

LIMNOPERNA FORTUNEI VERSUS DREISSENA POLYMORPHA: POPULATION DENSITIES AND BENTHIC COMMUNITY IMPACTS OF TWO INVASIVE FRESHWATER BIVALVES

ALEXANDER Y. KARATAYEV,^{1*} LYUBOV E. BURLAKOVA,^{1,2} VADIM A. KARATAYEV³ AND DEMETRIO BOLTOVSKOY⁴

¹Great Lakes Center, Buffalo State College, 1300 Elmwood Avenue, Buffalo, NY 14222; ²The Research Foundation of The State University of New York, Buffalo State College, Office of Sponsored Programs, 1300 Elmwood Avenue, Bishop Hall B17, Buffalo, NY 14222-1095; ³City Honors School, 186 East North Street, Buffalo, NY 14204; ⁴Department of Ecology, Genetics and Evolution, University of Buenos Aires, C1428EHA Buenos Aires; Consejo Nacional de Investigaciones Científicas y Técnicas, and Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Argentina

ABSTRACT In this study, for the first time, using similar methods, we compared the population density and distribution across different substrate types of *Limnoperna fortunei* and *Dreissena polymorpha*, as well as their impacts on the composition of benthic communities. Data on *L. fortunei* were obtained in Rio Tercero Reservoir, Argentina, whereas studies on *D. polymorpha* were conducted in North America and Europe. We found that, similar to the zebra mussel, *L. fortunei* creates high densities on hard substrates in the littoral zone, and avoids soft substrates in the profundal zone; however, the overall population density of *L. fortunei* in a water body seems to be higher than that of zebra mussels. Additional studies on *Limnoperna* are needed to confirm this hypothesis. The effect of *L. fortunei* on macrobenthos is very similar to the effect of *D. polymorpha* and is associated with an increase in the overall diversity, density, and biomass of native macroinvertebrates in druses compared with bare sediments. The presence of *L. fortunei* druses in the littoral zones of Rio Tercero has increased the average species richness of native benthic invertebrates per sample by almost 70% and their density and biomass by threefold, positively affecting epifaunal organisms and negatively burrowing invertebrates and unionids. In the near future, the freshwaters of North America may be colonized by *L. fortunei*, resulting in strong impacts on entire invaded ecosystems and devastating impacts on native unionids, especially in the southern regions of the United States, which are not colonized with dreissenids.

KEY WORDS: invasive species, *Limnoperna fortunei*, zebra mussel, *Dreissena polymorpha*, distribution, density, impacts on zoobenthos

INTRODUCTION

The strong ecological and economic impacts of the zebra mussel (*Dreissena polymorpha* (Pallas, 1771)), well documented both in Europe and in North America, make this mollusc the most aggressive freshwater invader in the northern hemisphere (reviewed in Karatayev et al. 1997, O'Neill 1997, Karatayev et al. 2002, Karatayev et al. 2007b). Much less information is available on the other invasive byssate bivalve, the golden mussel (*Limnoperna fortunei* Dunker, 1857). *L. fortunei* is a freshwater mytilid native to mainland China that was introduced into Hong Kong, Taiwan, and Japan between 1965 and 1990 (Morton 1975, Nakai 1995). In 1989 to 1990, *L. fortunei* invaded South America (Pastorino et al. 1993), where it has already spread across Argentina, Uruguay, Paraguay, Bolivia, and Brazil, having significant economic and ecological impacts (Boltovskoy et al. 2006, Boltovskoy et al. 2009). The overall impacts of both species on the areas invaded are scale dependent and are determined by the number of water bodies colonized (regional scale) and the population density in each of them (water body scale). Different factors govern the spread and distribution of *L. fortunei* and *D. polymorpha* at different spatial scales, affecting their population densities and environmental impacts (Karatayev et al. 2007b). Both species have similar length (typically approximately 20–30 mm; maximum, about 42–46 mm), and usually live about 3–4 y (reviewed in

Karatayev et al. 2007a). They are sessile suspension feeders with a planktonic larval stage and high reproductive capacity, which allows them to colonize large areas quickly, producing significant local and systemwide effects (reviewed in Karatayev et al. 2007a, Karatayev et al. 2007b). Although the local effects are chiefly associated with their ability to form aggregations (druses) and physically change substrates, providing shelter and food for other benthic organisms, the systemwide effects are associated with their filtering activities. Being powerful suspension feeders, they greatly enhance benthic–pelagic coupling in the ecosystems they invade (reviewed in Karatayev et al. 1997, Darrigran 2002, Karatayev et al. 2002, Vanderploeg et al. 2002, Boltovskoy et al. 2006, Karatayev et al. 2007a, Boltovskoy et al. 2009). Because both local and systemwide effects depend primarily on the presence and activity of individual organisms, the magnitude of the overall impact strongly correlates with their population densities. Therefore, information on their distribution and abundance is critically important for understanding and predicting their ecological impacts. Although for *Dreissena* such surveys are numerous (e.g., reviewed in Karatayev et al. 1998, Patterson et al. 2005, Burlakova et al. 2006), for *Limnoperna*, information on population densities over large areas is restricted to a single comprehensive survey (Boltovskoy et al. 2009), all other abundance data being isolated records of peak densities (Darrigran 2002, Boltovskoy et al. 2006). Although this constraint imposes limitations on comparisons between the 2 bivalves, the fact that we have had extensive experience with both species and used similar methods allows us to address several

*Corresponding author. E-mail: karatay@buffalostate.edu

key issues involving parallels and contrasts between these mussels. In this study we compare the population density and distribution across different substrate types of *L. fortunei* and *D. polymorpha*, as well as their impacts on the composition of benthic communities.

METHODS

Limnoperna fortunei Distribution

Samples were collected in Embalse Río Tercero, a medium-size reservoir located in Córdoba Province, central Argentina (32°11'S, 64°13'W). The surface area of the reservoir is 47 km², its average depth is 10.1 m, and its volume is 0.48 km³ (Boltovskoy et al. 2009). The reservoir was built in 1936 for hydroelectric power supply, and became a cooling reservoir for a 600-MW nuclear power plant in 1983. Large water-level fluctuations (up to 10 m) were typical for this water body before 1983. After the nuclear power plant was built, these fluctuations were substantially reduced, although during dry periods more than 17% of the reservoir bottom is occasionally exposed to air (Mariazzi et al. 1992). The littoral zone is dominated by rocks and sand, whereas deeper areas are mostly covered with mud. At the time of sampling, macrophytes were scarce, most likely because of the high water-level fluctuations.

All samples used to determine the distribution and abundance of *L. fortunei* were collected in December 2006 along 18 transects as a part of a larger survey (Boltovskoy et al. 2009). All transects were initiated on the shore and ran perpendicularly to the shore toward the center of the reservoir. Transects were distributed based on bathymetry and types of bottom sediments to represent all major habitat types adequately (Boltovskoy et al. 2009). For each transect, samples were collected from 3–10 sites at depths ranging from 2–19 m. Shallower areas were not sampled because all mussels in depths of less than 3 m were dead as a result of a recent drawdown. Each sample was collected by a scuba diver who retrieved all the specimens encompassed by a 50 × 50-cm metal frame (0.25 m² area quadrat) randomly placed from the boat. On hard bottoms, all rocks with mussels encompassed by the quadrat were removed or, when they were immobile or too large to remove, all adhering mussels were detached manually. On soft bottoms, the surface sediments within each quadrat down to 5 cm were examined and all mussels removed. Within 48 h of sampling, mussels were counted and weighed to the nearest 0.01 g, after removing water from their mantle cavity (wet weight, soft tissue plus shell).

Dreissena polymorpha Distribution

To compare the population densities and distribution of *L. fortunei* with *D. polymorpha* statistically, we needed primary data from other water bodies colonized by *D. polymorpha* obtained with similar methods of collection. Therefore, we used data obtained during our previous study in Belarus with a very similar experimental design and collection methods (Karatayev 1983, Burlakova et al. 2006). For these studies, *Dreissena* samples were collected from the glacial lakes Lukomskoye (data collected in 1978), Naroch (1993 to 1995, 1997, 2002), Myastro (1993, 1995, 2002), Batorino (1993, 1995, 2002), and Reservoir Drozdy (1995; Table 1). Lake Lukomskoye was sampled in July 1978 along 14 transects. For each transect, samples were collected at 0.5, 1, 2, 3, 4, 5, 6 m using scuba gear, and on silt sub-

strates at 8 m using an Eckman grab (Karatayev 1983). The Eckman grab was very effective for sampling silt sediments, where only occasionally small *Dreissena* druses were found. Lakes Naroch, Myastro, and Batorino were sampled each year in July or August. We sampled 8 transects in Lake Naroch and 5 transects in lakes Myastro and Batorino. For each transect in these 3 lakes, up to 10 replicate samples were collected at 0.5-, 1-, 1.5-, 2-, and 3-m depths, and then at an interval of 1 or 2 m down to the maximum depth where *D. polymorpha* was found. At less than 8 m, samples were collected by divers based on a 0.25-m² quadrat, whereas at deeper sites on silt substrates an Eckman grab was used. A detailed description of our *Dreissena* sampling protocol was published previously (Karatayev 1983, Burlakova et al. 2006). Similarly to the *L. fortunei* study, all *D. polymorpha* samples were washed through a 550- μ m mesh, and within 48 h of sampling all zebra mussels larger than 1 mm in shell length were counted, opened with a scalpel to remove water from the mantle cavity, and the entire sample was weighed to the nearest 0.01 g after blotting dry on absorbent paper (wet weight, soft tissue plus shell) (Burlakova et al. 2006).

Impact on the Benthic Community

The impact of *L. fortunei* on the benthic community was studied in Río Tercero Reservoir in Córdoba, Argentina, in December 2006. Twenty samples were collected at 3.5 m depth on silty sand within the same 5 × 10-m area: 10 samples of *L. fortunei* aggregations (druses) and 10 samples of bare sediments (without *L. fortunei* druses). *L. fortunei* druses were collected with their substrates by a diver, placed in zip-locked bags, and brought to the surface. Benthic samples were collected with a tube dredge sampler 7.2 cm in diameter (surface area, 0.004 m²). All samples were washed through a 500- μ m sieve and fixed with 10% buffered formaldehyde. All organisms from all samples were identified to the lowest possible taxonomic level, counted, and weighed after blotting dry on absorbent paper (total wet weight). Druse surface area was estimated as the projection on the surface; the mean area of the druses analyzed was 0.0058 ± 0.002 m².

To compare the effect of *L. fortunei* on benthic invertebrates with those of *D. polymorpha*, we used our data obtained in June 2007 in Lower Nashotah Lake, Wisconsin. In this lake we collected 12 samples at 2.5 m depth on silty sand within a single 5 × 10-m area, including 6 samples of *Dreissena* druses and 6 samples of bare sediments. Samples were analyzed using the same protocol as for *L. fortunei*.

Statistical Analyses

The average mass of the mussels in a sample was calculated as the ratio between the total mass of the animals and their number in the sample. To compare the average mass, density, and biomass of *D. polymorpha* and *L. fortunei*, we used Kruskal-Wallis tests (because many samples contained no mussels; density = 0), separately for each substrate (Zar 1996), and multiple comparisons of mean ranks for all groups. All statistical tests were performed with the aid of Statistica software (STATISTICA version 6, StatSoft, Inc.). Effects were considered statistically significant at $P < 0.05$. When multiple tests were conducted on the same data, we used a sequential Bonferroni correction to adjust the critical alpha considered for statistical significance.

TABLE 1.

Limnoperna fortunei and *Dreissena polymorpha* densities (per square meter), and total wet biomass (grams per square meter) across different substrates in water bodies in Argentina and in Belarus.

Water Body	Substrate				
	Rocks	Gravel	Sand	Silty Sand	Silt
<i>Limnoperna fortunei</i> (Argentina)					
Rio Tercero Reservoir					
Density	3,909 ± 917 (14)	3,938 ± 1,121 (6)	1,302 ± 1,046 (7)	1,007 ± 596 (10)	29 ± 27 (31)
Biomass	2,302 ± 508 (100)	2,859 ± 945 (100)	576 ± 456 (71)	554 ± 298 (90)	24 ± 23 (7)
<i>Dreissena polymorpha</i> (Belarus)					
Lake Lukomskoye					
Density	NR	NR	267 ± 90 (32)	3,620 ± 1,091 (16)	140 ± 57 (37)
Biomass			55 ± 16 (69)	1,055 ± 255 (100)	69 ± 27 (41)
Lake Naroch					
Density	2,206 ± 378 (22)	1,456 ± 296 (6)	119 ± 39 (215)	NR	116 ± 60 (42)
Biomass	804 ± 163 (100)	378 ± 148 (100)	31 ± 9 (25)		26 ± 14 (10)
Lake Myastro					
Density	1,644 ± 806 (4)	248 ± 25 (3)	699 ± 340 (12)	NR	91 ± 91 (22)
Biomass	1,024 ± 567 (100)	72 ± 11 (100)	402 ± 231 (58)		56 ± 56 (5)
Lake Batorino					
Density	NR	NR	965 ± 517 (6)	NR	43 ± 41 (29)
Biomass			215 ± 97 (50)		13 ± 13 (7)
Drozdy Reservoir					
Density	4,048 ± 1,552 (2)	2,281 ± 954 (6)	5,829 ± 2,808 (6)	808 ± 664 (4)	0 (7)
Biomass	845 ± 303 (100)	1,065 ± 466 (100)	2,310 ± 891 (69)	470 ± 403 (100)	
All water bodies					
Density	2,257 ± 339 (28)	1,545 ± 427 (15)	307 ± 85 (271)	3,058 ± 913 (20)	97 ± 29 (137)
Biomass	839 ± 147 (100)	591 ± 214 (100)	105 ± 30 (34)	938 ± 221 (100)	38 ± 13 (16)
<i>P</i> Kruskal-Wallis test					
Density	0.31	0.073	0.030	0.035	0.177
Biomass	0.055	0.024*	0.017*	0.159	0.190

* Significant at $P < 0.025$ (Kruskal-Wallis test with Bonferroni correction).

Cell values are means ± SE of sample size (top number) and percent of quadrats with zebra mussels (bottom number in parentheses). Tests of significance (Kruskal-Wallis test) compared the density and biomass of *D. polymorpha* and *L. fortunei*. NR, not recorded.

(Rice 1989). When appropriate, we present the critical alpha with the results of each statistical test.

Macroinvertebrate community structures were assessed using macroinvertebrate abundance (density, measured in individuals per square meter; and biomass, measured in grams per square meter) and diversity indices. PRIMER 6 version 6.1.6, Primer E-Ltd.) was used to analyze differences in benthic communities. To assess and visualize differences between macroinvertebrate community composition, we used nonmetric multidimensional scaling, which calculates a set of metric coordinates for samples, most closely approximating their nonmetric distances (Legendre & Legendre 1998). The sample-to-sample similarity of macroinvertebrate community composition (density and biomass) was assessed with the aid of the Bray-Curtis index (Bray & Curtis 1957, Clarke 1993) based on square root transformed abundance data. Differences between assemblages were assessed by analysis of similarities (ANOSIM). ANOSIM is a resampling technique that uses permutation/randomization methods on Bray-Curtis similarity matrices to identify differences among groups of samples with subsequent pairwise comparisons (Clarke 1999). The SIMPROF test routine was used to test for structure in the data. To characterize diversity in druse and sediment communities, we used the univariate Margalef's index of species richness; to describe the variability in the multivariate structure of these communities, we used relative multivariate dispersion. The compar-

ative index of multivariate dispersion (Warwick & Clarke 1993) was calculated as a measure of increased variability between druse and sediment communities; this index varies between 0 (no difference) and 1 (maximum difference).

RESULTS

Distribution Within a Water Body

L. fortunei was found in 36 of the 68 samples obtained. Densities and biomass of *L. fortunei* varied significantly with substrate type ($P < 0.001$, Kruskal-Wallis test), being lowest on silt, medium on sandy substrates, and very high on rocks and gravel (Tables 1 and 2). The rocky and sandy substrates were most common at 4–8.5 m, resulting in the highest densities and biomass of *L. fortunei* at these depths. Because of the recent drawdown, all *L. fortunei* found above 3 m were dead. Silty bottoms were generally barren of *L. fortunei*, except for isolated druses formed around solid objects lying on the sediment, such as wood debris, bottles, and so forth, that occasionally were very large. In fact, one of the largest druses recorded was found on silt below 10 m, on a plastic bottle. On sandy substrates we found numerous *L. fortunei* druses that used sand grains or small pebbles glued together with byssal threads as a substrate for their attachment (Fig. 1). At the time of our sampling, the

TABLE 2.

Limnoperna fortunei and *Dreissena polymorpha* average individual mass (total wet mass of body and shell, measured in grams, mean \pm SE) across different substrates.

Water Body	Substrate				
	Rocks	Gravel with Sand	Sand	Silty Sand	Silt
<i>Limnoperna fortunei</i>					
Río Tercero Reservoir	0.640 \pm 0.076	0.638 \pm 0.067	0.504 \pm 0.030	0.594 \pm 0.088	0.770 \pm 0.066
<i>Dreissena polymorpha</i>					
Lake Lukomskoye	NR	NR	0.290 \pm 0.056	0.357 \pm 0.041	0.402 \pm 0.075
Lake Naroch	0.452 \pm 0.139	0.242 \pm 0.043	0.373 \pm 0.033	NR	0.207 \pm 0.025
Lake Myastro	0.633 \pm 0.071	0.291 \pm 0.033	0.549 \pm 0.143	NR	0.618
Lake Batorino	NR	NR	0.256 \pm 0.051	NR	0.253 \pm 0.053
Drozdy Reservoir	0.211 \pm 0.006	0.466 \pm 0.029	0.431 \pm 0.057	0.469 \pm 0.096	NR
<i>P</i> , Kruskal-Wallis test	0.001*	0.005*	0.064	0.0162*	0.060

* Significant at $P < 0.0167$ (Kruskal-Wallis test with Bonferroni correction)/

Tests of significance (Kruskal-Wallis test) compared the average individual mass of *D. polymorpha* and *L. fortunei*.

population consisted of subadult and adult individuals. The smallest *L. fortunei* found was 2 mm; the largest was 50.5 mm long (Fig. 1).

Comparison of the distributional data for *L. fortunei* in Río Tercero Reservoir with that of *D. polymorpha* in 5 European lakes indicates that in both cases, the largest densities and wet biomass were usually found on rocks and gravel, whereas the lowest densities were always found on silt (Table 1). We found that on gravel and sand, *L. fortunei* densities and biomass were significantly higher than those of zebra mussels (Table 1). We also found that the average mass of *L. fortunei* was higher than that of *D. polymorpha* on rocks, gravel, and silty sand (Table 2).

Impacts on the Benthic Community

We found a total of 20 taxa (species and higher taxa) of macroinvertebrates in druses of *L. fortunei* (excluding *Limnoperna*), and 16 taxa in the bare sediments near the druses (Table 3). Nine taxa were found both in druses and in the sediments.

The average diversity of native benthic invertebrates per sample was significantly higher ($P < 0.0003$, *t*-test) in *L. fortunei* druses than in the sediments. Communities in bare sediments were also characterized by a much larger variability between samples; the very high index of multivariate dispersion values (0.9–1.0, Table 3) allows rejecting the null hypothesis of no differences in the variability between these communities.

The average number of species, total density, and biomass of benthic communities were significantly higher in *L. fortunei* druses ($P < 0.001$, 2-sided *t*-test, Table 3). Nearly all taxa were much more abundant in druses than in bare sediments (Table 4). Differences were especially large for gastropods, leeches, caddisflies, mayflies, and chironomids. Only oligochaetes were more abundant in the sediments than in *Limnoperna* druses.

Similarly, a significant increase in the diversity, density, and biomass of bottom invertebrates (diversity and density, $P < 0.001$; biomass, $P = 0.0023$; 2-sided *t*-test) was found in *Dreissena* druses compared with bare sediments (Tables 3 and 4). Burrowing mayflies (*Hexagenia* sp.) were found in bare sediments but not in *Dreissena* druses.



Figure 1. (A, B) A single individual (A) and druse (B) of *Limnoperna fortunei* attached to coarse sand grains glued together with byssal threads. (C) The largest *L. fortunei* found. (D) Mussels attached to live *Anodontites* sp. (E) Recently dead *Anodontites* sp. with attached *L. fortunei*.

TABLE 3.

Total and average species richness (number of taxa found), density (per square meter), wet biomass (grams per square meter), and the coefficient of variation of density (CV) of native macroinvertebrates (excluding *L. fortunei* and *D. polymorpha*) in Río Tercero Reservoir, Argentina, and Lake Lower Nashotah, Wisconsin.

Parameters	Río Tercero Reservoir		Lake Lower Nashotah	
	Sediments	<i>Limnoperna</i> Druses	Sediments	<i>Dreissena</i> Druses
Total species recorded	16	20	9	32
Species per sample	5.6 ± 0.9	10.3 ± 0.6	2.7 ± 0.8	16.5 ± 1.2
Density/m ²	4,650 ± 123	15,313 ± 284	833 ± 21	18,165 ± 156
CV of density (%)	11	8	7	4
Biomass (g/m ²)	8.91 ± 0.25	30.75 ± 0.50	2.71 ± 0.13	33.03 ± 0.30
CV of biomass (%)	11	7	14	5
Relative multivariate dispersion	1.449	0.551	1.484	0.516
IMD substrate vs. druse communities		0.908		1.0
Margalef's species richness	1.776	1.972	1.19	3.161

Cell values are means ± SE. Diversity indices (calculated on densities), including relative multivariate dispersion, index of multivariate dispersion (IMD), and Margalef's species richness are given for each community.

Assemblages of native benthic invertebrates associated with the druses differed significantly from those found in the nearby bare substrate (global $R = 0.46$, $P = 0.001$, ANOSIM; $P = 0.01$, SIMPROF test; Fig. 2). These conclusions held when we aggregated data from species to higher taxonomic levels (genus, family, order, and class, all $P = 0.001$, ANOSIM).

DISCUSSION

Population Density and Potential Systemwide Effect

The ecological impact of both *L. fortunei* and *D. polymorpha* is associated with their role as biofilters and is therefore determined by their filtration rate and the overall population density in a given water body. Being powerful suspension feeders, both species filter large volumes of water, transferring energy and material from the water column to the bottom, greatly enhancing benthic–pelagic coupling, and inducing major changes in the colonized ecosystems (reviewed in Karatayev et al. 2007a). Although for *L. fortunei* our comparisons are based on distribution and population density data from a single water body, abundant previous information indicates that, similar to *D. polymorpha*, the golden mussel clearly favors the hard substrates of the littoral zone and avoids the soft bottom of deeper areas (see review in Boltovskoy et al. 2006) (Table 1). Thus, the general pattern of distribution within a water body is generally similar for the 2 bivalves. However, because the numerical density of *L. fortunei* across all substrates combined appears to be higher than that of the zebra mussels, the overall population density of *L. fortunei* in a water body may be also higher. Furthermore, because filtration rate is tightly coupled with biomass, and because *L. fortunei* is larger than *D. polymorpha*, at similar densities it may attain higher biomass levels and is therefore a more powerful “biofilterer” than the zebra mussel. As a result, the time required for *L. fortunei* to filter a volume of water equivalent to that of the water body is often substantially shorter than that of *D. polymorpha* (Fig. 3). Thus, although further studies are needed, we anticipate that *L. fortunei* may have a stronger systemwide effect than *D. polymorpha*.

Impacts on the Benthic Community

Both European and North American studies have shown that aggregations of zebra mussels create new 3-dimensional habitats for different invertebrates, whereas their pseudofeces and feces provide an abundant food supply for detritivores (reviewed in Karatayev et al. 1997, Karatayev et al. 2002). Shelters created by *D. polymorpha* have been shown to be the primary mechanism for increased abundance of macroinvertebrates, especially snails and amphipods (Botts et al. 1996, Stewart et al. 1998). Similar to the zebra mussel, *L. fortunei* transforms a 2-dimensional surface of hard substrate into a 3-dimensional structure, altering the habitat and providing shelter and food for other benthic invertebrates (Sylvester et al. 2007, Sardiña et al. 2008). Therefore, the mechanism by which *L. fortunei* affects benthic assemblages is very similar to the one described for *D. polymorpha* (reviewed in Karatayev et al. 2002, Burlakova et al. 2005; Karatayev et al. 2007a, Karatayev et al. 2007b, Ward & Ricciardi 2007).

Dreissena druses have positive effects on the majority of native bottom invertebrates, including turbellarians, leeches, gastropods, some oligochaetes, and chironomids (Karatayev et al. 1983, Botts et al. 1996, Karatayev et al. 1997, Stewart et al. 1998). On the other hand, negative effects have been reported for several species of oligochaetes (Afanasyev 1987), and devastating effects on native unionid bivalves (reviewed in Burlakova et al. 2000). Our results show that the effects of *L. fortunei* on native benthic organisms are very similar to those of the zebra mussel (Table 3). The density of turbellarians, molluscs, leeches, mayflies, and chironomids was from 3–20 times higher in druses than in nearby sediments (Table 3). Crustaceans and caddisflies were found exclusively in *L. fortunei* druses. On the other hand, oligochaete densities were 25 times higher in the sediments than in *L. fortunei* druses (Table 3). Although we did not find any amphipods in Río Tercero, they were extremely abundant in *L. fortunei* druses collected in Río de la Plata (authors' unpublished data). Similarly to *D. polymorpha*, *L. fortunei*'s overgrowth may cause the mortality of native unionids

TABLE 4.

Density per square meter (average \pm SD) and occurrence (percent of samples with the taxon, in parentheses) of macroinvertebrates (excluding *L. fortunei* and *D. polymorpha*) in Río Tercero Reservoir, Argentina, and Lake Lower Nashotah, Wisconsin.

Taxon	Río Tercero Reservoir		Lake Lower Nashotah	
	Sediments	<i>Limnoperna</i> Druses	Sediments	<i>Dreissena</i> Druses
Turbellaria				
<i>Dugesia tigrina</i>	NR	NR	NR	840 \pm 467 (100)
<i>Planaria</i> sp.	NR	21 \pm 67 (10)	NR	29 \pm 72 (17)
Turbellaria total	NR	21	NR	869
Gastropoda				
<i>Amnicola limosus</i>	NR	NR	NR	27 \pm 66 (17)
<i>Biomphalaria</i> sp.	25 \pm 79 (10)	NR	NR	NR
<i>Gundlachia moricandi</i>	NR	172 \pm 109 (80)	NR	NR
<i>Gyraulus circumstriatus</i>	NR	NR	NR	184 \pm 157 (67)
<i>Physella</i> sp.	NR	NR	NR	966 \pm 1,034 (100)
<i>Stenophysa marmorata</i>	NR	289 \pm 322 (70)	NR	NR
Gastropoda total	25	461	NR	1177
Bivalvia				
<i>Pisidium</i> sp.	NR	NR	42 \pm 102 (17)	66 \pm 105 (33)
<i>Sphaerium</i> sp.	NR	12 \pm 36 (10)	NR	NR
Bivalvia total	NR	12	42	66
Oligochaeta				
<i>Branchiura sowerbyi</i>	50 \pm 105 (20)	NR	NR	NR
<i>Stylaria lacustris</i>	NR	NR	NR	27 \pm 66 (17)
Oligochaeta sp.	2,050 \pm 1,707 (100)	82 \pm 147 (30)	NR	570 \pm 388 (100)
Oligochaeta total	2,100	82	NR	597
Hirudinea				
<i>Glossiphonia</i> sp.	75 \pm 121 (30)	43 \pm 135 (10)	NR	NR
<i>Helobdella brasiliensis</i>	225 \pm 558 (20)	547 \pm 448 (100)	NR	NR
<i>Helobdella fusca</i>	NR	NR	NR	39 \pm 95 (17)
<i>Helobdella stagnalis</i>	325 \pm 528 (60)	4,181 \pm 2,132 (100)	NR	NR
Hirudinea total	625	4,771	NR	39
Decapoda				
<i>Aegla scamosa</i>	NR	136 \pm 295 (40)	NR	NR
Amphipoda				
<i>Hyalella azteca</i>	NR	NR	NR	2,668 \pm 1422 (100)
Ceratopogonidae				
<i>Culicoides</i> sp.	50 \pm 105 (20)	NR	NR	31 \pm 75 (17)
Chironomidae				
<i>Chironomus</i> sp.	NR	NR	167 \pm 204 (50)	27 \pm 66 (17)
<i>Cricotopus</i> sp.	NR	14 \pm 43 (10)	NR	NR
<i>Cryptochironomus</i> sp.	100 \pm 129 (40)	NR	NR	NR
<i>Dicrotendipes tritonus</i>	NR	NR	NR	1,569 \pm 661 (100)
<i>Dicrotendipes</i> sp.	50 \pm 158 (10)	3,744 \pm 1928 (100)	NR	NR
<i>Harnischia</i> sp.	150 \pm 394 (20)	NR	NR	NR
<i>Larsia</i> sp.	300 \pm 350 (60)	1,932 \pm 846 (100)	NR	158 \pm 140 (67)
<i>Microtendipes</i> gr. <i>chloris</i>	NR	205 \pm 319 (40)	NR	NR
<i>Microtendipes pedellus</i>	NR	NR	NR	2,148 \pm 953 (100)
<i>Nilothauma</i> sp.	NR	NR	NR	27 \pm 66 (17)
<i>Polypedilum halterale</i>	NR	NR	125 \pm 209 (33)	690 \pm 353 (100)
<i>Polypedilum illinoense</i>	NR	NR	NR	86 \pm 210 (17)
<i>Polypedilum</i> sp.	275 \pm 702 (30)	43 \pm 135 (10)	NR	NR
<i>Procladius</i> sp.	75 \pm 121 (30)	NR	NR	29 \pm 72 (17)
<i>Pseudochironomus</i> sp.	NR	NR	NR	347 \pm 620 (50)
<i>Tanytarsus</i> sp.	750 \pm 957 (80)	661 \pm 586 (80)	83 \pm 129 (33)	2,417 \pm 1,383 (100)
<i>Tribelos jucundus</i>	NR	NR	208 \pm 292 (50)	3,197 \pm 2,613 (100)
Chironomidae total	1,700	6,599	625	10,697
Coleoptera				
<i>Stenelmis</i> sp.	NR	NR	NR	26 \pm 65 (17)
Ephemeroptera				
<i>Caenis</i> sp.	25 \pm 79 (10)	2,382 \pm 1,576 (100)	42 \pm 102 (17)	1,257 \pm 1,083 (100)
<i>Ephemeroptera</i> sp.	NR	13 \pm 42 (10)	NR	NR

continued on next page

TABLE 4.
continued

Taxon	Río Tercero Reservoir		Lake Lower Nashotah	
	Sediments	<i>Limnoperna</i> Druses	Sediments	<i>Dreissena</i> Druses
<i>Hexagenia</i> sp.	NR	NR	83 ± 129 (33)	NR
<i>Maccaffertium mexicanum integrum</i>	NR	NR	NR	163 ± 399 (17)
Ephemeroptera total	25	2,395	125	1,419
Megaloptera				
<i>Sialis</i> sp.	NR	NR	42 ± 102 (17)	152 ± 203 (50)
Odonata				
<i>Argia</i> sp.	NR	NR	NR	167 ± 144 (67)
<i>Chromagrion</i> sp.	NR	NR	NR	60 ± 93 (33)
<i>Epitheca princeps princeps</i>	NR	NR	NR	56 ± 88 (33)
Odonata total	NR	NR	NR	283
Trichoptera				
<i>Agraylea</i> sp.	NR	21 + 66 (10)	NR	NR
<i>Cyrnellus fraternus</i>	NR	781 ± 907 (100)	NR	NR
<i>Cyrnellus</i> sp.	NR	NR	NR	27 ± 66 (17)
<i>Mystacides</i> sp.	NR	NR	NR	26 ± 65 (17)
<i>Oecetis</i> sp.	125 ± 317 (20)	NR	NR	NR
<i>Orthotrichia</i> sp.	NR	NR	NR	87 ± 151 (33)
Limnephiloidea sp.	NR	35 ± 75 (20)	NR	NR
Trichoptera total	125	837	NR	141

NR, not recorded.

(Darrigran & Drago 2000, Darrigran 2002). The only 3 unionid specimens (1 alive, 2 dead) found in our Río Tercero survey were heavily overgrown by *L. fortunei* (Fig. 1).

Although we used a different sampling protocol, our data largely agree with recent South American studies on the effects of *L. fortunei* on the associated fauna (Darrigran et al. 1998, Darrigran & Drago 2000, Sylvester et al. 2007, Sardiña et al. 2008). However, an interesting difference is that, in contrast

with these reports, our data indicate that the effect of the mussel on oligochaetes is negative (rather than positive). This difference suggests a species-specific effect, whereby different species are affected differently. Freshwater oligochaetes comprise both infaunal (burrowing), and epifaunal species; it is conceivable that the oxygen depletion associated with the large amounts of organic matter derived from the mussels' feces and pseudofeces (Sardiña et al. 2008) inhibits the development of burrowing

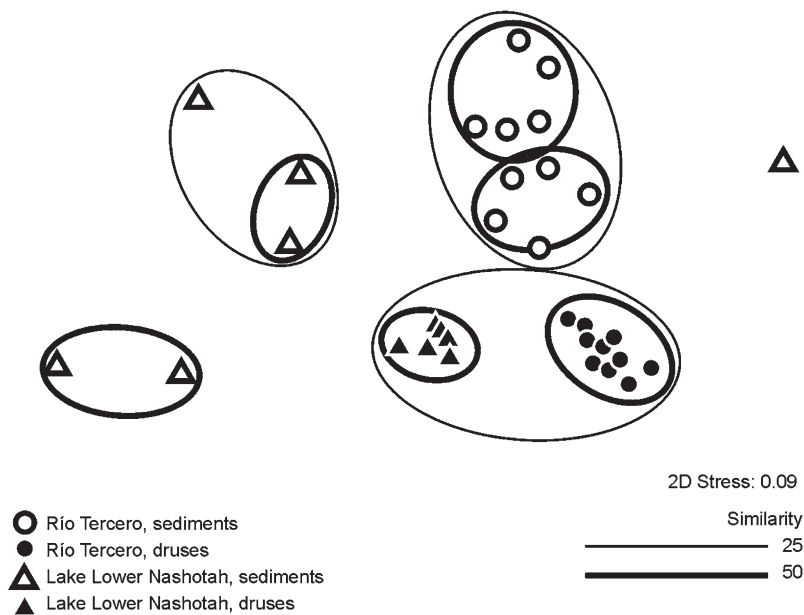


Figure 2. Nonlinear multidimensional scaling plot of benthic samples from Río Tercero Reservoir, Argentina, and Lake Lower Nashotah, Wisconsin. The samples were collected in *Dreissena polymorpha* (Lake Lower Nashotah) and *Limnoperna fortunei* (Río Tercero Reservoir) druses, and in nearby sediments. The Bray-Curtis similarity matrix used for this plot was calculated based on square root transformed density data for each taxon identified in each sample. Superimposed circles denote groups joined at 25% (fine line), and 50% (solid line) Bray-Curtis similarity.

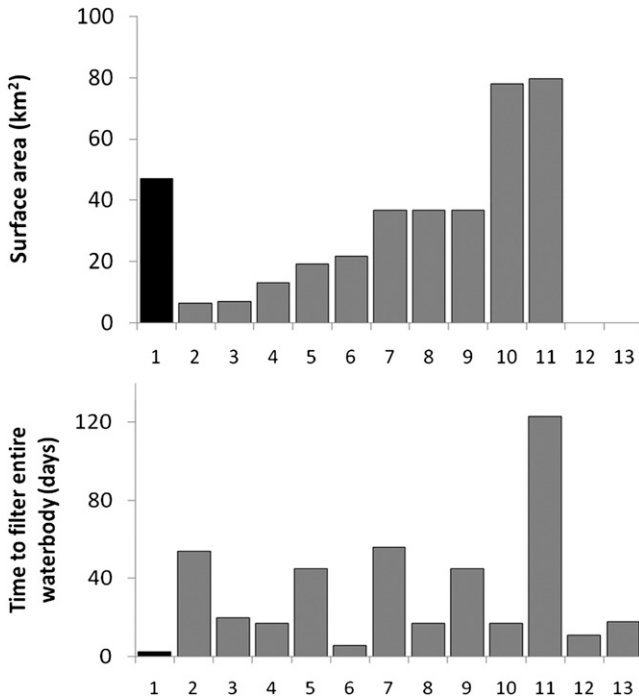


Figure 3. Estimated time for *Limnoperna fortunei* (1) and *Dreissena polymorpha* (2–13) to filter the volume of water equivalent to that of the water body. 1, Río Tercero Reservoir, Argentina, 2006 (Boltovskoy et al. 2009); 2, Lake Batorino, Belarus, 1993 (Karatayev & Burlakova 1995a); 3, Pyalovskoe Reservoir, Russia (Mikheev 1967); 4, Lake Myastro, Belarus, 1993 (Karatayev & Burlakova 1995a); 5, Uchinskoe Reservoir, Russia, 1967 (Lvova 1977); 6, cooling reservoir of Chernobyl nuclear station, Ukraine (Protasov et al. 1983); 7, Lake Lukomskoe, Belarus, 1978 (Karatayev 1983); 8, Lake Lukomskoe, Belarus, 1975 (Karatayev & Burlakova 1995b); 9, Lake Lukomskoe, Belarus, 1990 (Karatayev & Burlakova 1995b); 10, Long Point Bay, Lake Erie (Petrie & Knapton 1999); 11, Lake Naroch, Belarus, 1993 (Karatayev & Burlakova 1995a); 12, Lake Ijsselmeer, The Netherlands, 1985 (Reeders et al. 1989); 13, Lake Markermeer, The Netherlands, 1985 (Reeders et al. 1989).

species, while still providing an advantageous medium for the epifaunal forms. Incidentally, in Río Tercero Reservoir, the burrowing oligochaete *Branchiura sowerbyi* was found in the nearby sediments, but not in *L. fortunei* druses (Table 4). Similarly, in Lake Lower Nashotah, the burrowing mayfly *Hexagenia* was found in bare sediments, but not in *Dreissena* druses. Facilitation by habitat modifiers in general, and by filter-feeding bivalves in particular, is a well-known phenomenon, but effects on the benthic fauna are often modulated and even reversed by specific makeups (particularly in oligochaetes associated with mussels (Afanasiev 1987, Spooner & Vaughn 2006)), suspended sediment concentration (Norkko et al. 2006),

geographical location (Buschbaum et al. 2009), season (Spooner & Vaughn 2006), sediment characteristics (Radziejewska et al. 2009), and sometimes by more intricate relationships (multispecies interactions, nonlinear biotic/abiotic interactions, threshold effects) that elude straightforward generalizations (Cummins et al. 2001). In this case, both *L. fortunei* and *D. polymorpha*, being powerful ecosystem engineers, physically alter benthic substrates and change dramatically associated macroinvertebrate communities.

Potential Effect on North America

Although on the continental scale, as a result of temperature limits, *L. fortunei*'s northward spread in northern America may be limited when compared with that of *D. polymorpha*, in central and southern regions of North America, *Limnoperna* may colonize many more water bodies than zebra mussels (Ricciardi 1998, Karatayev et al. 2007a, Karatayev et al. 2007b, Oliveira et al. 2010). It was shown that *L. fortunei* has a much wider tolerance to several key abiotic factors than *D. polymorpha*, including upper temperature limit (35°C for *L. fortunei* vs. 33°C for *D. polymorpha*), salinity (15‰ for *L. fortunei* vs. 6‰ for *D. polymorpha*), low pH values (5.5 for *L. fortunei* vs. 7.3 for *D. polymorpha*), calcium (around 3 mg/L for *L. fortunei* vs. 25 mg/L for *D. polymorpha*), and dissolved oxygen (0.5 mg/L for *L. fortunei* vs. 1.8 mg/L for *D. polymorpha*) (reviewed in Karatayev et al. 2007a, Karatayev et al. 2007b). Thus, on a regional scale, *L. fortunei* has a clear advantage in spreading among water bodies that are too warm and/or too acidic for *D. polymorpha*. Hence, in the near future, the freshwaters of North America may be colonized by another invader that, in certain regions, may be even more aggressive than the zebra mussel. The ecological consequences of this invasion may be similar to or even stronger than those of zebra mussels, including strong positive effects on epifaunal benthos (e.g., exotic amphipods and gastropods), negative effects on burrowing organisms, and devastating impacts on native unionids. The negative effect on unionids may be especially strong in southern regions of the United States, particularly if *L. fortunei* invades soft-water habitats that serve as refuges for threatened unionids against zebra mussels infestation (Ricciardi 1998).

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LITERATURE CITED

- Afanasiev, S. A. 1987. The differences in oligochaete distribution in periphyton on substrate with different structure. In: O. L. Kachalova & E. A. Parele, editors. Water Oligochaeta. Transactions of the Sixth All-Union Symposium. Riga, Lithuania. pp. 38–41. [in Russian].
- Boltovskoy, D., N. Correa, D. Cataldo & F. Sylvester. 2006. Dispersion and ecological impact of the invasive freshwater bivalve *Limnoperna fortunei* in the Río de la Plata watershed and beyond. *Biol. Invasions* 9:947–963.
- Boltovskoy, D., A. Karatayev, L. Burlakova, D. Cataldo, V. Karatayev, F. Sylvester & A. Marinelarena. 2009. Significant ecosystem-wide effects of the swiftly spreading invasive freshwater bivalve *Limnoperna fortunei*. *Hydrobiologia* 636:271–284.
- Botts, P. S., B. A. Patterson & D. W. Schloesser. 1996. Zebra mussel effects on benthic invertebrates: physical or biotic? *J. North Am. Benthol. Soc.* 15:179–184.

- Bray, J. R. & J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27:325–349.
- Burlakova, L. E., A. Y. Karatayev & D. K. Padilla. 2000. The impact of *Dreissena polymorpha* (Pallas) invasion on unionid bivalves. *Int. Rev. Hydrobiol.* 85:529–541.
- Burlakova, L. E., A. Y. Karatayev & D. K. Padilla. 2005. Functional changes in benthic freshwater communities after *Dreissena polymorpha* (Pallas) invasion and consequences for filtration. In: R. Dame & S. Olenin, editors. The comparative roles of suspension feeders in ecosystems. NATO science series: IV: earth and environmental sciences. Vol. 47. Netherlands: Springer. pp. 263–275.
- Burlakova, L. E., A. Y. Karatayev & D. K. Padilla. 2006. Changes in the distribution and abundance of *Dreissena polymorpha* within lakes through time. *Hydrobiologia* 571:133–146.
- Buschbaum, C., S. Dittmann, J. S. Hong, I. S. Hwang, M. Strasser, M. Thiel, N. Valdivia, S. P. Yoon & K. Reise. 2009. Mytilid mussels: global habitat engineers in coastal sediments. *Helgol. Mar. Res.* 63: 47–58.
- Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* 18:117–143.
- Clarke, K. R. 1999. Non-parametric multivariate analysis in community-level ecotoxicology. *Environ. Toxicol. Chem.* 18:118–127.
- Cummins, V. J., S. F. Thrush, J. E. Hewitt & G. A. Funnell. 2001. Variable effect of a large suspension-feeding bivalve on infauna: experimenting in a complex system. *Mar. Ecol. Prog. Ser.* 209:159–175.
- Darrigran, G. 2002. Potential impact of filter feeding invaders on temperate inland freshwater environments. *Biol. Invasions* 4:145–156.
- Darrigran, G. & I. E. Drago. 2000. Invasion of the exotic freshwater mussel *Limnoperna fortunei* (Dunker, 1857) (Bivalvia: Mytilidae) in South America. *Nautilus* 114:69–73.
- Darrigran, G., S. M. Martin, B. Gullo & L. Armendariz. 1998. Macro-invertebrates associated with *Limnoperna fortunei* (Dunker, 1857) (Bivalvia, Mytilidae) in Río de la Plata, Argentina. *Hydrobiologia* 367:223–230.
- Karatayev, A. Y. 1983. Ecology of *Dreissena polymorpha* Pallas and its effects on macrozoobenthos of the thermal power plant's cooling reservoir. Candidate diss. Zoology Institute of Academy of Science of Belarusian SSR. 153 pp. [in Russian].
- Karatayev, A. Y., D. Boltovskoy, D. K. Padilla & L. E. Burlakova. 2007a. The invasive bivalves *Dreissena polymorpha* and *Limnoperna fortunei*: parallels, contrasts, potential spread and invasion impacts. *J. Shellfish Res.* 26:205–213.
- Karatayev, A. Y. & L. E. Burlakova. 1995a. Present and further patterns in *Dreissena* population development in the Narochanskaya lakes system. *Vesti Akademii Navuk Belarusi. Ser. Biyol. Navuk* 3:95–98. [in Belorussian].
- Karatayev, A. Y. & L. E. Burlakova. 1995b. The role of *Dreissena* in lake ecosystems. *Russ. J. Ecol.* 26:207–211. [in Russian].
- Karatayev, A. Y., L. E. Burlakova & D. K. Padilla. 1997. The effects of *Dreissena polymorpha* (Pallas) invasion on aquatic communities in eastern Europe. *J. Shellfish Res.* 16:187–203.
- Karatayev, A. Y., L. E. Burlakova & D. K. Padilla. 1998. Physical factors that limit the distribution and abundance of *Dreissena polymorpha* (Pall.). *J. Shellfish Res.* 17:1219–1235.
- Karatayev, A. Y., L. E. Burlakova & D. K. Padilla. 2002. Impacts of zebra mussels on aquatic communities and their role as ecosystem engineers. In: E. Leppäkoski, S. Gollasch & S. Olenin, editors. Invasive aquatic species of Europe: distribution, impacts and management. Monographiae biologicae series. Dordrecht: Kluwer Scientific Publishers. pp. 433–446.
- Karatayev, A. Y., D. K. Padilla, D. Minchin, D. Boltovskoy & L. E. Burlakova. 2007b. Changes in global economies and trade: the potential spread of exotic freshwater bivalves. *Biol. Invasions* 9:161–180.
- Karatayev, A. Y., G. M. Tishchikov & I. V. Karatayeva. 1983. The specific community of benthic animals associated with *Dreissena polymorpha* Pallas. *Biol. Vnutr. Vod. Inform. Bull.* 61:18–21. [in Russian].
- Legendre, P. & L. Legendre. 1998. Numerical ecology, 2nd edition. Amsterdam: Elsevier. 853 pp.
- Lvova, A. A. 1977. The ecology of *Dreissena polymorpha* (Pall.) in Uchinskoe Reservoir. Candidate diss. Moscow State University. 116 pp. [in Russian].
- Mariazzi, A. A., J. L. Donadelli, P. Arenas, M. A. Di Siervi & C. Bonetto. 1992. Impact of a nuclear power plant on water quality of Embalse der Río Tercero Reservoir (Córdoba, Argentina). *Hydrobiologia* 246:129–140.
- Mikheev, V. P. 1967. The nutrition of zebra mussels (*Dreissena polymorpha* Pallas). Summary of the candidate dissertation. Leningrad: State Research Institute for Lakes and Rivers Fishery Industry. 22 pp. [in Russian].
- Morton, B. 1975. The colonization of Hong Kong's raw water supply system by *Limnoperna fortunei* (Dunker 1857) (Bivalvia: Mytilacea) from China. *Malacol. Rev.* 8:91–105.
- Nakai, K. 1995. Intrusion of the freshwater mytilid mussel, *Limnoperna fortunei* (Dunker, 1857), into Japan. *Kansai Shizenhogo Kiko* 17:45–56.
- Norkko, A., J. E. Hewitt, S. F. Thrush & G. A. Funnell. 2006. Conditional outcomes of facilitation by a habitat-modifying subtidal bivalve. *Ecology* 87:226–234.
- Oliveira, M. D., S. K. Hamilton & C. M. Jacobi. 2010. Forecasting the expansion of the invasive golden mussel *Limnoperna fortunei* in Brazilian and North American rivers based on its occurrence in the Paraguay River and Pantanal wetland of Brazil. *Aquat. Invasions* 5:59–73.
- O'Neill, C. R., Jr. 1997. Economic impact of zebra mussels: results of the 1995 National Zebra Mussel Information Clearinghouse study. *Great Lakes Res. Rev.* 3:35–44.
- Pastorino, G., G. Darrigran, S. M. Martin & L. Lunaschi. 1993. *Limnoperna fortunei* (Dunker, 1857) (Mytilidae), nuevo bivalvo invasor en aguas del Río de la Plata. *Neotropica* 39:34.
- Patterson, M. W. R., J. J. H. Ciborowski & D. R. Barton. 2005. The distribution and abundance of *Dreissena* species (Dreissenidae) in Lake Erie, 2002. *J. Great Lakes Res.* 31:223–237.
- Petrie, S. & R. Knapp. 1999. Rapid increase and subsequent decline of zebra and quagga mussels in Long Point Bay, Lake Erie: possible influence of waterfowl predation. *J. Great Lakes Res.* 25:772–782.
- Protasov, A. A., S. A. Afanasiev & O. O. Ivanova. 1983. The distribution and role of *Dreissena polymorpha* in the periphyton of Chernobyl water cooling reservoir. In: I. M. Likharev, editor. Molluscs: systematics, ecology and patterns of occurrence. Abstracts of the 7th Meeting on the Molluscs Study. Leningrad: Nauka Press. pp. 220–222 [in Russian].
- Radziejewska, T., C. Fenske, B. Wawrzyniak-Wydrowska, P. Riel, A. Wozniczka & P. Gruszka. 2009. The zebra mussel (*Dreissena polymorpha*) and the benthic community in a coastal Baltic lagoon: another example of enhancement? *Mar. Ecol. (Berl.)* 30(Suppl. 1): 138–150.
- Reeders, H. H., A. bij de Vaate & F. J. Slim. 1989. The filtration rate of *Dreissena polymorpha* (Bivalvia) in three Dutch lakes with reference to biological water quality management. *Freshw. Biol.* 22:133–141.
- Ricciardi, A. 1998. Global range expansion of the Asian mussel *Limnoperna fortunei* (Mytilidae): another fouling threat to freshwater systems. *Biofouling* 13:97–106.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- Sardiña, P., D. Cataldo & 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. *Arch. Hydrobiol.* 173:135–144.
- Spooner, D. E. & C. C. Vaughn. 2006. Context-dependent effects of freshwater mussels on stream benthic communities. *Freshw. Biol.* 51: 1016–1024.

- Stewart, T. W., J. G. Miner & R. L. Lowe. 1998. Quantifying mechanisms for zebra mussel effects on benthic macroinvertebrates: organic matter production and shell-generated habitat. *J. North Am. Benthol. Soc.* 17:81–94.
- Sylvester, F., D. Boltovskoy & D. Cataldo. 2007. The invasive bivalve *Limnoperna fortunei* enhances benthic invertebrate densities in South American floodplain rivers. *Hydrobiologia* 589:15–27.
- Vanderploeg, H. A., T. F. Nalepa, D. J. Jude, E. L. Mills, K. T. Holeck, J. R. Liebig, I. A. Grigorovich & H. Ojaveer. 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species emerging in the Laurentian Great Lakes. *Can. J. Fish. Aquat. Sci.* 59:1209–1228.
- Ward, J. M. & A. Ricciardi. 2007. Impacts of *Dreissena* invasions on benthic macroinvertebrate communities: a meta-analysis. *Divers. Distrib.* 1:155–165.
- Warwick, R. M. & K. R. Clarke. 1993. Comparing the severity of disturbance: a meta-analysis of marine macrobenthic community data. *Mar. Ecol. Prog. Ser.* 92:221–231.
- Zar, H. J. 1996. Biostatistical analysis, 3rd edition. Englewood Cliffs, NJ: Prentice Hall. 662 pp.