FUNCTIONAL CHANGES IN BENTHIC FRESHWATER COMMUNITIES AFTER *DREISSENA POLYMORPHA* (PALLAS) INVASION AND CONSEQUENCES FOR FILTRATION

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Abstract: *Dreissena* is extremely abundant in waters it invades, and dramatically changes benthic invertebrate communities in terms of total biomass, species composition, and the relative abundance of functional groups. We analyzed the relative abundance of feeding functional groups of the benthic community before and after zebra mussel invasion in three Belarussian lakes, four lakes after invasion only, and one lake in the same region that has not been invaded. After invasion, benthic structure was dominated by one trophic group – filterers. This group accounted for greater than 96% of the total biomass of benthic invertebrates. We found that the relative abundance of feeding functional groups in the rest of the benthic community, without including *Dreissena* biomass, was also different in lakes examined before and after zebra mussel invasion. Before invasion and in the un invaded lake, planktonic invertebrates filtered a volume equivalent to the volume of the lake within few days, and were more than 200 times more effective than benthic filterers, which would take about 4 years to filter an equivalent volume. After *Dreissena* invaded the lakes, the total average biomass of all benthic invertebrates (including zebra mussels) increased more than 20 times. The filtration efficiency of the benthic community increased greater than 70 times, and the time required to filter the volume of the lake was not significantly different than that for zooplankton. These dramatic changes will alter the relative roles of the plankton and benthos in a variety of ecosystem functions, especially the movement of carbon from the plankton to the benthos.

Key words: Zebra mussels, benthic community, trophic structure, feeding functional groups, filtration efficiency.

INTRODUCTION

The zebra mussel, *Dreissena polymorpha* Pallas (1771), continues to spread throughout the freshwaters of Eurasia and North America, and new lakes and rivers are constantly being invaded (Kinzelbach 1992, McMahon and Bogan 2001, Minchin et al. 2002, Karatayev et al. 2003). Species of

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Dreissena are the only bivalves in freshwater to attach to hard substrates and possess a dispersing planktonic larval stage. *D. polymorpha* is extremely abundant in waters it invades, is frequently competitively dominant over native freshwater fauna, and has large impacts on all parts of the ecosystem, especially benthic animals (reviewed in Karatayev et al. 1997, 2002).

Characterizing the feeding functional group composition in lakes before and after invasion by zebra mussels can provide insights into how benthic communities respond to invasion. The feeding functional group approach enables a quantitative assessment of the degree of dependence of the invertebrate biota on particular food resources, and the linkages between food sources and morphological and behavioral adaptations (Merritt and Cummings 1996).

Although the effect of *D. polymorpha* invasion on species composition and abundance within the benthic community has been documented for certain lakes, to date there are few studies of resultant changes in the trophic structure of communities (Sokolova et al. 1980a, Karatayev and Burlakova 1992). When zebra mussels invade, they create a large population of effective suspension-feeders that can cause radical changes in the benthic community (Lvova-Kachanova and Izvekova 1978, Sokolova et al. 1980a, Karatayev and Burlakova 1992, Karatayev et al. 1997). Native suspension-feeders can be out-competed by *D. polymorpha*, and decrease in abundance, while animals feeding on the sediments can increase in abundance (Sokolova et al. 1980a, Karatayev and Burlakova 1992, Karatayev et al. 1994). In this study, we assessed the impacts of invasion by zebra mussels on the structure of the benthic communities by examining feeding functional groups within the benthic community of 8 Belarussian lakes. By comparing the structure of communities without zebra mussels with those that have been invaded, we can assess the impacts of invasion on trophic processes and some aspects of ecosystem function.

MATERIALS AND METHODS

Study Sites and Sampling

To study the trophic structure of benthic invertebrates in lakes with and without *Dreissena*, we used data collected from glacial lakes (Karatayev et al. 2003), as part of a larger survey of Belarussian lakes. The Republic of Belarus is situated between Poland and Russia, and was part of the former Soviet Union. A variety of chemical, geological, physical, and biological data were collected in mid-summer for each of these lakes by the Lakes Research Laboratory of the Belarussian State University. We collected additional data for some lakes in the summer of 1998 and 1999. For three lakes we have data before and after invasion, for four lakes we have data after invasion only, and we have data for one lake, in the same region, that has not been invaded (Table 1).

To determine the species composition, density and biomass of benthic invertebrates 7 – 16 samples were collected from each lake, depending on the lake size. Sample sites were selected to maximize coverage of the lake bottom and include all major habitat types. For all benthic samples we used a Petersen grab for hard substrates and an Eckman grab for soft substrates (sample area 0.025 m^2). Samples were washed through a 500 μm mesh. Retained macroinvertebrates were preserved with 10% neutral buffered formalin. All macroinvertebrates were identified to the lowest possible taxon, counted and weighed to the nearest 0.0001 g after being blotted dry on absorbent paper (wet mass).

For three lakes, Myadel, Boginskoe, and Svir, we had data both before and after invasion, which allowed us to do paired comparisons (Table 1). We also had data for four additional lakes, Bolshie Shvakshty, Volchin, Dolzha, and Bolduk that have been invaded by zebra mussels. All of these lakes were invaded by *Dreissena* between 1980 and the mid-1990s, however, unfortunately, we do not know the exact years of invasion.

Table 1. Limnological parameters of the studied Belarussian lakes.

Lake	Year Studied Before invasion	After invasion	Surface area (km^2)	Volume (10^6 m^3)	Maximum depth (m)	Secchi depth (m)	Trophic status
Boginskoe	1973	1999	1.2	9.12	16.2	2.4	eutrophic
Svir	1980	1998	22.3	104.3	8.7	1.8	eutrophic
Myadel	1980	1998	16.4	102.0	24.6	4.8	mesotrophic
Dolzha	-	1998	1.0	5.4	13.7	2.6	eutrophic
Bolshiye Shvakshty	-	1998	9.6	22.3	5.3	3.1	eutrophic
Volchin	-	1998	0.5	7.9	32.9	3.8	mesotrophic
Bolduk	-	1999	0.8	11.9	39.7	4.5	oligomeso-trophic
Ikazn	1973	not invaded	2.4	7.9	8.4	1.4	eutrophic

Functional Groups

We used the classification scheme by Merritt and Cummins (1996) for functional feeding groups. For invertebrates that were identified to species, we used data from Izvekova (1975), Sokolova et al. (1980b) and Monakov (1998, 2003) to assign feeding functional group. For invertebrates identified to genus, we used Merritt and Cummins (1996) and Thorp and 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 cloris*, *Bithynia tentaculata*, *B. leachi*, *Tanytarsus* sp.)

(Izvekova 1975, Merritt and 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 group "collectors".

To determine if there were changes in the relative abundance of feeding functional groups associated with zebra mussel invasion, we compared the relative proportions of biomass of each functional group before and after zebra mussel invasion.

Functional Consequences

Shifts in the feeding functional groups in a lake will have functional consequences for both the processing of benthic carbon, and for links between the benthic and the planktonic communities (benthic-pelagic coupling).

To estimate the filtration capability of the zooplankton community in each lake we used Kryuchkova's (1989) estimate that zooplankton can filter 120 mL mg wet mass^{-1}d^{-1} in a cladoceran dominated eutrophic lake. To estimate the filtration capacity of the benthos, we used the literature values for the filtration rates, based on wet total mass, of individual species (Izvekova 1975, Alimov 1981, reviewed in Monakov 1998) weighted by the average biomass (wet total mass (body plus shell), g m^{-2}) of that species in the lake. For species whose filtration rates were not known, we used the rates for the closest related taxon whose rate was known. The total filtration capacity of the benthic community was estimated by multiplying the filtration rates by the average biomass of each taxon determined to be in the filtering collectors functional group. As it is very difficult to determine the relative proportion of time a species filters or gathers (references in Monakov 1998), the impact of members of the filtering + gathering collectors was divided in half. For zebra mussels, we used a filtration rate of 58 mL g^{-1} h^{-1} (literature estimates range from 35 - 110 mL g^{-1} h^{-1}, Karatayev et al. 1997). To estimate the total filtration capacity of zebra mussels, we multiplied the average biomass of zebra mussels (g m^{-2}) by this filtration rate. In this way we were able to compare the filtration rate of the entire community of zooplankton with the amount of filtration for the entire benthic community.

Statistical Analyses

To compare the relative abundance of trophic groups in lakes with and without zebra mussels, we used either a *t*-test or Mann-Whitney U test on percentage data for each lake (Zar 1996). To compare the structure of functional trophic groups of benthic community before and after zebra mussel invasion we used Fisher-Freeman-Halton test (a generalization of the Fishers Exact test to *r* by *c* contingency table) with a Monte Carlo estimate of the P-value to test for homogeneity in contingency tables. Effects were considered statistically significant at P < 0.05. Analyses were performed with StatXact-4 (version 4.0.1, Cytel Software Corp.) and Statistica software (STATISTICA version 6, StatSoft, Inc. 2001). When multiple tests were conducted on the same data, we used a sequential Bonferroni correction (Rice 1989) to adjust the critical alpha considered for statistical significance. Where appropriate, we present the critical alpha (α) with the results of each statistical test.

RESULTS

Feeding Functional Group Composition

Before Invasion

Collectors (filterers, filterers + gatherers and gatherers) dominated the benthic macroinvertebrate community in lakes uninhabited by zebra mussels, and comprised approximately 70% of the total biomass of the community. Filterers + gatherers were the largest group (50% of total biomass). Predators constituted about 17% of the total biomass, comparable to shredders, scrapers and scavengers combined (Table 2).

Table 2. Relative proportions of feeding functional groups of benthic macroinvertebrates (% of total biomass) in Belarussian lakes with and without zebra mussels (average ± SE).

Feeding functional group	Lakes without zebra mussels (n = 4)	Zebra mussel invaded lakes excluding zebra mussels (n = 7)	Zebra mussel invaded lakes including zebra mussels (n = 7)
Collectors: Filterers	4.2 ± 0.9	7.6 ± 2.0	96.7 ± 0.8
Collectors: Filterers + Gatherers	50.4 ± 5.1	34.4 ± 8.5	1.5 ± 0.7
Collectors: Gatherers	14.5 ± 5.2	21.9 ± 3.2	0.7 ± 0.2
Shredders	2.5 ± 2.3	0.3 ± 0.3	< 0.01
Scarpers	9.6 ± 3.5	6.0 ± 1.5	0.2 ± 0.1
Scavengers	2.3 ± 1.1	7.4 ± 3.2	0.3 ± 0.2
Predators	16.5 ± 1.8	22.5 ± 5.2	0.7 ± 0.1

After Invasion, excluding Dreissena: Lakes with before and after data

For the three lakes where we had before and after invasion data, the changes in functional group structure (excluding *Dreissena* biomass) were significant (Lake Boginskoe: P = 0.0008, α = 0.017; Lake Myadel: P = 0.004, adjusted critical α = 0.025; Lake Svir: P = 0.044, α = 0.05; Fisher-Freeman-Halton test) (Table 3).

Table 3. Relative proportions of feeding functional groups of benthic macroinvertebrates (% of total wet biomass) excluding *Dreissena* biomass in three Belarussian lakes studied before (B) and after (A) zebra mussel invasion.

Feeding functional group	Lake Myadel B	Lake Myadel A	Lake Boginskoe B	Lake Boginskoe A	Lake Svir B	Lake Svir A
Collectors: Filterers	5.7	2.4	5.1	10.6	1.6	12.4
Collectors: Filterers + Gatherers	36.0	36.4	55.9	51.3	50.9	51.0
Collectors: Gatherers	29.8	12.7	7.9	21.4	11.1	13.6
Total Collectors	71.5	51.5	68.9	83.3	63.6	77
Shredders	0.0	0.0	0.8	0.0	0.0	0.0
Scarpers	2.3	4.5	14.8	4.0	16.4	7.7
Scavengers	5.4	3.7	0.8	5.4	1.9	2.5
Predators	20.8	40.3	14.7	7.3	18.1	12.8

After Invasion, excluding Dreissena: Pooled data from all lakes

The pooled data for all invaded (7 invaded lakes - Myadel, Bolshie Shvakshty, Boginskoe, Svir, Bolduk, Dolzha, and Volchin) and uninvaded (4 uninvaded lakes - Myadel, Boginskoe, Svir and Ikazn) lakes were tested for differences in the relative biomass of different feeding functional groups. For these pooled data, the changes in the functional trophic groups after zebra mussel invasion were not significant ($P = 0.068$, adjusted critical $\alpha = 0.013$, Fisher-Freeman-Halton test). Collectors remained more than 60% of total community biomass (excluding *D. polymorpha*), and the relative abundance of filterers + gatherers did not change significantly ($P = 0.12$, adjusted critical $\alpha = 0.017$, *t*-test). The portion of collectors-gatherers and filterers also did not significantly change ($P > 0.30$, adjusted critical $\alpha = 0.025$) (Table 2). The change in the relative abundance of all types of collectors before and after invasion was also not significant ($P = 0.065$, Fisher-Freeman-Halton test adjusted critical $\alpha = 0.010$). The portion of scavengers increased, but this change was not significant ($P = 0.039$, Mann-Whitney U test, adjusted critical $\alpha = 0.008$) and the proportion of predators also did not change ($P = 0.36$, *t*-test, critical $\alpha = 0.05$).

After Invasion, including Dreissena

If *D. polymorpha* is considered with the rest of the benthic community, the trophic structure of the benthic community was characterized by an extremely high dominance of one trophic group – collectors filterers, which accounted for > 96 % of the total biomass of benthic invertebrates in lakes populated by zebra mussels (Table 2). The relative proportions of feeding functional groups (in terms of biomass) in the benthic community before and after zebra mussel invasion were significantly different (P << 0.001, Fisher-Freeman-Halton test).

Filtration Capacity of Planktonic versus Benthic Community

After *Dreissena* invasion, the total average biomass of the benthic community including zebra mussels increased 22 times, from 10.3 ± 3.8 (mean ± SE) to 225.5 ± 18.9 g m^{-2} (P = 0.002, adjusted critical α = 0.025, paired *t*-test). Before the zebra mussel invasion, planktonic invertebrates filtered the equivalent of the volume of the lake in 4 - 9 days (6.5 ± 1.1) (Table 4). The benthic community, however, would take 0.2 - 10 years (3.8 ± 1.9) to filter the same volume, an average 213 times slower than for zooplankton.

After invasion, the filtration ability of benthic community increased > 70 times. The time required for the benthic community to filter the volume

Table 4. Mean biomass of zooplankton and benthic communities, and the time required to filter a volume of water equal to the lake volume before and after zebra mussel invasion.

Parameter		Lake Bolshie Shvakshty	Lake Svir	Lake Volchin	Lake Dolzha
Before *Dreissena* invasion					
Zooplankton*:	biomass (g m^{-3})	0.97	1.55	1.03	2.08
	days to filter	9	5	8	4
Zoobenthos:	biomass (g m^{-2})	20.0	10.1	1.2	9.8
	days to filter	63	59	3688	1732
After *Dreissena* invasion					
Zooplankton*:	biomass (g m^{-3})	0.52	2.78	1.37	1.25
	days to filter	16	3	6	7
Zoobenthos excluding *Dreissena*:	biomass (g m^{-2})	22.7	16.2	9.1	4.4
	days to filter	77	39	303	506
Dreissena:	biomass (g m^{-2})	163	238	192	257
	days to filter	10	14	55	15
Zoobenthos including *Dreissena*:	biomass (g m^{-2})	185	254	202	261
	days to filter	4	10	47	14

*data from Karatayev and Makritskaya (1999) equivalent to that of the lake decreased to 19 ± 10 days, and was not significantly different from that for the planktonic community (8 ± 3 days, P = 0.40, paired *t*-test). The total biomass of benthic invertebrates excluding *Dreissena* did not change significantly after zebra mussel invasion (P = 0.41, paired *t*-test). There was also no significant difference in the biomass of zooplankton before and after zebra mussel invasion (1.4 ± 0.3 g m^{-3} vs. 1.5 ± 0.5 g m^{-3}, paired *t*-test, P = 0.88), nor in the time to filter the equivalent of the volume of the lake (6.5 ± 1.1 vs. 7.9 ± 2.8, P = 0.65, *t*-test). The high filtration rate for the zoobenthos in Lake Bolshie Shvakshty was attributed to an unusually large biomass of chironomids, which can have a very high filtration rate (> 1,700 mL g^{-1} hr^{-1}, Izvekova 1975).

DISCUSSION

Feeding Functional Group Composition

We found a dramatic shift in the benthic trophic structure after *D. polymorpha* invasion. The structure of feeding functional groups in the community including *Dreissena* was overwhelmingly dominated by collectors-filterers. *D. polymorpha* was the dominant benthic species in terms of biomass.

These results are consistent with findings from other lakes and reservoirs in the former Soviet Union including Uchinskoe Reservoir, Russia (Lvova-Kachanova and Izvekova 1978, Sokolova et al. 1980a, Sokolova et al. 1980b) and Lake Lukomskoe, Belarus (Karatayev and Burlakova 1992, Karatayev et al. 1997). The invasion of *D. polymorpha* in Uchinskoe Reservoir resulted in the replacement of the dominant species, the chironomid filter-feeder *Glyptotendipes paripes,* and drastic changes in the relative abundance of different species and trophic groups (Lvova-Kachanova and Izvekova 1978, Sokolova et al. 1980a, 1980c). Following the invasion of *D. polymorpha* in Lake Lukomskoe the benthic community was characterized by an exceedingly high dominance of filterers, which accounted for 95% of the total benthic animal biomass (Karatayev and Burlakova 1992). As a result, the trophic structure of the littoral zone was impoverished, and the remaining trophic groups contributed relatively little to the total biomass. Similar patterns were found for six other waterbodies across the Former Soviet Union, where *Dreissena* comprised > 93% of the total biomass of benthic community (Karatayev et al. 1994, 1997).

Other studies of benthic communities in zebra mussel beds have shown dramatic differences in the density and biomass of associated taxa compare to substrates without mussels (reviewed in Karatayev et al. 1997, 2002). The creation of new habitat is perhaps the most important effect that zebra mussels have on the benthic community. Several experimental studies have shown that the structure created by zebra mussels provides refuge for a variety of species, and this impact is seen even in the absence of the biological activity of filtering mussels (Slepnev et al. 1994, Ricciardi 1997, Stewart et al. 1998, 1999).

Another possible mechanism through which zebra mussels may impact benthic community functional structure is through trophic impacts. Some studies have reported increases in the relative abundance of collectors due to enrichment of the benthos with organic substances from feces and pseudofeces created by zebra mussels or decreases in filterers due to competition for food with zebra mussels (Izvekova Lvova-Katchanova 1972, Stewart et al. 1998, Berezina 1999). All of these changes may be obvious within zebra mussel beds and areas with high mussel densities. However, in all lakes with zebra mussels much of the bottom is not covered by mussels, especially in the profundal zone (Stánczykowska and Lewandowski 1993, Burlakova, Karatayev, personal observations). Therefore, the overall effect on the entire benthic community might be much less pronounced than in areas with high zebra mussel densities.

When the average structure of benthic trophic groups was pooled across lakes with and without zebra mussels, differences in the relative abundance of the feeding functional groups did not significantly change after zebra mussel invasion. However, we had relatively few lakes in our sample, limiting the power of our statistical tests. With greater sample sizes, the quantitative changes in scavengers could be significant. These results suggest that the major change in the community was the addition of zebra mussels rather than the displacement of other functional groups. However, the data for individual lakes indicated significant changes in several functional groups before and after zebra mussel invasion, but the changes were not in concert, and were often in opposite directions for the same functional group. Thus, these changes were masked when the data were pooled. These results do, however, highlight the importance and power of before and after data. To fully understand the impacts of zebra mussels on communities we need much more community data on lakes before and after invasion, and, unfortunately, these data are rare.

Suspension-feeders are an integral component of aquatic ecosystems. They feed upon a very dilute food resource and convert previously dispersed, minute materials to larger animal biomass, i.e., their own bodies (Wallace and Merritt 1980). The overpowering dominance of collectors-filterers after zebra mussel invasion will drive changes in ecosystem function as they greatly enhance the rates of deposition of both organic and inorganic material on the bottom and thus build a direct connection between the planktonic portion of the water body and the benthos (benthic-pelagic coupling) (reviewed in Karatayev et al. 2002). In addition, *Dreissena* as well as many associated benthic animals are prey for benthivorous fishes (reviewed in Molloy et al.

1997, Karatayev et al. 1994). They may also provide an important path for moving energy from the benthic community to higher trophic levels.

Zebra Mussel as a Biofilter

The role of bivalves in and impacts on aquatic ecosystems has long been recognised for marine and estuarine ecosystems (reviewed in Dame 1993, 1996). Bivalves can affect nutrient cycling by consuming particulate and dissolved organic matter and excreting inorganic nutrients. They affect community structure (both in the water column and on the benthos) and can influence community stability, diversity and interspecies links (Dame 1996). Zebra mussels create high densities over large areas in lakes and efficiently filter large volumes of water. They deposit substantial amounts of pseudofeces and feces on the bottom. Thus, they play the same ecosystem engineering role as marine bivalves (Karatayev et al. 2002).

We found that before invasion by zebra mussels, the planktonic community filtered the equivalent to the volume of each lake within a few days, and were on average > 200 times more effective than the benthic community, which took four years to filter the same volume. We found no significant changes in the total biomass or filtration capacity of the zooplankton community in lakes after zebra mussel invasion. However, the total average biomass of the benthic community, including zebra mussels, increased 22 times, and filtration ability of the benthic community increased > 70 times. Consequently, the time required to filter the volume of each lake for the benthos was no different than that for the zooplankton community. The impacts of increased benthic filtration on the ecosystem will depend on the size of the *Dreissena* population, lake morphometry and rate of water exchange, and will be more pronounced in littoral zone where zebra mussels are most dense and less in profundal areas of deep lakes where zebra mussels are rare or absent.

Our results are consistent with the findings of other studies. During the summer, *D. polymorpha* has been estimated to filter the volume of water equivalent to that of an entire waterbody from 5 to 90 days (Mikheev 1967, Stanczykowska 1977, Lvova et al. 1980, Protasov et al. 1983, Reeders et al. 1989, Karatayev and Burlakova 1995a, Petrie and Knapton 1999). After *D. polymorpha* invaded Lake Lukomskoe (Belarus), the filtration capacity of the benthic community increased 320 times, and the time to filter the equivalent of the volume of the lake decreased from 15 years to 17 days. At the same time zooplankton abundance declined, and the time required for the zooplankton community to filter the equivalent of the volume of the lake increased from 5 to 17 days (Karatayev and Burlakova 1992, 1995b).

In most freshwater ecosystems, benthic production is driven by the slow rain of suspended organic material to the bottom and to a lesser extent by the filtration activity of bottom suspension-feeders where most species feed on detritus or other benthic organisms. Consequently, the typical benthic freshwater system is considered to be detritus dominated, rather than relying on large amounts of primary productivity or direct links to planktonic processes. Usually, the benthos are not capable of controlling processes or dynamics in the planktonic system. Zebra mussels, filtering vast amount of water in a short period of time, provide a direct link between processes in the plankton and those in the benthos and by their deposition of pseudofeces and feces, provide a direct conduit for primary productivity in the water column to the benthos. Thus, they are able to control pelagic processes by removal of particulate matter, increasing water transparency and hence the volume of the photic zone, impacting phytoplankton standing stock, and, therefore, they can influence planktonic trophic interactions (reviewed in Karatayev et al. 2002). As a result, the role of the benthic community in lakes populated by zebra mussels increases tremendously and the benthos become capable of controlling processes and dynamics in the planktonic system and, therefore, the whole freshwater ecosystem. All of these effects are the direct result of changes in the trophic structure of the benthic community after zebra mussel invasion and the overwhelming dominance of one trophic group – filterers.

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