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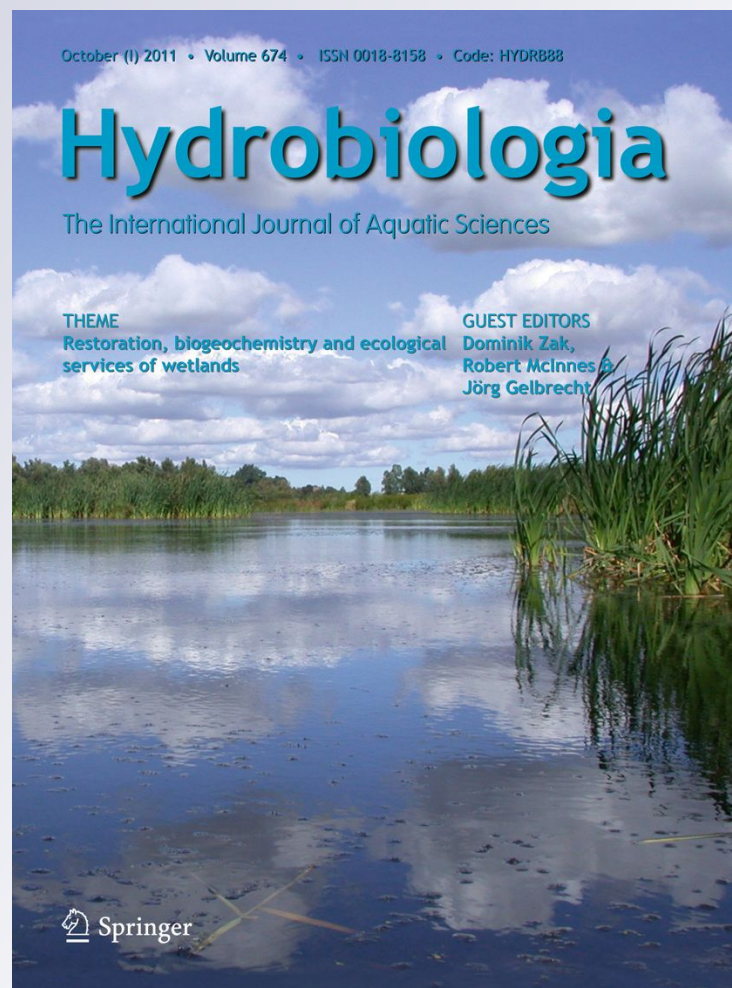
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HABITAT COMPLEXITY

Invasive mussels induce community changes by increasing habitat complexity

Lyubov E. Burlakova · Alexander Y. Karatayev · Vadim A. Karatayev

Abstract Habitat complexity is among the most important factors affecting the diversity, structure, and density of natural communities. The invasive byssate bivalves zebra mussel (*Dreissena polymorpha* (Pallas, 1771)) and golden mussel (*Limnoperna fortunei* (Dunker, 1857)) are sessile suspension feeders that form aggregations (druses), physically changing sediments and increasing habitat complexity, and providing shelter and food for other benthic organisms. In this study, we explored the impact of the change in habitat complexity on benthic community created by druses of *L. fortunei* and *D. polymorpha*, formed on various sediments. *D. polymorpha* was studied in Europe (Naroch Lake, Belarus) and in North America (Glen Lake and Lower Nashotah Lake, USA), and *L. fortunei* was studied in South America (Río Tercero Reservoir, Argentina). Druses of *D. polymorpha* or *L. fortunei* and samples of bare nearby sediment (without druses of exotic mussels) were collected at each sampling site. We found significant changes in species richness, density, biomass, taxonomic, and trophic structure of communities formed in druses compared to the nearby bare sediments. Community taxonomic richness increased threefold, and density increased sevenfold with increasing complexity of habitat from sand to druse. The feeding functional group approach indicated that the impact of increased complexity was reinforced by an increase in food supply in *D. polymorpha* and *L. fortunei* druses. Along with increasing species richness and densities, byssate bivalves homogenized benthic communities.

Keywords Invasive species · Community effect · Habitat complexity · *Dreissena polymorpha* · *Limnoperna fortunei* · Taxonomic structure · Trophic structure · Byssate bivalve

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Introduction

Habitat complexity, along with a variety of ecological processes, has a strong and pervasive influence on community diversity, structure, and abundance (Bell

et al., 1991; Schluter & Ricklefs, 1993; Rahbek & Graves, 2001). It has been documented in terrestrial, freshwater, and marine environments and for both vertebrate and invertebrate species, that physically complex habitats contain more species than simple habitats (Bell et al., 1991). Higher densities in physically complex habitats may simply be due to greater living space or surface area. However, the effects may be more complex, as heterogeneity of the environment is essential for species co-existence, and complex habitats offer a variety of different micro-habitats and niches, allowing resource partitioning (Schoener, 1974; Pianka, 1988; Levin, 1992; Downes et al., 2000). Understanding the mechanisms that influence benthic community diversity, structure, and abundance is one of the major goals of aquatic ecology (Ritchie & Olff, 1999; Almany, 2004; Taniguchi & Tokeshi, 2004).

The invasive bivalves zebra mussel (*Dreissena polymorpha* (Pallas, 1771)) and golden mussel (*Limnoperna fortunei* (Dunker, 1857)) are sessile suspension feeders that produce byssal threads to form aggregations (druses) and not only physically change substrates, increasing habitat complexity for other benthic organisms, but also affect trophic relationships and nutrient cycling locally and system-wide via their filtering activities (Karatayev et al., 1997, 2002, 2010). Most of the impacts of these invasive mussels in freshwater systems are a direct result of their functioning as ecosystem engineers (Karatayev et al., 1997, 2002, 2007a, b; Sousa et al., 2009). Ecosystem engineers are defined as species that "directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials" (Jones et al., 1994, 1997). Many different species have been identified as ecosystem engineers of aquatic habitats (Flecker, 1996; Wotton et al., 1998; Statzner et al., 2000), and particularly bivalves (Dame, 1993, 1996; Ruesink et al., 2005). The main ecosystem level roles of bivalves include structural, trophic, and nutrient cycling (Dame, 1996). Physically, bivalves create three-dimentional structures with their shells and can stabilize sediments (Gutierrez et al., 2003; Ruesink et al., 2005). Biologically, they affect community structure (both in the water column and in the benthos), and can influence community stability, diversity, and interspecies links (Karatayev et al., 2002). *D. polymorpha* and *L. fortunei* have all of the properties of ecosystem engineers

(Karatayev et al., 1997, 2002, 2007a, b; Sousa et al., 2009), and although less information is available on *L. fortunei*, we hypothesize that their effect on benthic community will be similar to that of *D. polymorpha*. This knowledge is important, considering that *L. fortunei* may colonize many more waterbodies in central and southern regions of North America than zebra mussels (Ricciardi, 1998; Karatayev et al., 2007a, b; Oliveira et al., 2010). Although facilitation by habitat modifiers in general, and by filter-feeding bivalves in particular, is a well-known phenomenon, the effects on the benthic fauna are often modulated and even reversed by specific species composition (Afanasiev & Protasov, 1987; Spooner & Vaughn, 2006), suspended sediment concentration (Norkko et al., 2006), sediment characteristics (Radziejewska et al., 2009), and geographic location (Buschbaum et al., 2009).

In this study, we explore the impact of the change in habitat complexity on the benthic community created by druses of two exotic byssate bivalves *L. fortunei* and *D. polymorpha*, and investigate how these impacts vary depending on sediment type. We hypothesize that druses augment the habitat's structural complexity and enhance trophic conditions for associated invertebrates, resulting in large changes in the benthic community. We assess the impact by evaluating changes in diversity, density, biomass, taxonomic composition, and trophic structure of the community.

Materials and methods

Dreissena polymorpha impact on macroinvertebrates was studied in Europe and in North America, and *L. fortunei* was studied in South America using previously described methods (Burlakova et al., 2005; Karatayev et al., 2010). The effect of *D. polymorpha* on benthic community was assessed in Lake Naroch (Republic of Belarus, July 2006), in Lower Nashotah Lake (Waukesha Co., Wisconsin, June 2007), and in Glen Lake (Warren Co., New York, July 2003). The effect of *L. fortunei* on benthos was studied in 2006 in Embalse Río Tercero, a reservoir located in the province of Córdoba, central Argentina, during a similar season (mid-summer, December) (Boltovskoy et al., 2009; Karatayev et al.,

2010). In each lake, samples were collected at one or more sites. Each sampling site had the same sediment within a site (e.g., sand). Samples of *D. polymorpha* or *L. fortunei* druses and the same amount of bare sediment samples not immediately adjacent to the druse (without druses, "sediments") were collected at each sampling site. Druses were collected together with contained sediments and invertebrates (but without underlying sediments) by a diver, carefully placed in zip-lock bags, and brought to the surface. Benthic samples of bare sediments (without druses) were collected with a tube dredge sampler 7.2 cm in diameter. All samples were washed through a 500 μm sieve and fixed with 10% buffered formaldehyde. All organisms from all samples were identified to the lowest possible taxonomic level, except for oligochaetes, where only two species (*Stylaria lacustris* (Linnaeus) and *Branchiura sowerbyi* (Beddard)) were identified, while all others were categorized as Oligochaeta. All organisms were counted, and weighted after blotting dry on absorbent paper (total wet weight). Wet biomass was not recorded for macroinvertebrates collected from Glen Lake. Druse surface area was estimated as its projection onto a two-dimensional plane (two-dimensional area of mussels covering the benthos) and was on average 0.0047 ± 0.0002 m^2, $n = 54$ (mean $\pm$ standard error here and elsewhere unless noted) across all samples, comparable to the tube sampler catch area (0.004 m^2). Druses and tube samples were approximately similar in total volume, as the height of an average druse was comparable to the depth of the tube sample (5–7 cm).

In Glen Lake, nine druses and nine sediment samples were collected in July 2003 at 1 to 1.5 m depth from sand (Table 1). In Naroch Lake, we collected 10 druses and 10 sediment samples from two sites at 1 m depth each, one site was on bare sand and another on sand with *Chara* sp. In the Lower Nashotah Lake, we collected six *D. polymorpha* druses and six samples of bare sediments at three sites with different sediments: on silt and shells (2.5 m depth), sand and gravel (1 m depth), and rocks (1 m depth, rocks incrusted with zebra mussels, vs. non-incrusted rocks of a similar size). In Río Tercero Reservoir, we collected 10 samples of *L. fortunei* druses and 10 samples of coarse sand with silt at 3.5 m depth (all mussels in <3 m depth were dead due to the recent drawdown) (Table 1).

To assign invertebrates found in the benthic samples to feeding functional groups, we used the classification suggested by Merritt & Cummins (1996). For invertebrates that were identified to species, we used data from Izvekova (1975), Sokolova et al. (1980b), and Monakov (1998, 2003) to assign the feeding functional group. For invertebrates identified to genus, we used Merritt and Cummins (1996) and Thorp & Covich (2001). However, some species and genera fit into more than one group. For example, some collectors are known to filter-feed and gather (e.g., *Microtendipes chloris* (Meigen, 1818), *Bithynia tentaculata* (Linnaeus, 1758), *B. leachi* (Scheppard, 1823), *Tanytarsus* sp.) (Izvekova, 1975; Merritt & Cummins, 1996; Monakov, 1998). As these species were abundant in the lakes sampled, we considered them as "filtering + gathering collectors", a sub-group within the "collectors" group.

To characterize the convolution of all sampled substrates, we arranged them in four groups according to their sediment particle size and increased complexity: 1—sand; 2—silt with shells, and coarse sand with silt; 3—sand with *Chara* sp., rocks (40–100 mm), and sand with gravel; 4—druses. Sediment particle size classification has proven to be useful in studies of bivalve ecology and impacts on benthic communities (Strayer, 1999; Ward & Ricciardi, 2007; Sousa et al., 2007).

Statistical analyses

Macroinvertebrate community structures were assessed using density, wet biomass, and diversity indices. PRIMER 6 (Version 6.1.6, Primer E-Ltd. 2006) package was used to analyze differences in benthic communities. The sample-to-sample similarity of macroinvertebrate community composition (density and biomass) was assessed with the aid of the Bray-Curtis index (BC) (Bray & Curtis, 1957; Clarke, 1993), based on fourth-root transformed density or biomass data. To visualize the differences among communities, we used nonmetric multi-dimensional scaling (NMDS), which calculates a set of metric coordinates for samples, most closely approximating their nonmetric distances (Legendre & Legendre, 1998). NMDS was found to be consistently reliable in a comparative study of ordination methods for community data (Kenkel & Orlóci, 1986; Clarke, 1993). To test the significance of differences among communities, we used a non-parametric analogue of ANOVA—analysis of Similarities

Table 1 Mean density, wet biomass, taxon richness, and diversity indices (Margalef's index of species richness calculated on density data) of benthic communities formed in *Limnoperna fortunei* and *Dreissena polymorpha* druses, and in nearby bare sediments (number of samples collected from each substrate, equal to the number of druses, in parentheses)

Lake, substrate	Mean density (m^{-2})			Mean biomass (g m^{-2})			Taxa richness			Margalef's index		
	S	D	d	S	D	d	S	D	d	S	D	d
Naroch Lake												
Sand (10)	3,238	11,355	3.5	4	75	19	9	30	3.3*	1.36	2.54	1.9
Sand and *Chara* sp. (10)	9,975	19,356	1.9	29	115	4.0	23	20	0.9	2.38	1.93	0.8
Mean	6,606	15,355	2.3	16	95	5.9	25	32	1.3	2.73	3.21	1.2
Glen Lake												
Sand (9)	1,571	27,615	17.6	n.r.	n.r.	n.r.	11	27	2.5*	1.36	2.54	1.9
Lower Nashotan												
Silt and shells (6)	833	18,165	21.8	3	33	11	9	32	3.6*	1.19	3.16	2.7
Rocks (6)	10,254	21,764	2.1	7	30	4.3	18	30	1.7*	1.84	2.90	1.6
Sand and gravel (6)	5,708	22,928	4.0	15	26	1.7	20	33	1.7*	2.20	3.19	1.5
Mean	5,599	20,952	17.6	8	30	3.8	30	47	1.6	3.36	4.62	1.4
Rio Tercero												
Silt and sand (10)	4,650	15,313	3.3	9	31	3.5	16	20	1.3*	1.78	1.97	1.1
All lakes (57)	5,280	19,051	3.6*	11	57	4.9*	64	105	1.6*	7.35	10.55	1.4

Density and biomass of invasive bivalves were excluded from this analysis. Samples were collected in Río Tercero Reservoir, Argentina (*L. fortunei*), Lake Naroch (Belarus), Lake Lower Nashotah and Glen Lake (USA) (*D. polymorpha*). *S* bare sediment community, *D* community in *Dreissena/Limnoperna* druses, *d* ratio between druse and sediment community parameters, *n.r.* not recorded. For taxa richness and Margalef's index instead of the mean, total values for the lake are given

* These changes were tested and found significant at $P < 0.001$ (2-sided *t* tests)

(ANOSIM), a resampling technique that uses permutation/randomization methods on BC similarity matrices to identify differences among groups of samples (Clarke, 1993). Large values of the test statistic (Global *R*) indicate complete separation of groups, and small values (close to 0) indicate little or no separation. To decrease the effect of natural differences in species composition among continents, this analysis was done on different taxonomic levels including species, genus, family, order, and class levels.

We used SIMPER ("Similarity Percentage") analysis to examine the contribution of each taxon to the average BC similarity within each druse and sediment communities. To reveal the contribution of different functional groups to similarity among druse and sediment communities, we used SIMPER on density and biomass data by taxa aggregated to functional feeding groups using the classification scheme by Merritt & Cummins (1996). Density and biomass of *D. polymorpha* and *L. fortunei* were excluded from the community for this analysis.

Univariate diversity indices are used to reduce the data on the community's multivariate complexity into a single index. Different diversity indices emphasize the species richness (total number of species present or some adjusted form) or equitability (how evenly the individuals are distributed among the different species) components of diversity to varying degrees. To demonstrate between-sample relationships obtained from the full range of diversity information extracted (evenness + richness) (Clarke & Gorley, 2006) we used PRIMER to create a similarity matrix of diversity indices (total number of taxa in each sample, Margalef's species richness, Pielou's evenness, Shannon–Wiener diversity index (Log *e* base), and Simpson's diversity index). We applied ANOSIM to this matrix to test for differences in community composition in druses versus bare sediments. This analysis was then contrasted with the usual NMDS ordination done on original data (species density). For all tests, effects were considered statistically significant at $P < 0.05$.

Results

Changes in diversity, density, and biomass

When we combined all data across three continents, we found that there were a total of 105 species in all *D. polymorpha* and *L. fortunei* druses, compared to 64 taxa found in all nearby sediments. This increase in taxa richness was significant for each substrate in each lake except for sand and *Chara* sp. in Naroch Lake ($P < 0.001$, 2-sided *t* tests, Table 1).

The complex 3D structure of druses increased both density and biomass of associated communities in all waterbodies studied (Table 1). Excluding density and biomass of *D. polymorpha* and *L. fortunei*, invertebrate densities in druses increased from 1.9 to 22 times and biomass from 1.7 to 19 times, depending on substrate (Table 1). The effects of druse and sediment type on the community were both significant (density—druse: $R = 0.425$, $P = 0.001$; sediment type: $R = 0.466$, $P = 0.001$; biomass—druse: $R = 0.812$, $P = 0.001$; sediment type: $R = 0.88$, $P = 0.001$; two-way ANOSIM). The average density and biomass of native benthic invertebrates per sample was significantly higher in druses than in the sediments ($P < 0.001$, *t* test, Table 1).

When we included *D. polymorpha* and *L. fortunei* into the analysis, we found drastic changes in community density and biomass. On average, the mean difference between druses and communities in nearby bare sediments in density was 10 times (from 5 times in Naroch Lake to 18 in Glen Lake), and in biomass 994 times (from 624 times in Naroch Lake to 1,281 in Rio Tercero Reservoir) higher in druses than in bare sediments. Both *D. polymorpha* and *L. fortunei* were the dominant species in the druse community.

Taxonomic changes

The presence of *D. polymorpha* and *L. fortunei* druses significantly affected the density and biomass of benthic communities on all sediments ($R = 0.53$, $P = 0.001$); however, due to natural differences in species composition among lakes and sediments, there was a high dissimilarity among benthic communities in different lakes ($R = 0.85$, $P = 0.001$, two-way ANOSIM, Fig. 1A). When the species matrix was aggregated to the taxonom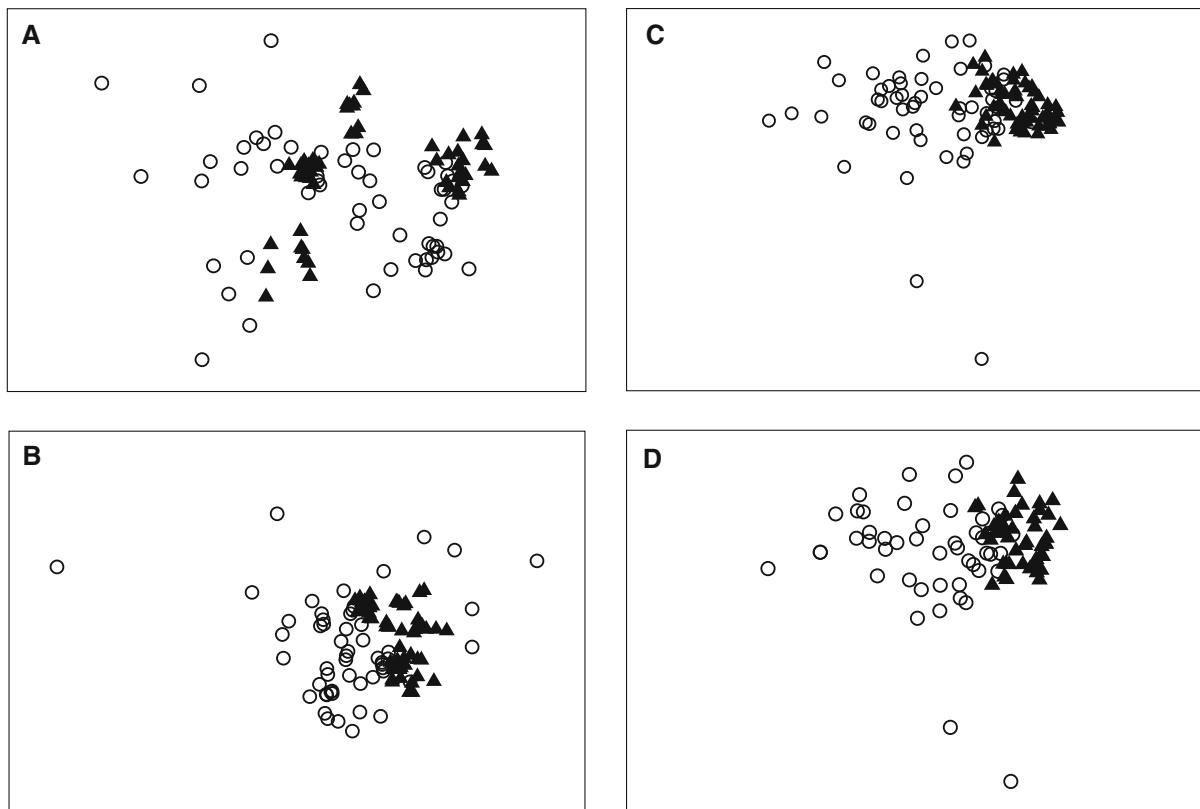ical level of genus and higher, the druse community appeared more homogenous, and the changes were better pronounced (genus level—druse: $R = 0.54$, lake: $R = 0.76$, both $P = 0.001$; family level—druse: $R = 0.58$, lake: $R = 0.70$, both $P = 0.001$, Fig. 1B).

We further tested these effects on a dataset obtained from the full range of diversity information, using matrix of diversity indices that involve both species richness and species evenness. With both dimensions of diversity considered, group separation was more distinct (2D stress decreased from 0.12 to 0.01, Fig. 2A, B), and the effect of druse was more important than the difference driven by species composition in different lakes and substrates (druse: $R = 0.44$, $P = 0.001$, lake: $P = 0.39$, $P = 0.001$, two-way ANOSIM).

Druse and bare sediment communities were dissimilar at 85%, and 20 macroinvertebrate species contributed each over 2% to the dissimilarity between the groups (e.g., leach *Helobdella stagnalis* (Linnaeus, 1758) (4.2%), chironomid *Dicrotendipes tritomus* (Kieffer, 1916) (4.1%), gammarid *Gammarus lacustris* G. O. Sars, 1863 (3.9%). Aggregation of the data to family level revealed that these differences were due to higher densities of Chironomidae, Glossiphonidae, Gammaridae, Caenidae, Asselidae, Planariidae, and unidentified Oligochaeta in druse communities. In general, Insecta were responsible for 41% of the differences between the groups, followed by Malacostraca (19%), Hirudinea (13%), and Gastropoda (11%); the input of other groups was <10% (Table 2).

Changes in community functional structure

Druse communities were more similar than those formed on bare sediments when each taxon was analyzed by its functional feeding mode (Fig. 1C, D; Table 3). Although gathering collectors and predators were the most abundant feeding groups in both communities, they reached higher densities and biomass in the presence of invasive bivalves (Table 3). Filtering collectors (excluding exotic bivalves), though having similar densities and biomass in both communities, had a lower relative abundance and thus a lower contribution to the similarity of druse communities (Table 3). Scrapers, in contrast, were more abundant in druse community (Table 3). Gathering collectors, predators, and scrapers contributed over 80% to the dissimilarity between druse and sediment communities (Table 4).

Fig. 1 Non-linear MDS plots of benthic samples from Lake Naroch (Belarus), Lake Lower Nashotah, and Glen Lake (USA), and Río Tercero Reservoir (Argentina). The samples were collected in *Limnoperna fortunei* (Río Tercero Reservoir) and *Dreissena polymorpha* (all other lakes) druses (filled triangles) and in nearby sediments (open circles). The Bray-Curtis similarity matrix used for this plot was calculated based on fourth -root transformed density data for each taxon

indentified in each sample. Densities of *L. fortunei* and *D. polymorpha* were excluded from the community for these analyses. **A** data for each species or taxon density (2D stress: 0.12). **B** species (taxon) density data aggregated to genus level (2D stress: 0.17). **C** density of each taxon aggregated by functional feeding groups according to Merritt & Cummins (1996) (2D stress: 0.11). **D** biomass of each taxon aggregated by functional feeding groups (2D stress: 0.12)

With inclusion of the exotic bivalves (both *D. polymorpha* and *L. fortunei* are filter-feeders), in all waterbodies druse community was characterized by extremely high dominance of one functional feeding group in their trophic structure—filtering collectors that comprised up to 99% of community's wet biomass.

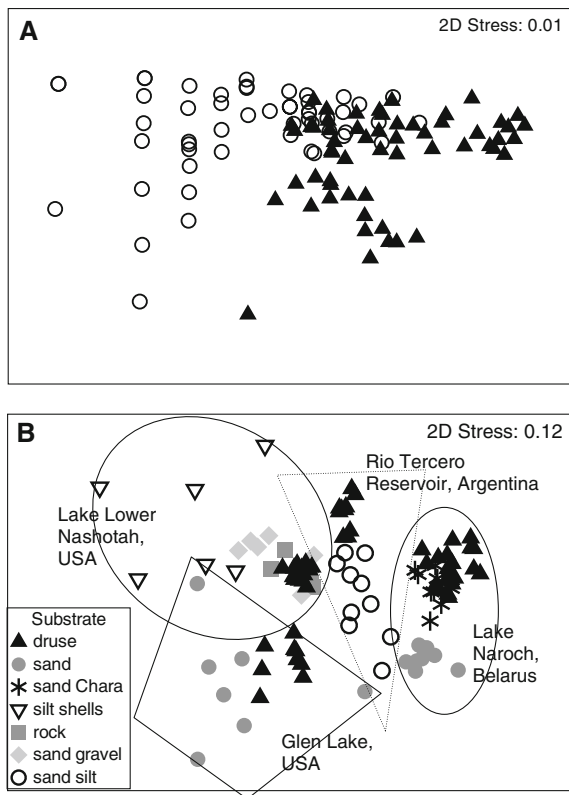### Druses increase substrate complexity and homogenize communities

Taxa richness increased along with the level of substrate complexity, from 4.1 (±0.4, range: 1–8) on sand, to 9.9 (±0.5, range 5–15) on more complex substrates (sand with *Chara* sp., rocks, and sand with gravel) (Fig. 3A). The highest taxa richness was found in druses (13.4 ± 0.6, range 6–22). A significant positive relationship was also found among habitat complexity and density of invertebrates that increased over sevenfold from sand to druses (Fig. 3B).

Macroinvertebrate communities formed in druses were more similar among themselves than to the communities in nearby sediments, independently of where they were formed: similarity of communities in druses was significantly higher than in bare sediments (average similarity in sediments: 48.4 ± 7.6, druses: 69.5 ± 2.5, $t = -2.64$, $P = 0.017$, one-sided t test) (Fig. 2B). Consequently, the dissimilarity between druse communities formed on different sediments in the same lake was significantly lower than the dissimilarity between bare sediments in the same lake

Fig. 2 Non-linear MDS ordination plots of benthic macroinvertebrate communities found in samples from Lake Naroch (Belarus), Lake Lower Nashotah, and Glen Lake (USA), and Río Tercero Reservoir (Argentina). The samples were collected in *Limnoperna fortunei* (Río Tercero Reservoir) or *Dreissena polymorpha* (all other lakes) druses, and in nearby sediments. Densities of *L. fortunei* and *D. polymorpha* were excluded from the community for these analyses. **A** NMDS ordination of similarity indices of the benthic community (taxon densities) based on normalized Euclidian distances of diversity indices of all samples. *Filled triangles L. fortunei* or *D. polymorpha* druses; *open circles* sediments. Diversity indices used were: total number of species in each sample, Margalef's species richness; Pielou's evenness, Shannon–Wiener diversity index (log *e*), and Simpson's index. **B** NMDS ordination of benthic macroinvertebrate communities found in *L. fortunei* or *D. polymorpha* druses and in nearby sediments. The Bray-Curtis similarity matrix used for this plot was calculated based on fourth-root transformed density data for each taxon indentified in each sample. *Reversed open triangles* silt and shells; *open circles* sand and silt; *grey filled circles* sand; *stars* sand with *Chara* sp.; *grey diamonds* sand and gravel; *grey squares* rocks; *filled triangles L. fortunei* or *D. polymorpha* druses. Samples from different lakes are indicated by *shapes*

(average dissimilarity in bare sediment: 77.4 ± 6.6, druse: 35.9 ± 4.3, $t = -5.13$, $P = 0.0018$, one-sided *t* test).

Discussion

We found large changes in species richness, density, biomass, taxonomic, and trophic structure of communities formed in byssate mussel aggregations compared to the nearby sediments. The mechanism of these changes is complex, but can be roughly divided into two main categories: structural and trophic.

Structural changes (physical alteration of the sediment) include increase in surface area due to sheer addition of bivalve shells, which serve as a substrate for the attachment of a variety of sessile organisms (e.g., algae, sponges, insect larvae, etc.), including the bivalves themselves. In addition, this complex two- and three-dimensional structure formed by the shells attached to each other with byssal threads provides the habitat heterogeneity and complexity in the form of interstices between living and dead shells, and cavities in empty shells from dead mussels. Empty shells do not decompose or dissolve readily in lakes but accumulate on the bottom, creating reef-like structures which provide additional hard-substratum habitat (Karatayev et al., 2002). These reefs made of live mussels and spent shells are used by various invertebrates (e.g. Gammaridae, Trichoptera, etc.) as refuges from predation and from physical (e.g., waves, currents) or physiological stresses (e.g., temperature, desiccation, lack of oxygen) (reviewed in Karatayev et al., 1997, 2002; Stewart et al., 1998a; Gutierrez et al., 2003). It has been shown that dreissenid aggregations create habitat for species that would otherwise be infrequent or absent in the environment, providing them with reliable shelter, and thus reducing the foraging success of predators (Botts & Patterson, 1996; Stewart et al., 1998b, 1999; Mayer et al., 2001; Cobb & Watzin, 2002; Beekey et al., 2004).

Community changes resulting from increased complexity of habitat have been seen in other environments. Surface roughness affects flow micro-environments and the ability of fauna to cling to stones (Lancaster & Mole, 1999), alters competitive outcomes (e.g., Fletcher & Underwood, 1987), or the local success of predators (e.g., Fairweather, 1988; Robson, 1996). Moreover, it has been demonstrated that patch size and structural complexity have independent effects on macroinvertebrate assemblages, suggesting that the relationship between the number of species and surface area is not a sampling

Table 2 Results of multivariate SIMPER ("Similarity Percentages—species contributions") analyses on benthic macroinvertebrate taxa in *Dreissena polymorpha* and *Limnoperna fortunei* druse communities (druse) and in communities in nearby sediments (sediment)

Taxa	Druse average density	Sediment average density	Contribution (%)	Cumulative contribution (%)
By Order (average dissimilarity = 60.0%)				
Diptera	25.91	17.34	26.29	26.29
Amphipoda	7.16	1.83	10.61	36.9
Rhynchobdellida	6.26	2.07	9.87	46.77
Basommatophora	5.69	0.73	8.46	55.23
Ephemeroptera	5.71	2.5	7.85	63.08
Trichoptera	3.96	0.61	6.58	69.66
Isopoda	3.52	0.45	6.44	76.11
Tricladida	3.3	0.22	5.16	81.27
Oligochaeta[a]	3.3	3.77	5.07	86.34
Haplotaxida	2.16	1.02	4.3	90.64
Arhynchobdellida	1.11	0.36	2.29	92.93
Veneroida	0.38	0.77	1.58	94.51
Neotaenioglossa	0.86	0.08	1.43	95.94
Megaloptera	0.68	0.14	1.14	97.08
Odonata	0.83	0.00	1.09	98.17
Coleoptera	0.44	0.07	0.67	98.84
Decapoda	0.28	0.00	0.56	99.4
Tubificida	0.00	0.14	0.28	99.68
Architaenioglossa	0.12	0.00	0.21	99.89
Hemiptera	0.00	0.07	0.11	100
By Class (average dissimilarity = 54.5%)				
Insecta	37.53	20.74	41.18	41.18
Malacostraca	10.96	2.28	18.72	59.90
Hirudinea	7.37	2.44	12.78	72.67
Gastropoda	6.66	0.82	10.98	83.66
Oligochaeta	5.46	4.93	8.90	92.55
Turbellaria	3.30	0.22	5.70	98.26
Bivalvia	0.38	0.77	1.74	100.00

Original data on species (and in some cases higher taxa) densities was aggregated to order and class level to decrease the natural differences in species composition among continents. Average density (fourth-root transformed), taxon contribution to the dissimilarity between druse and sediment communities (%), and cumulative contribution to the dissimilarity are given by taxa

[a] Only two species of oligochaetes (*Stylaria lacustris* and *Branchiura sowerbyi*) were identified to species; all others were categorized as oligochaetes

artifact due to more complex habitats having larger areas, and therefore sampling more individuals (Matias et al., 2010). In aggregations of byssate epifaunal bivalves the effect of increased habitat complexity is reinforced by trophic changes in the habitat. These filter-feeding bivalves greatly enhance the rates of deposition of both organic and inorganic material on the bottom, increasing sedimentation rates by several orders of magnitude. Filtered particles are sorted, and either consumed, or rejected. Rejected particles are bound in mucus, expelled as pseudofeces, and deposited onto the bottom. This results in greatly increased organic content of sediments, and provides an enhanced food subsidy for benthic deposit feeders (Karatayev et al., 1983, 1994,

2002, 2007a, b; Karatayev & Burlakova, 1992, 1995; Botts & Patterson, 1996; Stewart et al., 1998a).

Another source of food for benthic invertebrates inhabiting druses is the algal and bacterial communities flourishing on bivalve shells and in their aggregations. Over 150 algae species, mostly belonging to Bacillariophyta and Chlorophyta, were identified in periphyton samples collected from *D. polymorpha* shells in Lake Naroch, Belarus (Makarevich et al., 2008). The total area of hard substrate presented by *D. polymorpha* shells in Lake Naroch is equal to 11% of the lake surface area (Makarevich et al., 2008). *D. polymorpha* clusters were shown to increase heterotrophic bacterial density, induce changes in community structure, and enhance bacterial activity and

Table 3 Results of multivariate SIMPER ("Similarity Percentages—species contributions") analyses on benthic macroinvertebrate taxa in *Dreissena polymorpha* and *Limnoperna fortunei* druse communities (druse) and in communities in nearby sediments (sediment)
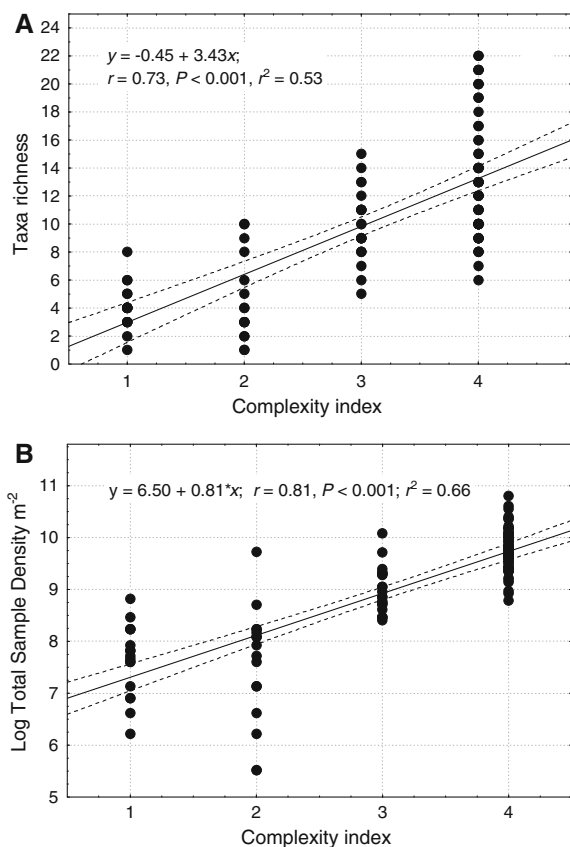
Functional feeding group	Average density	Average biomass	Contribution by density (%)	Contribution by biomass (%)
Sediment community (average similarity by density = 53.7; by biomass = 52.0)				
Gathering collectors	17.87	3.25	71.14	68.73
Predators	8.03	1.64	22.53	24.18
Shredders	1.68	0.22	2.27	1.63
Filtering collectors	1.86	0.34	1.99	2.09
Filtering gathering collectors	1.55	0.35	1.53	2.37
Scrapers	1.21	0.34	0.53	1.00
Druse community (average similarity by density = 74.3; by biomass = 72.7)				
Gathering Collectors	40.01	7.18	62.57	58.29
Predators	18.13	4.42	27.49	29.82
Scrapers	5.26	1.18	4.48	5.03
Filtering gathering collectors	3.89	0.96	2.95	4.09
Shredders	2.61	0.50	1.42	1.37
Filtering collectors	1.76	0.41	1.08	1.40

Original density and biomass data were aggregated by functional feeding groups according to (Merritt & Cummins, 1996). Average taxa density and biomass (fourth-root transformed), contribution to the Bray-Curtis similarity to the community (%), and cumulative contribution to the similarity are given by each group. Density and biomass of invasive bivalves were excluded from this analysis

Table 4 Results of multivariate SIMPER analyses on benthic macroinvertebrate taxa in *Dreissena polymorpha* and *Limnoperna fortunei* druse communities (druse) and in communities in nearby sediments (sediment)

Functional feeding group	Sediment average	Druse average	Contribution (%)	Cumulative contribution (%)
Density (average dissimilarity = 49.8)				
Gathering collectors	17.87	40.01	47.51	47.51
Predators	8.03	18.13	24.94	72.45
Scarpers	1.21	5.26	9.50	81.95
Filtering gathering collectors	1.55	3.89	7.34	89.29
Shredders	1.68	2.61	5.45	94.74
Filtering collectors	1.86	1.76	5.26	100.00
Biomass (average dissimilarity = 51.5)				
Gathering collectors	3.25	7.18	40.71	40.71
Predators	1.64	4.42	30.18	70.88
Scarpers	0.34	1.18	10.67	81.55
Filtering gathering collectors	0.35	0.96	8.52	90.07
Filtering collectors	0.34	0.41	5.22	95.29
Shredders	0.22	0.50	4.71	100.00

Original density and biomass data were aggregated by functional feeding groups according to (Merritt & Cummins, 1996). Average taxa density and biomass (fourth-root transformed), contribution to the Bray-Curtis dissimilarity between druse and sediment communities (%), and cumulative contribution to the dissimilarity are given by each group. Density and biomass of invasive bivalves were excluded from this analysis

Fig. 3 Relationship between macroinvertebrate taxa richness (**A**) and log-transformed total density (**B**) in each sample, and the degree of habitat complexity expressed in increasing order from sand (*1*), to silt with shells, or coarse sand with silt (*2*), sand with *Chara* sp., rocks, and sand and gravel (*3*). Druses on all sediments were given a complexity index of 4. The line represents linear regression with 95% confidence bands, regression equation is given on each graph

metabolic diversity compared to bare sediments (Lohner et al., 2007). Microbial community in druses can mineralize a significant portion of the nutrients contained in the *D. polymorpha* feces and pseudofeces, increasing bioavailable nutrients and altering nutrient cycling and nutrient concentrations in and near *D. polymorpha* druses (Lohner et al., 2007). In addition, aggregations of bivalve shells alter water flow and infiltration into sediments, affecting the transport of particles and solutes (Dame, 1996; Gutierrez et al., 2003). Due to structural and trophic complexity, the druse community was the richest, both in terms of diversity and density (Table 1; Fig. 3).

The intricate nature of habitat complexity, i.e., the interplay of structural and trophic components that

enhance taxonomic and numerical richness, has been demonstrated in other environments (e.g., Bell et al., 1991; Schluter & Ricklefs, 1993; Rahbek & Graves, 2001). More complex substrates often have higher trophic values, e.g., plants recolonize rough substrates more quickly that smooth surfaces (Downes et al., 2000). Sand with *Chara* in Lake Naroch attracted more animals compared to bare sand not only due to the larger area and structural complexity provided by *Chara*, but also due to an additional food source—periphyton growing on *Chara*. Downes et al. (2000) showed experimentally that both surface texture and macroalgae increase species richness of stream invertebrates independently of each other, and both sources of structure are important during colonization.

Increase in habitat complexity due to aggregations of exotic byssate bivalves, coupled with organic enrichment, induced profound changes in community diversity, taxonomic and trophic structure, and interspecies links. Often, community changes induced by increased habitat complexity are revealed by either increased species richness or density, and to date there are few studies of resultant changes in the trophic structure of communities (Lvova-Kachanova & Izvekova, 1978; Sokolova et al., 1980a; Karatayev & Burlakova, 1992; Burlakova et al., 2005; Ward & Ricciardi, 2007). The feeding functional group approach enables a quantitative assessment of the degree of dependence of the invertebrate biota on particular food resources (Merritt & Cummins, 1996). This approach is also a key to understanding the taxonomical changes in a community as a result of changes in their habitat.

We found a dramatic shift in the benthic trophic structure in both *D. polymorpha* and *L. fortunei* aggregations. The structure of feeding functional groups in the new community, including invasive bivalves, was overwhelmingly dominated by collectors-filterers. Both *D. polymorpha* and *L. fortunei* were the dominant benthic species in terms of biomass. Feces and pseudofeces, organic matter deposited actively and passively, and the phyto-, zooperiphyton and bacteria thriving on shells provide food for collectors and scrapers, which increased in density (Table 3), explaining the dominance of isopods, amphipods, gastropods, mayflies, and some trichopterans, oligochaetes, and chironomids (Table 2). All these animals are characteristic of druse communities (Sokolova et al., 1980a; Karatayev & Lyakhnovich,

1990; Karatayev & Burlakova, 1992; Botts & Patterson, 1996; Ricciardi et al., 1997; Stewart et al., 1998a; Karatayev et al., 2002; Ward & Ricciardi, 2007).

Abundance of food and shelter in druses also attracted predators, explaining the higher densities of leeches, dragonflies, and Megaloptera in druses compared to bare sediments nearby. Similar changes were found in *D. polymorpha* aggregations in both Europe and North America (reviewed in Karatayev et al., 1983, 1997, 2002, 2007a; Ward & Ricciardi, 2007). Small-grain sediments such as sand were dominated by small animals that live within the sediment (e.g., chironomids and oligochaetes), while the druse community was composed of larger animals (snails, amphipods, isopods, trichopterans, and leeches). This explains the almost threefold increase in biomass of druse communities (without consideration of the biomass of exotic bivalves, Table 1). Druses of *D. polymorpha* and *L. fortunei*, including the exotic bivalves themselves, increased local densities by a factor of ten, and biomass—by a factor of a thousand, and both bivalves dominated the resulting community in terms of the density and biomass.

In agreement with our hypothesis, we found that the mechanism by which *L. fortunei* affects benthic assemblages was the same as that of *D. polymorpha*, both in terms of species richness and density of benthic macroinvertebrates (Table 1). Although the effects on the benthic fauna were modulated by distinct species assemblages in different substrates, lakes, and continents, when we aggregated the species matrix to higher taxonomical levels, the druse community appeared more homogenous than the communities in bare sediments nearby, independently of which bivalve was forming the druse. Thus, we further hypothesize that similar trophic and taxonomic community changes should be expected as a result of the introduction of other freshwater or marine epifaunal byssal bivalves.

Druse inhabitants are predominantly epifaunal organisms which are likely to take advantage of both the resources and structural complexity provided by druses. Infaunal invertebrates (e.g., burrowing oligochaetes, mayflies) may avoid druses. As a result, species dominant in bare substrates often were not found in druses nearby (e.g., burrowing oligochaete *B. sowerbyi* in Rio Tercero and burrowing mayfly *Hexagenia* sp. in Lake Lower Nashotah). Epifaunal organisms are also highly mobile and may rapidly colonize druses on soft sediments (Mörtl & Rothhaupt, 2003), while many infaunal species are less mobile (Merritt et al., 1984).

Due to the variety of sampled substrates (e.g., sand, sand and *Chara*, rocks, silt and shells, druses etc.), we used a categorical measure of habitat convolution based on substrate particle size and complexity. While this measure demonstrated the increase in both diversity and species richness with increasing habitat complexity, a uniform index describing both area and structural complexity (e.g., refuge space, fractural dimension, Kostylev et al., 2005; Warfe et al., 2008) will be very useful for further studies that involve comparing habitats very different in nature.

We found a large increase in both species' diversity and density with increasing habitat complexity from sand to druses (Table 1, Fig. 3). The largest similarity was found among communities formed on druses on rocks, and druses on sand and gravel (Fig. 2B). The druse communities, independently of the substrate where the druses were found, included organisms more typical of rocky substrata, such as gammarid amphipod and isopod crustaceans, hydroids, flatworms, leeches, and snails (Karatayev et al., 1997, 2002, 2007b; Bially & Macisaac, 2000; Beekey et al., 2004; Ward & Ricciardi, 2007). Likewise, in marine sedimentary environments, epifauna normally unable to occupy soft sediments are restricted in their occurrence to the mussel bed (Dittmann, 1990; Robinson & Griffiths, 2002). The most dissimilar were druse communities from communities formed in soft sediments (e.g., sand, Fig. 2B).

Macroinvertebrate communities formed in druses were more similar among themselves than to the communities in nearby sediments, independently of where they were formed (Fig. 2B). In addition, they were less dissimilar among themselves than communities formed on bare substrates in the same lake. Therefore, along with increasing species richness and densities, both bivalves homogenize freshwater benthic communities, making them more similar independently of which substrate or part of the lake they colonize.

Conclusions

We found significant changes in species richness, density, biomass, taxonomic, and trophic structure of

communities formed in druses of *D. polymorpha* and *L. fortunei* compared to the nearby bare sediments. The feeding functional group approach allowed us to understand the taxonomical changes in community as a result of habitat change, and indicated that the effect of increased habitat complexity in druses was reinforced by increased food availability. We found a threefold increase in community taxonomic richness and a sevenfold increase in density with increasing complexity of habitat from sand to druse. Along with increasing species richness and densities, both bivalves also homogenized freshwater benthic communities, making them more similar independently of which substrate or part of the lake they colonized.

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