stoner 1980, 1982, 1983, Lewis and Stoner 1982).

At greater distances from the colonies (i.e., 5 and 15 m), site-specific environmental conditions seemed to be the primary factor structuring faunal communities.

Differences in community structure at Río Luján and Canal del Este reflected dissimilar degrees of environmental disturbance in these rivers. Oligochaetes had the highest densities and biomass at downstream sites in Río Luján, and many species (50%) occurred only in this river. Some of these species, such as *Limnodrilus hoffmeisteri* and *Limnodrilus claparedeanus*, typically are associated with high levels of organic pollution (Lauritsen et al. 1985, Verdonschot 1996, Lang 1997, Fletcher et al. 2001). Río Luján also was characterized by comparatively low numbers of Chironomidae and the absence of Tanytarsini, which are typical of oligomesotrophic conditions. In contrast, Chironomidae were important in the cleaner and less organic-matter-enriched Canal del Este. These findings are in agreement with many studies showing that organic enrichment results in an increase of oligochaetes and a reduction of Chironomidae (Brinkhurst and Cook 1974, Milbrink 1980, Saether 1980, Mastrantuono 1986).

Ecosystem effects of L. fortunei *under different environmental conditions*

Contrary to expectations, facilitation by *L. fortunei* was stronger in Canal del Este than in Río Luján, but only in terms of invertebrate abundance. Richness, mean total abundance, and mean total biomass of benthic invertebrates tended to be higher in mussel beds than downstream of beds, but differences were not significant because of high variation among samples at Canal del Este. At Río Luján, snails (*H. piscium*) and epibenthic crustaceans (tanaidaceans, amphipods, and harpacticoid copepods) responded most markedly to *L. fortunei*-related enhancement. At Canal del Este, those taxa and oligochaetes, isopods, caddisflies, and flatworms were better represented in the mussel beds than downstream of them. These results suggest that facilitation by *L. fortunei* is highly species- and site-specific, in contrast to theory that proposes more general facilitative effects under more stressful conditions.

One of the main environmental differences brought about by *L. fortunei* is the transfer of organic matter from the water column to the surrounding sediments. In Río Luján, pollution levels are high and these biodeposits could be of lower quality than in Canal del Este and even than other organic deposits in Río Luján. Ingestion of biodeposits also might carry higher risks to other invertebrates than ingestion of sediment detritus. This increased risk may result from a selection process whereby contaminants or contaminant-rich particles are selectively rejected by mussels and deposited as pseudofeces. This redirection of contaminants could result in biomagnifications of contaminants, as previously found for zebra mussels. For example, gammarid amphipods fed hexachlorobiphenyl-contaminated zebra mussel feces had 20× higher tissue concentrations than did tissue from zebra mussels exposed to contaminated algae (Bruner et al. 1994). Other investigators have found that zebra mussel pseudofeces were equally or more polluted than ingested particles (Reeders and de Vaate 1992, Gossiaux et al. 1998).

Our results suggest that *L. fortunei* strongly affects benthic communities in the Río Paraná delta but these effects are highly variable. Like some other ecosystem engineers (Karatayev et al. 2007), *L. fortunei* may influence benthic invertebrate communities by providing refuge from predation, reducing physical stress (e.g., currents and waves), and enhancing food availability (Sylvester et al. 2007, Sardiña et al. 2008). Our results show that understanding the effect of *L. fortunei* requires accounting for scale- and species-specific effects. Temporal fluctuations in environmental conditions were not measured in our study but may result in changes in the magnitude (direction) of the interactions between *L. fortunei* and benthic communities. More detailed studies are needed to provide better understanding of the effects of *L. fortunei* under different environmental conditions that can influence the outcome of the species interactions.

Acknowledgements

We thank D. Cataldo, E. Paolucci, and A. Scilipoti for their help in the field, G. Alonso (Museo Argentino de Ciencias Naturales, Amphipoda), A. Paggi (Instituto de Limnología "Dr. Raúl A. Ringuelett" [ILPLA], Chironomidae), C. Laprida (Universidad de Buenos Aires, Ostracoda), and D. Roccatagliata (Universidad de Buenos Aires, Tanaidacea) for identification of invertebrates, and D. Boltovskoy for critical reading of our manuscript. We also thank Wendell Haag, Francisco Sylvester, and an anonymous referee for providing us with constructive comments and suggestions. This work was financed by grants PICT 25275 and PICT 01968 from the Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT) to D. Boltovskoy, and PICT 1011 from ANPCyT to PS.

Literature Cited

BENKE, A. C., A. D. HURYN, L. A. SMOCK, AND J. B. WALLACE. 1999. Length–mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society 18:308–343.

BERTNESS, M. D., AND R. CALLAWAY. 1994. Positive interactions in communities. Trends in Ecology and Evolution 9:191–193.

BERTNESS, M. D., AND G. H. LEONARD. 1997. The role of positive interactions in communities: lessons from intertidal habitats. Ecology 78:1976–1989.

BOLTOVSKOY, D., N. CORREA, D. CATALDO, J. STRIPEIKIS, AND M. TUDINO. 1997. Environmental stress on *Corbicula fluminea* (Bivalvia) in the Paraná River delta (Argentina): complex pollution-related disruption of population structures. Archiv für Hydrobiologie 138:483–507.

BOLTOVSKOY, D., N. CORREA, D. CATALDO, AND F. SYLVESTER. 2006. Dispersion and ecological impact of the invasive freshwater bivalve *Limnoperna fortunei* in the Río de la Plata watershed and beyond. Biological Invasions 8: 947–963.

BOLTOVSKOY, D., A. KARATAYEV, L. BURLAKOVA, C. CATALDO, V. KARATAYEV, F. SYLVESTER, AND A. MARIÑELARENA. 2009. Significant ecosystem-wide effects of the swiftly spreading invasive freshwater bivalve *Limnoperna fortunei*. Hydrobiologia 636:271–284.

BRINKHURST, R. O., AND D. G. COOK. 1974. Aquatic earthworms (Annellida: Oligochaeta). Pages 143–156 *in* C. W. Hart and S. L. H. Fuller (editors). Pollution ecology of freshwater invertebrates. Academic Press, New York.

BRUNER, K. A., S. W. FISHER, AND P. F. LANDRUM. 1994. The role of the zebra mussel, *Dreissena polymorpha*, in contaminant cycling. II. Zebra mussel contaminant accumulation from algae and suspended particles, and transfer to the benthic invertebrate, *Gammarus fasciatus*. Journal of Great Lakes Research 20:735–750.

BRUNO, J. F., AND M. D. BERTNESS. 2001. Habitat modification and facilitation in benthic marine communities. Pages 201–218 *in* M. D. Bertness, S. D. Gaines, and M. E. Hay (editors). Marine community ecology. Sinauer, Sunderland, Massachusetts.

BRUNO, J. F., J. J. STACHOWICZ, AND M. D. BERTNESS. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology and Evolution 18:119–125.

CATALDO, D., J. C. COLOMBO, D. BOLTOVSKOY, C. BILOS, AND P. LANDONI. 2001. Environmental toxicity assessment in the Paraná River delta (Argentina): simultaneous evaluation of selected pollutants and mortality rates of *Corbicula fluminea* (Bivalvia) early juveniles. Environmental Pollution 112:379–389.

CLARKE, K. R., AND R. N. GORLEY. 2006. PRIMERv6: user manual/tutorial. PRIMER-E, Plymouth, UK.

CLARKE, K. R., AND R. M. WARWICK. 2001. Change in marine communities: an approach to statistical analysis and interpretation. 2nd edition. PRIMER-E, Plymouth, UK.

COLWELL, R. K. 2009. EstimateS: statistical estimation of species richness and shared species from samples. Version 8.2. User's guide and application. (Available from: http://purl.oclc.org/estimates)

CROOKS, J. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97:153–166.

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

DEPETRIS, P. J., AND S. KEMPE. 1993. Carbon dynamics and sources in the Paraná River. Limnology and Oceanography 38:382–395.

DUMONT, H. J., I. VAN DE VELDE, AND D. DUMONT. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. Oecologia (Berlin) 19: 75–97.

FELLER, R. J., AND R. M. WARWICK. 1988. Energetics. Pages 181–196 *in* H. P. Higgins and H. Thiel (editors). Introduction to the study of meiofauna. Smithsonian Institution Press, Washington, DC.

FIELD, J. G., K. R. CLARKE, AND R. M. WARWICK. 1982. A practical strategy for analysing multispecies distribution patterns. Marine Ecology Progress Series 8:38–52.

FLETCHER, R., T. B. REYNOLDSON, AND D. W. TAYLOR. 2001. The use of benthic mesocosm for assessment of sediment contamination. Environmental Pollution 115:173–182.

GOSSIAUX, D. C., P. F. LANDRUM, AND S. W. FISHER. 1998. The assimilation of contaminants from suspended sediment and algae by the zebra mussel, *Dreissena polymorpha*. Chemosphere 36:3181–3197.

GREENLEE, J. T., AND R. M. CALLAWAY. 1996. Abiotic stress and the relative importance of interference and facilitation in montane bunchgrass communities in western Montana. American Naturalist 148:386–396.

GRENZ, C., M. N. HERMIN, D. BAUDINET, AND R. DAUMAS. 1990. In situ biochemical and bacterial variation of sediments enriched with mussel biodeposits. Hydrobiologia 207: 153–160.

GROSHOLZ, E. D., G. M. RUIS, C. A. DEAN, K. A. SHIRLEY, J. L. MARON, AND P. G. CONNORS. 2000. The impacts of a nonindigenous marine predator in a California bay. Ecology 81:1206–1224.

KARATAYEV, A. Y., D. BOLTOVSKOY, D. K. PADILLA, AND L. E. BURLAKOVA. 2007. The invasive bivalves *Dreissena polymorpha* and *Limnoperna fortunei*: parallels, contrasts, potential spread and invasion impacts. Journal of Shellfish Research 26:205–213.

KAUTSKY, N., AND S. EVANS. 1987. Role of biodeposition by *Mytilus edulis* in the circulation of matter and nutrients in a Baltic coastal ecosystem. Marine Ecology Progress Series 38:201–212.

KERANS, B. L., M. F. DYBDAHL, M. M. GANGLOFF, AND J. E. JANNOT. 2005. *Potamopyrgus antipodarum*: distribution, density, and effects on native macroinvertebrate assemblages in the Greater Yellowstone Ecosystem. Journal of the North American Benthological Society 24:123–138.

LANG, C. 1997. Oligochaetes, organic sedimentation, and trophic state: how to assess the biological recovery of sediments in lakes? Aquatic Sciences 59:26–33.

LAURITSEN, D. D., S. C. MOZLEY, AND D. S. WHITE. 1985. Distribution of oligochaetes in Lake Michigan and comments on their use as indices of pollution. Journal of Great Lakes Research 11:67–76.

LEWIS, F. G., AND A. W. STONER. 1982. Distribution of macrofauna within seagrass beds: an explanation for patterns of abundance. Bulletin of Marine Science 33: 296–304.

LODGE, D. M., R. A. STEIN, K. M. BROWN, A. P. COVICH, C. BRÖNMARK, J. E. GARVEY, AND S. P. KLOSIEWSKI. 1998. Predicting impact of freshwater exotic species on native biodiversity: challenges in spatial scaling. Australian Journal of Ecology 23:53–67.

LOEZ, C. R., AND A. SALIBIAN. 1990. Premières données sur le phytoplancton et les caractéristiques physico-chimiques du Río Reconquista (Buenos Aires, Argentine). Une rivière urbaine polluée. Revue d'Hydrobiologie Tropicale 23:283–296.

MASTRANTUONO, L. 1986. Littoral sand zoobenthos and its relation to organic pollution in Lake Nemi (Central Italy). Hydrobiological Bulletin 19:171–178.

MERRITT, R. W., AND K. W. CUMMINS (EDITORS). 1984. An introduction to the aquatic insects of North America. 2nd edition. Kendall/Hunt, Dubuque, Iowa.

MEYER, E. 1989. The relationship between body length parameters and dry mass in running water invertebrates. Archiv für Hydrobiologie 117:191–203.

MILBRINK, G. 1980. Oligochaete communities in pollution ecology: the European situation with the special reference to lakes in Scandinavia. Pages 433–455 *in* R. O. Brinkhurst and D. G. Cook (editors). Aquatic Oligochaeta biology. Plenum Press, New York.

MÖRTL, M., AND K. O. ROTHHAUPT. 2003. Effects of adult *Dreissena polymorpha* on settling juveniles and associated macroinvertebrates. International Review of Hydrobiology 88:561–569.

NALEPA, T. F., S. A. POTHOVEN, AND D. L. FANSLOW. 2009. Recent changes in benthic macroinvertebrate populations in Lake Huron and impact on the diet of lake whitefish (*Coregonus clupeaformis*). Aquatic Ecosystem Health and Management 12:2–10.

NORKKO, A., J. E. HEWITT, S. F. THRUSH, AND G. A. FUNNEL. 2006. Conditional outcomes of facilitation by a habitat-modifying subtidal bivalve. Ecology 87:226–234.

NYSTRÖM, P., O. SVENSSON, B. LARDNER, C. BRÖNMARK, AND W. GRANÉLI. 2001. The influence of multiple introduced predators on a littoral pond community. Ecology 82: 1023–1039.

PAOLUCCI, E. M., E. V. THUESEN, D. CATALDO, AND D. BOLTOVSKOY. 2010. Veligers of an introduced bivalve, *Limnoperna fortunei*, are a new food resource that enhances growth of larval fish in the Paraná River (South America). Freshwater Biology 55:1831–1844.

PARKER, I. M., D. SIMBERLOFF, W. M. LONSDALE, K. GOODELL, M. WONHAM, P. M. KAREIVA, M. H. WILLIAMSON, B. VON HOLLE, P. B. MOYLE, J. E. BYERS, AND L. GOLDWASSER. 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions 1: 3–19.

PASTORINO, G., G. DARRIGRAN, S. MARTIN, AND L. LUNASCHI. 1993. *Limnoperna fortunei* (Dunker, 1957) (Mytilidae) nuevo bivalvo invasor en aguas del Río de la Plata. Neotrópica 39:101–102.

PAVLOV, A. M., AND I. M. ZUBINA. 1990. Relationship of weight to body dimensions in dragonfly larvae. Hydrobiological Journal 26:99–103.

RAHEL, F. J. 2002. Homogenization of freshwater faunas. Annual Review of Ecology and Systematics 33:291–315.

REEDERS, H. H., AND A. B. DE VAATE. 1992. Bioprocessing of polluted suspended matter from the water column by the zebra mussel (*Dreissena polymorpha*). Hydrobiologia 239:53–63.

REISE, K. 1978. Experiments on epibenthic predation in the Wadden Sea. Helgoland Marine Research 31:55–101.

RICCIARDI, A. 2003. Predicting the impacts of an introduced species from its invasion history: an empirical approach applied to zebra mussel invasions. Freshwater Biology 48:972–981.

RICCIARDI, A., AND H. J. MACISAAC. 2000. Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. Trends in Ecology and Evolution 15:62–65.

RILEY, L. A., M. F. DYBDAHL, AND R. O. HALL. 2008. Invasive species impacts: asymmetric interactions between invasive and endemic freshwater snails. Journal of the North American Benthological Society 27:509–520.

ROJAS MOLINA, F., AND S. JOSÉ DE PAGGI. 2008. Zooplankton in the Paraná River floodplain (South America) before and after the invasion of *Limnoperna fortunei* (Bivalvia). Wetlands 28:695–702.

SAETHER, O. A. 1980. The influence of eutrophication on deep lake benthic invertebrate communities. Progress in Water Technology 12:161–180.

SAKAI, A. K., F. W. ALLENDORF, J. S. HOLT, D. M. LODGE, J. MOLOFSKY, K. A. WITH, S. BAUGHMAN, R. J. CABIN, J. E. COHEN, N. C. ELLSTRAND, D. E. MCCAULEY, P. O'NEIL, I. M. PARKER, J. N. THOMPSON, AND S. G. WELLER. 2001. The population biology of invasive species. Annual Review of Ecology and Systematics 32:305–332.

SALA, O. E., F. S. CHAPIN, J. J. ARMESTO, E. BERLOW, J. BLOOMFIELD, R. DIRZO, E. HUBER-SANWALD, L. F. HUENNEKE, R. B. JACKSON, A. KINZIG, R. LEEMANS, D. M. LODGE, H. A. MOONEY, M. OESTERHELD, N. L. POFF, M. T. SYKES, B. H. WALKER, M. WALKER, AND D. H. WALL. 2000. Global biodiversity scenarios for the year 2100. Science 287: 1770–1774.

SARDIÑA, P., D. CATALDO, AND D. BOLTOVSKOY. 2008. The effects of the invasive mussel, *Limnoperna fortunei*, on associated fauna in South American freshwaters: importance of physical structure and food supply. Fundamental and Applied Limnology 173:135–144.

SIMON, K. S., AND C. R. TOWNSEND. 2003. Impacts of freshwater invaders at different levels of ecological organization, with emphasis on salmonids and ecosystem consequences. Freshwater Biology 48:982–994.

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

STEWART, T. W., J. G. MINER, AND R. L. LOWE. 1999. A field experiment to determine *Dreissena* and predator effects on zoobenthos in a nearshore, rocky habitat of western Lake Erie. Journal of the North American Benthological Society 18:488–498.

STITES, D. L., A. C. BENKE, AND D. M. GILLESPIE. 1995. Population dynamics, growth, and production of the Asiatic clam, *Corbicula fluminea*, in a blackwater river.

Canadian Journal of Fisheries and Aquatic Sciences 52: 425–437.

STOECK, T., AND B. P. ALBERS. 2000. Microbial biomass and activity in the vicinity of a mussel bed built up by the blue mussel *Mytilus edulis*. Helgoland Marine Research 54:39–46.

STONER, A. W. 1980. Perception and choice of substratum by epifaunal amphipods associated with seagrasses. Marine Ecology Progress Series 3:105–111.

STONER, A. W. 1982. The influence of benthic macrophytes on the foraging behavior of pinfish, *Lagodon rhomboides* (Linneaus). Journal of Experimental Marine Biology and Ecology 58:271–284.

STONER, A. W. 1983. Distributional ecology of amphipods and tanaidaceans associated with three seagrass species. Journal of Crustacean Biology 3:505–518.

STRAYER, D. L. 1999. Effects of alien species on freshwater mollusks in North America. Journal of the North American Benthological Society 18:74–98.

SYLVESTER, F., D. CATALDO, AND D. BOLTOVSKOY. 2007. The invasive bivalve *Limnoperna fortunei* enhances benthic invertebrate densities in South America floodplain rivers. Hydrobiologia 289:15–27.

SYLVESTER, F., J. DORADO, D. BOLTOVSKOY, A. JUÁREZ, AND D. CATALDO. 2005. Filtration rates of the invasive pest bivalve *Limnoperna fortunei* as a function of size and temperature. Hydrobiologia 534:71–80.

VERDONSCHOT, P. F. M. 1996. Oligochaetes and eutrophication: an experiment over four years in outdoor mesocosms. Hydrobiologia 334:169–183.

VITOUSEK, P. M., C. M. D'ANTONIO, L. L. LOOPE, AND R. WESTBROOKS. 1996. Biological invasions as global environmental change. American Scientist 84:218–228.

WARD, J. M., AND A. RICCIARDI. 2007. Impacts of *Dreissena* invasions on benthic macroinvertebrate communities: a meta-analysis. Diversity and Distributions 13:155–165.

WARD, J. M., AND A. RICCIARDI. 2010. Community-level effects of co-occurring native and exotic ecosystem engineers. Freshwater Biology 55:1803–1817.

Received: 20 December 2010
Accepted: 27 July 2011

APPENDIX. Mean (SE) total individuals (ind.)/m^2 of the taxa found in Río Luján (L) and Canal del Este (CE) in the lower delta of the Río Paraná. Species-specific data for nematodes, oligochaetes, amphipods, and chironomids are presence/absence (+/−) only. LBED and CEBED = samples taken from *Limnoperna fortunei* beds; L0 and C0 = samples taken at 0 m downstream of *L. fortunei* beds; L5, L15, CE5, and CE15 = samples taken at 5 m and 15 m downstream of *L. fortunei* beds. At L0 only 1 sample was obtained, so SE could not be calculated for this site.

Taxon	LBED	L0	L5	L15	CEBED	CE0	CE5	CE15
Nematoda	379.8 (191.1)	3720.9 (−)	39,806.2 (18,101.3)	8682.2 (3100.8)	1629.6 (412.4)	930.2 (0.0)	1899.2 (786.7)	2403.1 (387.6)
Tobrilus sp.	+	−	+	−	−	−	−	−
Tripyla sp.	−	+	+	+	+	+	−	−
Ironus sp.	−	−	−	−	−	−	+	−
Aquatides sp.	−	+	−	−	−	−	−	−
Longidorus sp.	−	−	−	−	−	−	−	+
Aetholaimus sp.	−	−	−	+	−	−	−	−
Actinca sp.	−	−	−	−	−	−	−	+
Aporcelaimellus sp.	−	−	−	−	−	−	−	+
Qudsianematinae	−	−	−	−	−	−	−	+
Xiphidorus sp.	−	−	−	−	−	−	−	+
Mermithidae	−	−	+	−	−	+	+	+
Hexamermis sp.	−	−	−	−	−	−	+	+
Amphimermis sp.	−	−	−	−	−	+	−	−
Mononchus sp.	−	−	+	−	−	−	−	+
Cobbonchus sp.	−	−	−	−	−	+	−	−
Mylonchulus sp.	−	−	−	−	+	−	−	−
Panagrolaimus sp.	+	−	−	−	−	−	−	−
Monhystera sp.	−	−	+	−	−	−	−	−
Anonchus sp.	−	−	+	+	−	−	+	+
Aphanolaimus sp.	−	+	−	−	−	−	−	−
Plectidae	−	−	+	−	−	−	−	−
Annelida								
Oligochaeta	37,638.5 (12,275.3)	17,209.3 (−)	30,736.4 (3332.7)	12,558.1 (4724.7)	9666.7 (2524.8)	9573.6 (3721.1)	2635.7 (476.3)	1472.9 (1141.9)
Limnodrilus hoffmeisteri	−	+	−	+	−	−	−	−
Limnodrilus claparedeanus	−	−	−	+	−	−	−	−
Paranadrilus descolei	−	−	−	−	−	+	−	−
Aulodrilus pigueti	−	−	−	+	−	−	−	−
Aulodrilus limnobius	−	+	−	−	−	−	−	−
Immature	−	−	−	+	−	+	+	−
Tubificinae								
Pristina americana	−	−	+	+	−	−	−	−
Pristina leidyi	+	−	−	−	+	−	−	−
Pristina aequiseta	−	−	−	−	+	−	−	−
Pristina osborni	+	−	−	−	−	−	−	−
Pristina acuminata	−	−	+	−	−	−	−	−

APPENDIX. Continued.

Taxon	LBED	L0	L5	L15	CEBED	CE0	CE5	CE15
Pristina jenkinae	−	−	+	−	−	−	+	+
Nais variabilis	+	−	−	−	+	−	−	−
Nais communis	−	−	−	−	+	−	−	−
Dero nivea	+	−	−	−	−	−	−	−
Dero multibranchiata	−	−	−	+	−	−	−	−
Stephensoniana trivandrana	−	+	−	−	−	−	−	−
Enchytraeidae	+	−	−	−	−	−	−	−
Megadrili	+	−	−	−	−	−	−	−
Hirudinea	202.0 (202.0)	0.0	426.4 (271.3)	775.0 (559.0)	296.3 (296.3)	0.0	77.5 (77.5)	38.8 (38.8)
Mollusca								
Bivalvia:*Corbicula fluminea*	0.0	116.3 (−)	155.0 (38.8)	426.4 (369.7)	0.0	348.8 (348.8)	38.8 (38.8)	0.0
Gastropoda								
Potamolithus sp.	1084.1 (525.3)	0.0	8682.2 (1240.3)	2674.4 (1347.7)	166.7 (84.9)	0.0	1860.5 (710.5)	620.2 (620.2)
Heleobia piscium	1084.1 (525.3)	6046.5 (−)	0.0	0.0	574.1 (129.6)	426.4 (369.7)	116.3 (116.3)	0.0
Heleobia parchappei	0.0	0.0	0.0	0.0	0.0	0.0	193.8 (102.5)	310.1 (310.1)
Planorbidae	0.0	2325.6 (−)	0.0	0.0	0.0	155.0 (155.0)	0.0	0.0
Ancylidae:*Gundlachia* sp.	348.7 (174.5)	1860.5 (−)	0.0	155.0 (155.0)	0.0	38.8 (38.8)	0.0	0.0
Crustacea								
Tanaidacea:*Sinelobus* sp.	27,203.1 (7515.9)	0.0	0.0	0.0	611.1 (361.5)	348.8 (177.6)	0.0	0.0
Amphipoda	2489.5 (692.1)	0.0	0.0	0.0	314.8 (66.8)	0.0	0.0	0.0
Hyalella sp. 1	+	−	−	−	−	−	−	−
Hyalella sp. 2	−	−	−	−	+	−	−	−
Isopoda	170.9 (170.9)	0.0	0.0	0.0	240.7 (18.5)	0.0	0.0	0.0
Copepoda								
Calanoidea	0.0	4651.2 (−)	4961.2 (4961.2)	620.2 (620.2)	74.1 (74.1)	0.0	0.0	0.0
Cyclopoida	0.0	0.0	0.0	0.0	0.0	0.0	232.6 (134.3)	0.0
Harpacticoidea	550.7 (28.3)	0.0	0.0	0.0	1463.0 (796.3)	0.0	155.0 (155.0)	0.0
Cladocera:Sididae	0.0	0.0	3720.9 (2148.3)	620.2 (620.2)	0.0	0.0	0.0	0.0
Ostracoda: *Cyprideis hartmanni*	0.0	0.0	310.1 (310.1)	7286.8 (1378.0)	0.0	0.0	0.0	0.0
Insecta								
Diptera								
Ceratopogonidae: *Culicoides* sp.	0.0	0.0	0.0	0.0	0.0	155.0 (155.0)	271.3 (168.9)	310.1 (310.1)
Chironomidae	0.0	0.0	116.3 (0.0)	620.2 (620.2)	0.0	77.5 (77.5)	1395.3 (348.8)	1860.5 (805.6)

APPENDIX. Continued.

Taxon	LBED	L0	L5	L15	CEBED	CE0	CE5	CE15
Chironominae								
Tanytarsini	−	−	−	−	−	−	+	+
Polypedilum sp.	−	−	−	+	−	−	−	+
Cryptochironomus sp.	−	−	−	−	−	−	+	+
Tanypodinae: *Coelotanypus* sp.	−	−	+	−	−	−	+	−
Ephemeroptera	0.0	0.0	0.0	0.0	92.6 (92.6)	0.0	0.0	0.0
Odonata: *Phyllocycla argentina*	0.0	0.0	0.0	0.0	0.0	38.8 (38.8)	0.0	0.0
Coleoptera	0.0	0.0	0.0	0.0	185.2 (185.2)	0.0	0.0	0.0
Trichoptera	0.0	0.0	0.0	0.0	333.3 (111.1)	0.0	0.0	0.0
Hydracarina	355.6 (355.6)	1860.5 (−)	0.0	0.0	0.0	0.0	155.0 (155.0)	0.0
Hydrozoa	0.0	0.0	0.0	0.0	74.1 (74.1)	0.0	0.0	0.0
Turbellaria	0.0	0.0	0.0	0.0	314.8 (66.8)	0.0	0.0	0.0
Total	71,507.1 (4818.1)	37,791 (−)	88,914.7 (27,989.6)	34,418.4 (8167.2)	16,037.0 (3140.3)	12,093.0 (3837.8)	9031.0 (2602)	7015.5 (2144.4)