

What a difference a species makes: a meta-analysis of dreissenid mussel impacts on freshwater ecosystems

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Abstract. We performed a meta-analysis of published studies and long-term monitoring data sets to evaluate the effects of dreissenid mussels (*Dreissena polymorpha* and *D. rostriformis bugensis*), two of the world's most problematic biological invaders, on the biogeochemistry, flora, and fauna of lakes and rivers across North America and Eurasia. Dreissenid effects were structured along two distinct energy pathways. For the pelagic–profundal pathway, large mean reductions in phytoplankton (–35% to –78%) and zooplankton (–40% to –77%) biomass occurred and were dependent on habitat type. The largest effects were found in rivers, followed by littoral and pelagic habitats in lakes. In contrast, benthic energy pathways within littoral habitats of lakes and rivers showed dramatic increases in mean benthic algal and macrophyte biomass (+170% to +180%), sediment-associated bacteria (about +2000%), non-dreissenid zoobenthic biomass (+160% to +210%), and total zoobenthic biomass, which includes dreissenid mussel soft tissues (+2000%). Our study quantifies the remarkable ability of these invasive mussels to shift aquatic food webs and energy flow from pelagic–profundal to benthic–littoral energy pathways, and it provides a basis for forecasting their impacts in diverse freshwater ecosystems. Our meta-analysis approach was a powerful tool for moving beyond the idiosyncrasies of individual case studies and may be equally powerful for assessing impacts of other biological invaders.

Key words: *benthic–pelagic coupling; biological invasion; cross-habitat subsidies; Dreissena spp.; ecosystem engineer; exotic species; facilitation; food web disruption; invasive species; quagga mussel; zebra mussel.*

INTRODUCTION

The introduction of species outside of their native range represents one of the greatest and most irreversible threats to the biological diversity and integrity of ecosystems on a global scale (OTA 1993, Simberloff 1996, Sala et al. 2000). Further, human-mediated biological invasions are now so pervasive throughout the world that their impacts constitute a major component of human-induced global change (Vitousek et al. 1997). Among the world's 100 most troublesome biological invaders (IUCN 2005) is the zebra mussel, *Dreissena polymorpha*. Native to the Ponto-Caspian basin, zebra mussels have spread widely across Eurasia and North America. A closely related species, *D. rostriformis bugensis*, commonly known as the quagga mussel, has also recently expanded from its native range

in the Ponto-Caspian region and invaded North America (Benson 2009). Total costs associated with zebra mussel bio-fouling of water intakes at drinking water and power facilities in North America from 1989 to 2004 were estimated to be ~267 million dollars, with an ongoing cost of ~11–16 million dollars per year (Connelly et al. 2007). The ecological impacts of dreissenids can be far reaching, affecting organisms as disparate as sediment bacteria (Frischer et al. 2000) and piscivorous fishes (Strayer et al. 2004), and causing large and sustained changes in physical and chemical attributes that define the habitat for all resident species (Nicholls et al. 1999, Strayer et al. 1999, Canale and Chapra 2002). Dreissenids have caused cyanobacterial and benthic algal blooms (Orlova et al. 2004, Higgins et al. 2008, Knoll et al. 2008) as well as the decline of native unionid and fish populations (Schloesser and Nalepa 1994, Ricciardi et al. 1998, Mills et al. 2003, Strayer et al. 2004, Strayer and Malcom 2007).

Despite the hundreds of studies on dreissenid mussels, mostly conducted at the subecosystem level, there has

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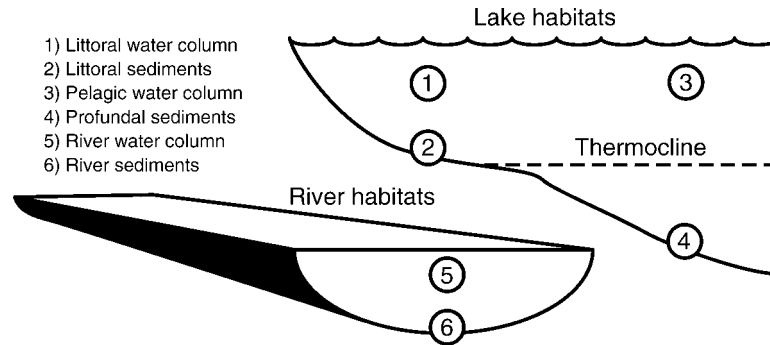


FIG. 1. Lake and river habitats used to evaluate the impacts of invasive dreissenids (zebra mussel *Dreissena polymorpha* and quagga mussel *D. rostriformis bugensis*) on the biogeochemistry, flora, and fauna of lakes and rivers across North America and Eurasia.

been no quantitative synthesis of their impacts on freshwater ecosystems. Indeed, there is only one quantitative synthesis of dreissenid effects for a particular ecosystem subcomponent, the zoobenthos (Ward and Ricciardi 2007). Thus, the range, variability, and magnitude of ecological impacts for lake and river ecosystems have not been quantified. Considering that dreissenids have invaded thousands of lakes and rivers throughout Eurasia and North America (Stanczkowska and Lewandowski 1993, Karatayev and Burlakova 1995, Son 2007, Zoltak and Brown 2008, Benson 2009), they continue their range expansion, and can have dramatic effects on whole ecosystems (Karatayev et al. 1997, 2002, Strayer et al. 1999), an ecosystem-scale assessment of their impacts on the world's freshwater ecosystems is urgently needed.

Here, we have compiled nearly 200 studies and conducted a quantitative meta-analysis in order to estimate the mean, variance, and statistical significance of dreissenid mussel impacts on freshwater ecosystems. We examine dreissenid impacts on well-studied biogeochemical parameters and major floral and faunal groups within benthic and pelagic habitats of lakes and rivers (Fig. 1). We test the significance of these effects using a common statistical approach in meta-analysis, the log response ratio (LR) (Gurevitch and Hedges 1999). Our general hypotheses were that dreissenid invasions induced significant changes in: (1) the biomass or abundance of major trophic groups; (2) the patterns of energy flow through freshwater ecosystems; and (3) that these impacts would be structured across two alternate energy pathways, a pelagic–profundal pathway dominated by phytoplankton, zooplankton, and profundal zoobenthos, and a benthic pathway dominated by benthic autotrophs and littoral zoobenthos.

BACKGROUND ON DREISSENIDS

Both *D. polymorpha* and *D. rostriformis bugensis* are relatively small (25–35 mm length) suspension-feeding mussels, commonly reaching densities >10 000 individuals/m², and sometimes exceeding 100 000 individuals/m² in localized areas (Ludyanskiy et al. 1993, Effler and

Siegfried 1994, Patterson et al. 2005). The density of *D. polymorpha* varies as a function of substrate size, with densities on hard (e.g., boulder, gravel) substrates orders of magnitude higher than on sand or mud substrata (Mellina and Rasmussen 1994, Berkman et al. 1998). In contrast, *D. bugensis* commonly occupies hard and soft substratum, is commonly found at depths >20 m, and has been found in profundal sediments to depths >100 m (Mills et al. 2003, Nalepa et al. 2007, Watkins et al. 2007). Dreissenids are *r* strategists with a short maturation time (1–2 years), high fecundity (>1 million eggs produced per female per spawning event), and a remarkable ability for dispersal, aided by a planktonic veliger stage and an adult stage that adheres strongly to most hard surfaces (Ludyanskiy et al. 1993).

During the mid-1800s, *D. polymorpha*, native to the Azov and Black Sea region of Eastern Europe, penetrated into other eastern and western European nations through the opening of canal systems connecting these regions (Zhadin 1946, Ludyanskiy et al. 1993). The dispersal of *D. polymorpha* to most eastern and western European nations has been described previously (Stanczkowska 1977, Walz 1991, Stanczkowska and Lewandowski 1993, McCarthy et al. 1997, Coughlan 1998, Pollux et al. 2003). The invasion of *D. polymorpha* into North America was facilitated through the ballast water of trans-Atlantic ships, and was first identified in the western basin of Lake Erie during 1986 (Carlton 2008). Within a few years of establishment, *D. polymorpha* expanded its range to include all five of the Laurentian Great Lakes. *D. polymorpha* reached the upper Mississippi River by 1991 (Cope et al. 1997), began invading connecting rivers and lakes, and by 1993 had expanded its range southward by >3500 km to the Gulf of Mexico (Benson 2009). *D. rostriformis bugensis* was first identified in North America in 1991, within Lake Ontario and connecting waterways (May and Marsden 1992). However, it is thought that this species first arrived in 1989 (Mills et al. 1993). *D. rostriformis bugensis* has since largely replaced *D. polymorpha* in the lower Laurentian Great Lakes (Patterson et al. 2005, Wilson et al. 2006, French et al. 2007). The North

TABLE 1. Morphometric characteristics and densities of invasive dreissenids (zebra mussel *Dreissena polymorpha* and quagga mussel *D. rostriformis bugensis*) in ecosystems included in the meta-analysis.

Characteristic	Lakes	Rivers	Enclosure experiments
<i>N</i>	68	11	18
Mean depth (m)	1.0–161	<0.9–8.3	0.2–10
Surface area (km ²):	<0.1–58 000		0.1–8
Volume (m ³)	<0.01–4900		0.001–49‡
Width (m)		15–800	
Annual discharge (m ³ /s)		2–900	
Dreissenid density† (no./m ²)	<1–40 000	50–26 000	150–10 000

† The range of dreissenid densities based on reported whole-ecosystem averages, rather than site-specific densities.

‡ Units for volume of enclosure experiments are m².

American distribution of this species outside of the Laurentian Great Lakes is currently estimated to be <50 lakes or reservoirs, compared with >650 lakes or reservoirs for *D. polymorpha* (Benson 2009).

METHODS

Data collection

We searched the literature, several databases, and government reports for studies and long-term data sets examining the effects of dreissenid (*D. polymorpha* and *D. rostriformis bugensis*) mussel invasions on the biogeochemistry, flora, and fauna of the world's lake and river ecosystems. All data came from North American and European ecosystems. A complete listing of ecosystems is available in the Appendix. Literature searches were conducted on three online databases (Science Citation Index, Web of Science, and Aquatic Sciences and Fisheries Abstracts) for articles containing the key words dreissen*, or zebra mussel, or quagga mussel, in combination with other key words including algae, autotroph*, bacteria, benthic, benthos, experiment, fish*, invertebrate, lake, macrophyte, mesocosm, microcosm, periphyton, phyto-benthos, phytoplankton, river, sediment*, stream, vertebrate, zoobenthos, or zooplankton (asterisks in database searches allowed for the detection of multiple derivatives of a word, e.g., fish* = fish, fishes, fishing, fishery, etc.). Database searches were conducted for the years 1965–2008. Reference lists from these literature sources were searched for additional sources. In addition to the peer-reviewed literature, long-term data sets for dreissenid-invaded lakes and rivers were obtained from several sources including: the EPA STORET database, the National Waters Resource Institute of Environment Canada, the Ontario Ministry of the Environment, the USGS Upper Midwest Environmental Sciences Center, the Lake Champlain water quality and biological monitoring project, and the Onondaga County Department of Water Environment Protection. In total, our search identified >500 studies, of which 190 provided sufficient information to test dreissenid effects in >65 lakes and 11 rivers, spanning large gradients in size, discharge, and trophic status (Table 1). Twenty-five

mesocosm and microcosm experiments on dreissenid effects were also included in the analysis. These were treated separately from natural systems except where specifically noted. A complete listing of lakes, rivers, and literature sources is available in the Appendix.

Metrics and criteria

Meta-analyses are often conducted using weighted statistical analysis, where replication and variance within experiments are accounted for (Gurevitch and Hedges 1999). Weighted analyses require information on the mean value for each group, the standard deviation within each group, and the number of individuals within each group to be compared (Gurevitch and Hedges 1999). However, many studies often fail to report all necessary information. For this reason meta-analyses may also use unweighted statistical analyses, such as the log response ratio (LR), where only mean values for each group are required (Gurevitch and Hedges 1999). For our purposes, we considered the use of an unweighted metric superior to a weighted metric, since the latter approach would have excluded a large number of studies. While reducing statistical power, the use of an unweighted analysis had an additional benefit that each experiment (in our case each dreissenid-invaded ecosystem) was given equal weighting. Since the effect of dreissenid invasions on a parameter of interest (e.g., invertebrate biomass) was assessed only once for each ecosystem (even though multiple studies may have occurred within that ecosystem), our approach ensured that ecosystems that were intensively studied because dreissenid effects were large were not overemphasized in our analysis.

The unweighted log response ratio was calculated as $LR = \log_e(X_{+D}/X_{-D})$, where X_{+D} equals the mean parameter value in the presence of dreissenid mussels, and X_{-D} equals the mean parameter value in the absence of dreissenid mussels. In the majority of cases, LR values were calculated from studies examining changes in biogeochemical parameters, flora, or fauna over time, and in these cases X_{-D} and X_{+D} represent parameter values for pre- and post-dreissenid periods, respectively. In some cases we incorporated data from studies

TABLE 2. Dreissenid mussel impacts (between pre- and post-dreissenid invasion periods) on the biogeochemical parameters and major floral and faunal groups of freshwater ecosystems and enclosure experiments.

Parameter	Lake (all habitats)				Pelagic-profundal				Littoral			
	<i>n</i>	%	SE	<i>P</i>	<i>n</i>	%	SE	<i>P</i>	<i>n</i>	%	SE	<i>P</i>
Biogeochemistry												
Secchi	46	38.5	4.7	<0.001	27	30.7	5.5	<0.001	19	50.5	10.7	<0.001
Turbidity	10	-40.7	21.5	0.025	5	-34.7	21.2	0.178	5	-46.2	23.3	0.118
SS†	21	-39.7	10.8	<0.001	9	-72.2	8.0	<0.001	12	-46.0	10.1	0.001
Alkalinity	6	2.8	24.2	0.902	5	5.8	27.0	0.842				
Chloride	12	-0.8	3.2	0.804	4	0.3	5.5	0.960	8	-1.3	4.1	0.762
DIN	17	7.6	8.1	0.361	8	8.2	16.7	0.637	9	7.0	5.4	0.230
TDN	14	-1.2	6.0	0.839	7	-6.1	10.5	0.584	7	4.0	4.4	0.396
TKN	16	-14.6	9.0	0.088	8	-17.3	15.8	0.311	8	-11.8	3.7	0.015
NO ₃	22	-4.0	21.8	0.837	12	-23.7	30.5	0.452	10	26.4	9.7	0.024
NH ₃	14	-21.0	24.6	0.303	7	6.6	35.7	0.859	7	-41.6	19.0	0.072
SRP	18	-1.8	15.5	0.902	7	39.1	22.6	0.134	11	-21.3	15.7	0.203
TP	42	-19.5	3.8	<0.001	24	-20.8	4.0	<0.001	18	-17.9	5.8	0.006
SiO ₂	16	30.0	13.6	0.058	6	75.6	37.9	0.103	10	8.4	8.8	0.364
Sed. org. C‡									12	93.1	33.7	0.019
Water column flora/fauna												
Chl <i>a</i>	45	-47.3	6.5	<0.001	26	-37.8	8.1	<0.001	19	-58.1	9.5	<0.001
Phytoplankton§	19	-58.5	12.2	<0.001	10	-34.6	15.9	0.057	9	-74.9	12.4	<0.001
Zooplankton	15	-51.3	13.1	0.002	5	-40.1	20.9	0.128	10	-56.1	16.6	0.008
Benthic flora/fauna												
Littoral depth¶									6	39.4	26.4	0.015
Periphyton									4	170.5	95.3	0.037
SAV (% cover)#									7	182.1	155	0.021
Bacteria††									6	2115	879	0.061
Zoobenthos‡‡	15	61.4	38.2	0.130	5	-46.6	34.8	0.066	8	211.7	48.3	0.003
Zoobenthos§§	15	749	220	0.004	5	-11.1	63.5	0.853	8	1976	505	0.006

Note: While dreissenid effects are reported as percentage change, statistical analyses were conducted using a two-tailed *t* test on the population of log response ratio values for each parameter (see *Methods*).

† Some suspended solids (SS) data were derived from turbidity values using a derived empirical relationship between turbidity and SS.

‡ Sediment organic carbon.

§ Phytoplankton biomass estimates from cell counts and biovolume estimates using microscopy.

|| Data reported as change in biomass.

¶ Littoral depth refers to maximum depth colonized by rooted macrophytes.

SAV refers to submerged aquatic vegetation (macrophytes).

†† Data reported as change in numerical abundance.

‡‡ Biomass of zoobenthos excluding dreissenid mussels. Data for zoobenthos in rivers is for abundance rather than biomass.

§§ Biomass of zoobenthos including dreissenid mussels.

utilizing experimental dreissenid additions (tile colonization experiments) or space-for-time substitutions (e.g., upstream-downstream) to test for dreissenid effects on benthic invertebrate communities.

The use of X_{-D} and X_{+D} was restricted to <15 years before and after dreissenid invasion. Further, we excluded studies where dreissenid effects were estimated between year groupings that were ≥ 10 years apart. For long-term monitoring data sets, potential outliers (outside two standard deviations of the seasonal mean value) within pre- or postinvasion periods were excluded from further analyses. The mean parameter value for each year's ice-free period was used to calculate the grand mean value (X_{-D} and X_{+D}) for pre and post-invasion years. When data for multiple sites were provided, site averages were calculated for each habitat type. If the data sets contained raw data for multiple depths, mean values for the epilimnion were calculated for each sampling date.

Where data were sufficient, the effects of dreissenid mussels were assessed in four lake habitats and two river habitats (Fig. 1). For biogeochemical parameters, the littoral was defined as the portion of the lake where complete mixing occurred from the lake surface to the sediments, and included shallow lakes and embayments of large lakes where $\geq 80\%$ of the lake area was above the mixing depth. Where mixing depths were unreported, they were estimated based on lake surface area (Hanna 1990). The pelagic zone was defined as the offshore, upper-surface layer above the thermocline (Fig. 1). Profundal habitats were defined as the benthic portion of a lake at depths below the littoral zone. A potential fifth zone, the water column within the hypolimnion, was excluded due to lack of sufficient data for analysis. To limit problems of nonindependence (Gurevitch and Hedges 1999) we used only one effect size (i.e., one LR value) for each parameter within a lake or river habitat. Where there were multiple studies for a lake or river habitat, we used long-term monitoring data

TABLE 2. Extended.

River				Enclosures			
<i>n</i>	%	SE	<i>P</i>	<i>n</i>	%	SE	<i>P</i>
7	71.4	16.3	0.005				
3	-50.3	26.4	0.197				
4	-38.6	10.8	0.037	7	-58.8	15.5	0.009
				5	28.9	10.5	0.051
				5	28.7	10.3	0.050
4	73.7	48.5	0.226	15	34.2	8.9	0.002
5	429	157	0.052	13	393.8	117	0.005
6	-9.3	7.5	0.269	12	315.8	145	0.052
7	-78.3	17.3	0.004	15	-79.6	16.8	<0.001
3	-76.5	10.7	0.019	12	-51.1	21.2	0.034
5	156.0	38.5	0.050				

sets over shorter-term studies, and studies with the most robust sampling methodologies (largest sampling frequency and largest number of stations). Data sets from redundant studies were discarded.

The significance of dreissenid effects was tested using a two-tailed *t* test on the population of LR values for each parameter using the statistical software R (version 2.7.2). Dreissenid effects were considered statistically significant, or moderately significant, when the distribution of LR values deviated from 0 (no effect) at the *P* < 0.05 and *P* < 0.10 levels, respectively. In some cases, low sample size may have resulted in *P* values indicating dreissenid effects were nonsignificant, even though effect sizes were large. In some of these cases results may be ecologically relevant despite *P* values exceeding traditional criteria for statistical significance. We focus attention on these statistically nonsignificant, but potentially ecologically relevant, results to encourage further research in those areas. In all cases where we test the statistical significance of dreissenid effects, we report *P* values, *n* values, and estimates of variance. High natural variability in dreissenid effects was expected, since the magnitude of dreissenid effects should be related to dreissenid density and filtration capacity, both of which are unknown and unreported in most invaded ecosystems. While LR values were used to calculate the statistical significance of dreissenid effects, we converted these LR values to units of percentage change for presentation purposes, allowing for more accessible

interpretation of the results and assessment of their ecological relevance.

Due to a lack of data, we were unable to quantify or test the significance of dreissenid effects on fish populations. We have, however, qualitatively reviewed the current information on dreissenid effects on the fish community.

RESULTS

Water clarity and suspended solids

Dreissenid invasions were associated with significant decreases in suspended particulate matter (suspended solids and turbidity) and significant increases in water clarity (Secchi depth) in lakes and rivers (Table 2, Fig. 2a, b). An exception to this general dreissenid effect was

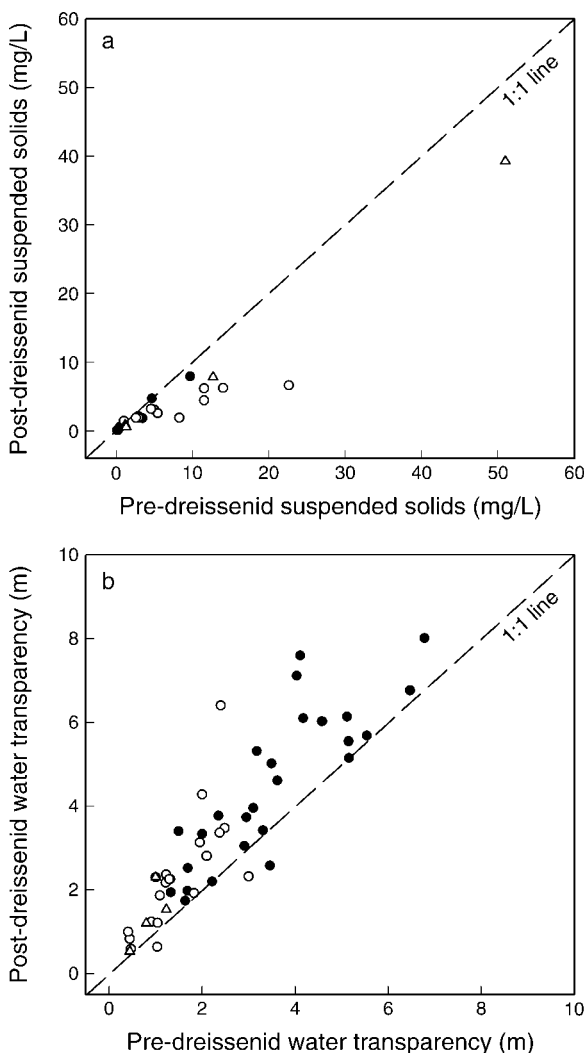


FIG. 2. The impacts of dreissenids on (a) suspended matter and (b) Secchi depth (water clarity) in freshwater ecosystems. Symbols represent pelagic (solid circles), littoral (open circles), and river (open triangles) habitats during pre- vs. post-dreissenid invasion periods. Values above the 1:1 line indicate an increase in parameter values after invasion, while values below the line indicate a decrease.

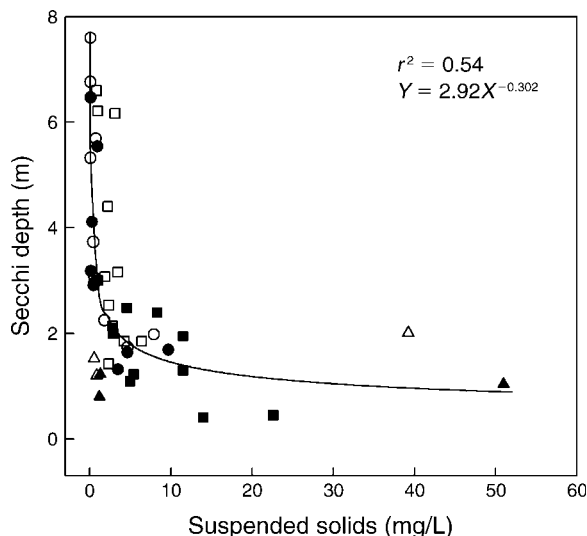


FIG. 3. The relationship between suspended solids and water transparency in pelagic (circles), littoral (squares), and river (triangles) habitats. Solid symbols refer to values during the pre-dreissenid mussel period, and open symbols the post-dreissenid mussel period.

a nonsignificant result for turbidity in rivers ($n = 3$, $X = -50\%$, $P = 0.197$ [Table 2]), though a low sample size reduced statistical power. Dreissenid invasions were associated with mean reductions in suspended solids (SS) concentrations by 30–46% across habitat types (Table 2), with the largest absolute declines in habitats where pre-dreissenid SS concentrations were high (Fig. 2a).

The nonlinear relationship between SS and water clarity (Fig. 3) is important for understanding dreissenid effects on water clarity. At SS concentrations above 2–3 mg/L, large changes in SS have only small effects on water clarity. As SS concentrations fall below this threshold, small changes in SS have increasingly large effects on water clarity. Changes in SS were an order of magnitude higher in river and littoral habitats (about 4.0 mg/L) than in pelagic habitats (0.4 mg/L). However, mean SS concentrations in river and littoral habitats were higher than the 2–3 mg/L threshold during pre- and postinvasion periods. In contrast, mean SS concentrations in pelagic habitats were below the threshold during both periods. As a result, despite much greater declines in suspended particulate matter in rivers and littoral zones, absolute changes in water clarity (Secchi depth) were lower in river (mean \pm SD = 0.6 ± 0.6 m, $n = 7$) and littoral (0.8 ± 1.0 m, $n = 19$) habitats than in pelagic habitats (1.0 ± 1.0 m, $n = 27$).

Major nutrients

Dreissenid effects on dissolved nitrogen compounds in natural ecosystems were complex and did not always follow the general increases noted in enclosure experiments (Table 2, Fig. 4a–c). In littoral lake habitats,

dreissenid effects on nitrate (NO_3) concentrations were similar in direction and magnitude to enclosure experiments. However, ammonia (NH_3) declined by 40% in littoral habitats, and there was no detectable change in total dissolved nitrogen (total dissolved nitrogen = dissolved inorganic N + dissolved organic N) between pre- and postinvasion periods (Table 2, Fig. 4a). In pelagic habitats, there was no significant effect of dreissenids on NO_3 , NH_3 , DIN (dissolved inorganic nitrogen), or TDN (total dissolved nitrogen) (Table 2). In rivers, sufficient data were available only to test dreissenid effects on NH_3 . While effects were generally positive (Fig. 4c), a low sample size and high variability between rivers contributed to a nonsignificant result (Table 2).

In river habitats, there was a large and moderately significant increase in soluble reactive phosphorus (SRP) following dreissenid invasion (Table 2). In four of the five rivers in our data set, SRP ranged from 1.0 to 11 $\mu\text{g/L}$ prior to dreissenid invasion, increasing to 17–40 $\mu\text{g/L}$ following invasion (Fig. 4d). The effect of dreissenids on SRP in lake littoral and pelagic habitats was nonsignificant (Table 2). In rivers, declines in particulate phosphorus (PP) were compensated by large increases in SRP, and total phosphorus (TP) remained unchanged after dreissenid invasion ($n = 6$, $P = 0.269$ [Table 2, Fig. 4e]). Within lakes, TP concentrations in both littoral and pelagic habitats declined by 18–20% (Table 2), or 5.1 ± 3.5 $\mu\text{g/L}$, following dreissenid invasion.

In pelagic or littoral habitats, dissolved silica (SiO_2) concentrations were not significantly different between pre- and post-dreissenid invasion periods (Table 2, Fig. 4f). When these habitat types were combined, there were moderately significant ($n = 16$, $P = 0.058$) increases in SiO_2 concentrations of 30%, or 0.12 ± 0.13 mg/L following dreissenid invasion (Table 2). Insufficient data precluded an assessment of dreissenid effects on SiO_2 in rivers.

We found sufficient data to test dreissenid effects on alkalinity only within pelagic habitats of lakes, and effect sizes were low and nonsignificant (Table 2). Changes in chloride in pelagic and littoral habitats were nonsignificant (Table 2). Insufficient data precluded assessment of changes in chloride concentrations in rivers. Data for examining dreissenid effects on sediment organic carbon was available only for littoral habitats in lakes. These data indicated that dreissenid mussels nearly doubled the organic carbon content of surrounding sediments (Table 2).

Water column biota

Phytoplankton.—Phytoplankton biomass was most often ($n = 52$) estimated using concentrations of the ubiquitous algal pigment chlorophyll *a* (chl *a*) and less often ($n = 21$) by cell-counting methods (reported as “biomass”). We reported the results of these methods separately (Table 2). Significant declines in phytoplankton biomass were identified across habitat types (Table

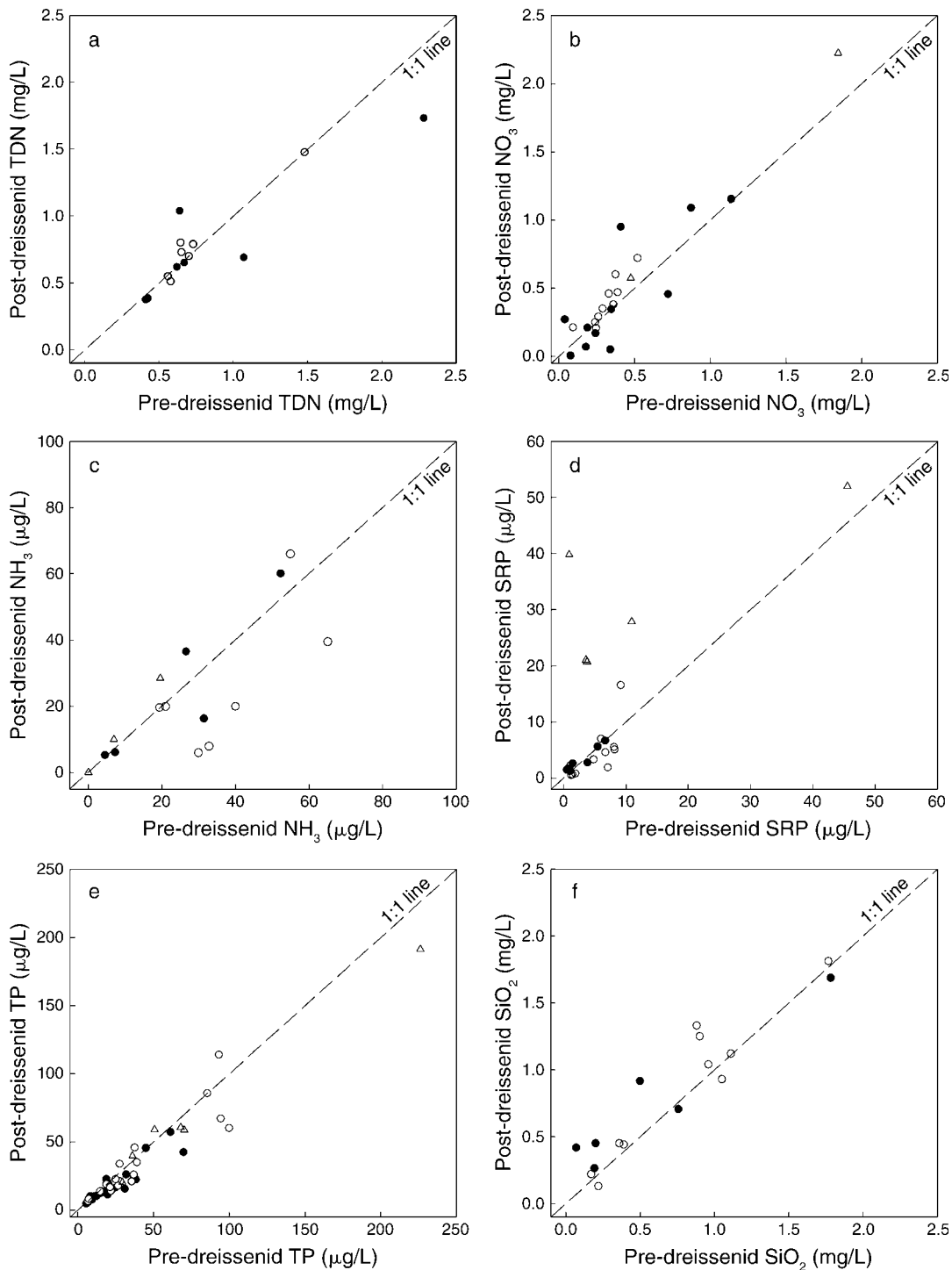


FIG. 4. The impact of dreissenid mussels on nutrient concentrations in freshwater ecosystems. Symbols are as in Fig. 2. Values above the 1:1 line indicate an increase in nutrient concentrations after dreissenid invasion, while values below the line indicate a decrease. TDN is total dissolved nitrogen; SRP is soluble reactive phosphorus; TP is total phosphorus.

2, Fig. 5). Mean chl *a* declined from 6.9 to 4.2 µg/L in pelagic habitats, from 19.9 to 8.7 µg/L in littoral habitats, and from 31.8 to 8.5 µg/L in rivers between pre- and postinvasion periods. Absolute changes in chl *a*

tended to be highest when pre-dreissenid chl *a* was elevated (Fig. 5a). Changes in phytoplankton biomass were nonlinearly correlated with dreissenid mussel filtration capacity (FC), which represents the fraction

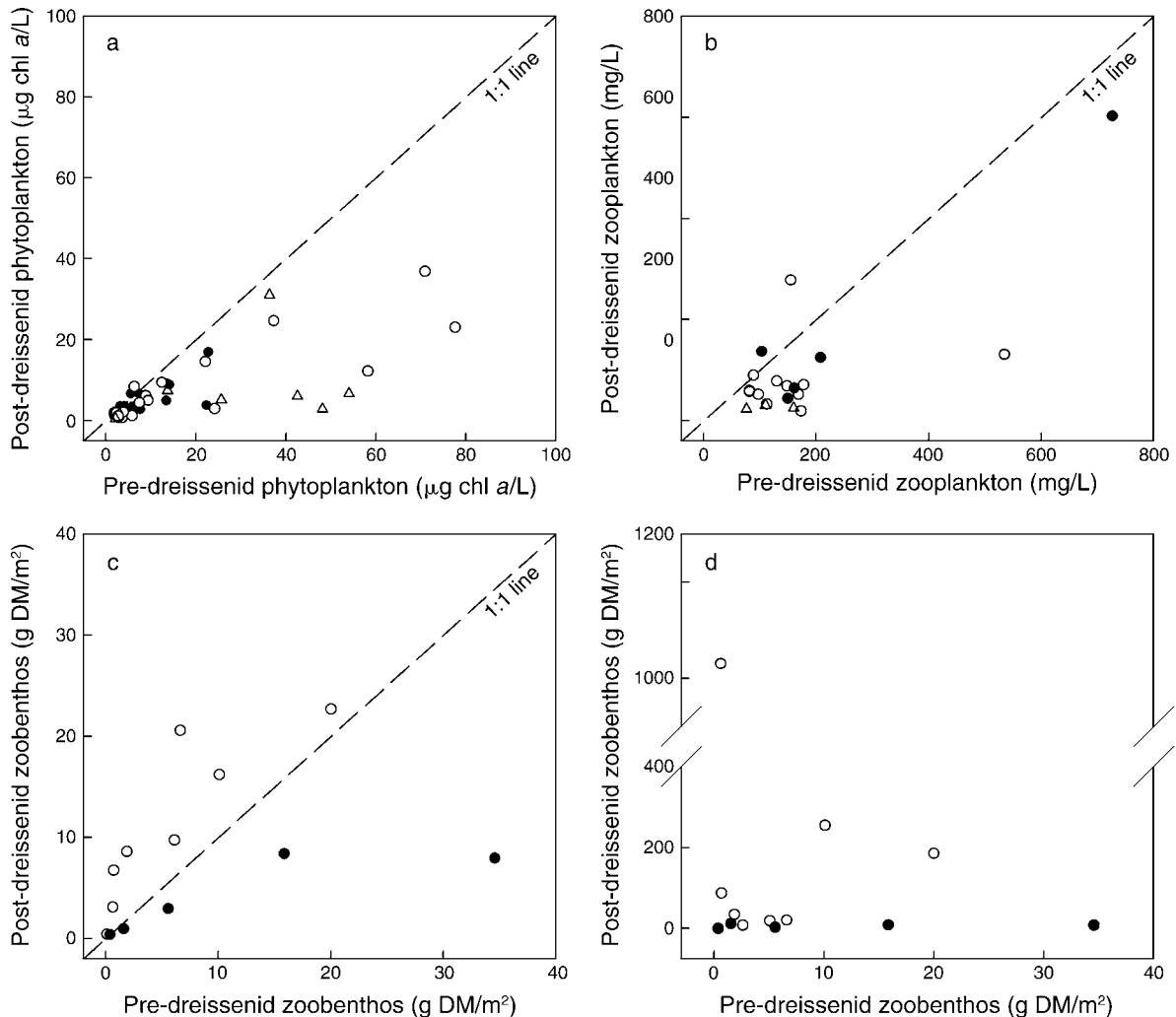


FIG. 5. The impact of dreissenid mussels on (a) phytoplankton, (b) zooplankton, and (c, d) zoobenthic biomass (c) excluding and (d) including dreissenid mussel soft tissues; DM is dry mass. Symbols are as in Fig. 2, except for panels (c) and (d) where closed symbols refer to zoobenthos in the profundal zone. Note the change in scale of x- and y-axes in panel (d).

of the water column that can be filtered in one day (Fig. 6). The changes in phytoplankton biomass leveled out at FC values >3 per day, with maximum declines between 90% and 95% (Fig. 6).

Changes in areal phytoplankton photosynthesis and photosynthetic parameters were also detected. Maximum rates of photosynthesis (P_{MAX}^b), normalized to biomass, increased by 17% following dreissenid invasion (Table 3). Dreissenid effects on α^b , the slope of light-limited portion of the photosynthesis–irradiance curve, were variable between studies and nonsignificant. Areal photosynthetic rates displayed moderately significant declines of about -47% (Table 3).

Dreissenid effects on the phytoplankton community composition were assessed at the division level of taxonomic resolution and pooled across lakes and rivers due to the low number of studies and level of taxonomic resolution therein. Dreissenid impacts on algal divisions

were either negative (Pyrrophyta, Cyanobacteria, Chlorophyta, Bacillariophyta) or neutral (Cryptophyta, Chrysophyta; Table 3).

Zooplankton.—Large and significant declines in zooplankton biomass were detected in littoral and river habitats in response to invasion (Table 2). Dreissenid mussels depressed zooplankton biomass within four of the five pelagic systems where data was available; however, these effects were not significant due to high variability between systems (Table 2, Fig. 5b). Due to the low number of studies, dreissenid effects on zooplankton community structure were pooled across habitat types. Within the zooplankton community, all taxonomic groups were negatively affected by dreissenid invasion, with largest effects on groups with the smallest body size. Most negatively affected by dreissenid invasion were rotifer, copepod nauplii, and flagellated protozoan abundance (-70% to -85%), while adult

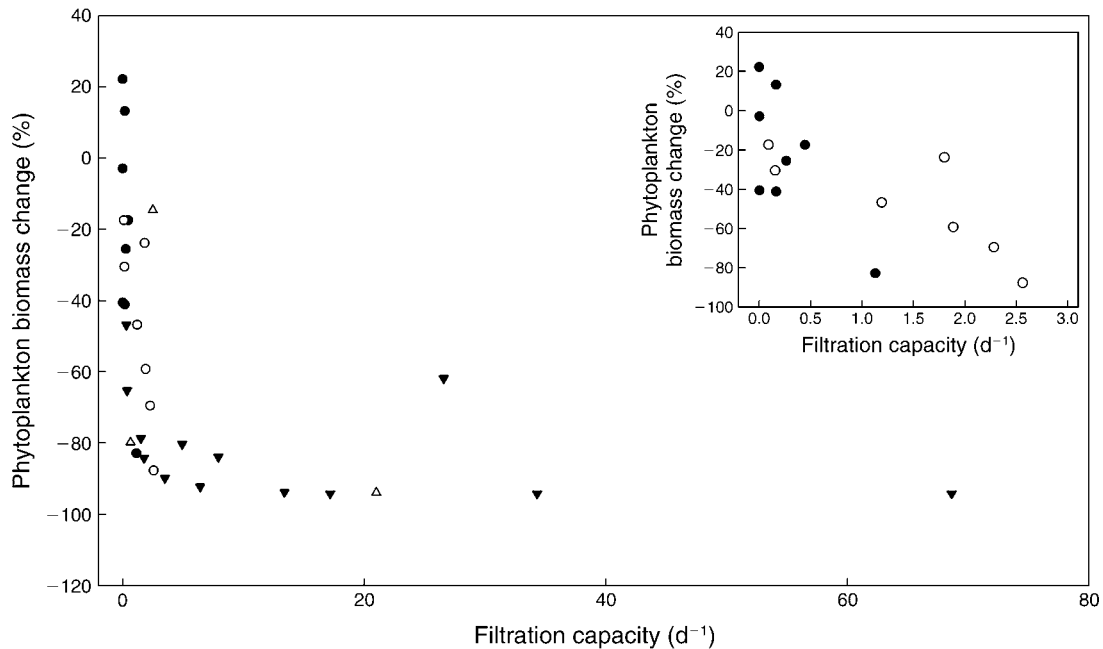


FIG. 6. The impact of dreissenid filtration capacity on phytoplankton dry biomass (DM) in freshwater ecosystems and enclosure experiments. Symbols are as in Fig. 2, except enclosure experiments (inverted triangle). Filtration capacity represents the proportion of the water column filtered in one day, and values were calculated using a filtration rate of $11.7 \text{ L} \cdot (\text{g DM})^{-1} \cdot \text{h}^{-1}$ and the mean depth of the ecosystem (sensu Vanderploeg et al. 2002). A mesocosm study ($X = 2.64$, $Y = 540\%$) was not included on plot. The inset figure represents pelagic and littoral habitats within lakes only, with identical symbols and units. The inset assesses the impact of filtration on lake ecosystems, which are obscured by the addition of enclosure experiments (main figure) that typically have much larger values of filtration capacity.

copepods and cladocerans displayed 56–67% reductions in abundance (Table 4).

Declines in total zooplankton biomass following invasion were moderately correlated with declines in phytoplankton biomass ($r = 0.46$, data not shown). Declines in cladoceran ($r = 0.84$), copepod ($r = 0.70$), and rotifer ($r = 0.70$) abundance were all linearly correlated with declines in phytoplankton biomass (data not shown).

TABLE 3. Dreissenid impacts (between pre- and post-dreissenid invasion periods) on phytoplankton photosynthetic parameters and taxonomic groups.

Parameter	<i>n</i>	%	SE	<i>P</i>
Chl <i>a</i>	52	-53.3	6.8	<0.001
Biomass	21	-62.3	11.6	<0.001
P_{MAX}^b	5	16.6	5.4	0.036
α^b	5	20.0	15.3	0.262
Areal photosynthesis	4	-47.0	17.7	0.077
Chrysophyta	7	-2.3	29.9	0.942
Cryptophyta	10	-34.8	21.9	0.147
Bacillariophyta	12	-40.1	21.7	0.092
Chlorophyta	10	-55.2	20.7	0.026
Cyanobacteria	10	-58.1	26.5	0.056
Pyrrophyta	7	-58.5	19.1	0.022

Notes: Phytoplankton biomass and areal photosynthesis results include data from both lakes and rivers, while photosynthetic parameters include lakes, rivers, and experiments. The superscript “b” in the maximum photosynthesis (P_{MAX}^b) and slope of the photosynthesis–irradiance curve (α^b) terms indicate that these values are normalized to algal biomass. The statistical analysis is as described in Table 2.

Benthic biota

Sediment-associated bacteria, macrophytes, and benthic algae.—The abundance of bacteria dramatically increased (+2000%) in sediments surrounding dreissenid mussel beds (Table 2). Insufficient information was available to assess the effects of dreissenids on these communities in sediments within river or profundal habitats.

Changes in macrophyte depth (i.e., depth of the littoral zone) in dreissenid-invaded lakes were strongly correlated to changes in water clarity ($n = 10$, $r^2 = 0.76$; data not shown). Since many studies reported the

TABLE 4. Dreissenid-induced changes in zooplankton biomass and abundance.

Parameter	<i>n</i>	%	SE	<i>P</i>
Total biomass	18	-56.9	11.4	<0.001
Total abundance	10	-70.2	21.8	0.010
Cladocera†	9	-56.2	29.0	0.089
Copepoda†	9	-67.3	30.2	0.056
Flagellated protozoans†,‡	7	-73.3	32.1	0.063
Copepod nauplii†,‡	4	-83.5	21.7	0.031
Rotifera†	7	-84.8	28.0	0.023

† Data for individual taxonomic groups are based on abundance.

‡ Results for flagellated protozoans and copepod nauplii include data from lakes, rivers, and experiments. The remaining groups are for lakes and rivers only. Statistical analyses are as per Table 2.

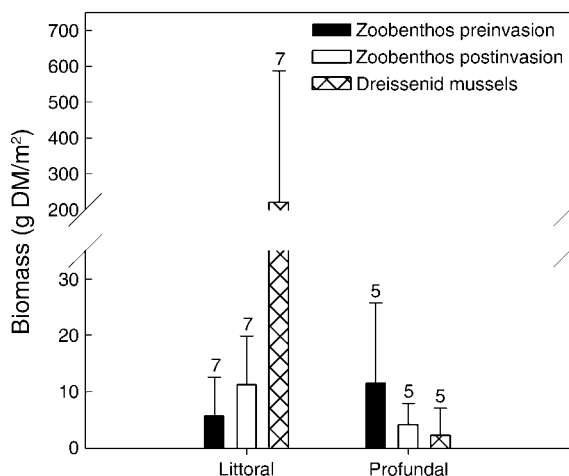


FIG. 7. The biomass (dry mass, DM) of zoobenthos (excluding dreissenid mussels) pre- and post-dreissenid mussel invasion, and dreissenid mussel biomass, in littoral and profundal habitats of lake ecosystems. Error bars represent one standard deviation, and the numbers above the error bars represent the number of lakes included in the analysis.

influence of dreissenids on water clarity, but did not measure changes in macrophytes, we applied the equation linking water clarity to macrophyte depth (macrophyte depth = $0.67 + 1.23 \times \text{Secchi depth}$, $n = 10$, $r^2 = 0.76$) to estimate how macrophyte depth would be expected to vary over a larger range of invaded ecosystems. The maximum depth of macrophyte colonization would increase, on average, by 1.0 ± 0.4 m in lakes ($n = 14$) and 0.8 ± 0.3 m in rivers ($n = 7$). Due to the low slope of most lakes, the modest increases in littoral depth increased total macrophyte coverage by $180\% \pm 40\%$ (Table 2). Benthic algal biomass increased by 170% following dreissenid mussel invasion (Table 2).

Zoobenthos.—For profundal habitats, the mean biomass of non-dreissenid taxa declined by 45% between pre- and post-dreissenid periods (Table 2, Figs. 5c, 7). *D. rostriformis bugensis* occurred in profundal habitats of some lakes, and when this taxon was included in the

analysis there was no significant effect of dreissenids on the total biomass of benthic invertebrates (Table 2). Within littoral zones of lakes, there were large and significant increases in the biomass of both non-dreissenid taxa (+210%) and all taxa including dreissenids (+1980%; Table 2, Fig. 5c, d). In littoral lake habitats the mean biomass of dreissenid mussels (220 g/m^2) was an order of magnitude higher than the mean biomass of all other taxa combined ($\sim 10 \text{ g/m}^2$; Fig. 7). In rivers, data for the biomass of benthic invertebrates were generally not reported, and we were not able to collect sufficient data to analyze dreissenid effects. Data on the areal abundance of benthic invertebrates were available from rivers, and there was a significant increase (+160%) between pre- and post-dreissenid periods (Table 2).

In general, taxonomic groups of benthic invertebrates from littoral and river habitats responded similarly to dreissenid invasion, with most taxa exhibiting neutral or positive responses (except filter feeders; Table 5). In the littoral zone of lakes, significant increases in abundance were noted for Hirudinea, Amphipoda, and Gastropoda (+240% to +1700%); nonsignificant responses were noted for Ephemeroptera, Oligochaeta, Turbellaria, Diptera, and Trichoptera; and significant declines were noted for Sphaeriidae and Unionidae (−78% to −93%; Table 5). In rivers, there were significant increases in the abundance of Amphipoda, Gastropoda, Oligochaeta, Turbellaria, Diptera, and Trichoptera (+130% to +270%); nonsignificant responses for Ephemeroptera; and significant declines for Unionidae (−90%; Table 5). Fewer taxonomic groups were present in profundal habitats, and responses to dreissenid invasion were either neutral (Diptera, Sphaeriidae) or negative (Amphipoda, Oligochaeta; Table 5).

DISCUSSION

Benthic–pelagic coupling

The suppression of phytoplankton, the channeling of nutrients and energy from the water column to the littoral benthos, and the facilitation of benthic autotrophic production by invasive dreissenid mussels (Fig. 8)

TABLE 5. Percentage change in benthic invertebrate abundance (no./m²) in rivers and littoral and profundal habitats of lakes between pre- and post-dreissenid invasion periods.

Taxon	Profundal				Littoral				River			
	<i>n</i>	%	SE	<i>P</i>	<i>n</i>	%	SE	<i>P</i>	<i>n</i>	%	SE	<i>P</i>
Hirudinea					3	1699.3	553.0	0.092				
Amphipoda	10	−60.4	25.5	0.042	8	855.4	268.8	0.013	4	273.2	91.2	0.058
Gastropoda					7	243.2	74.3	0.017	4	134.4	41.3	0.047
Ephemeroptera					5	210.8	346.7	0.576	3	64.9	27.3	0.141
Oligochaeta	9	−45.4	13.5	0.010	7	94.6	66.4	0.204	4	240.4	99.9	0.095
Turbellaria					5	119.9	232.0	0.633	4	322.1	77.4	0.025
Diptera	7	−18.4	21.2	0.419	10	19.4	41.5	0.651	6	135.1	52.7	0.050
Trichoptera					3	−27.2	170.2	0.847	4	130.9	53.2	0.091
Sphaeriidae	10	−32.6	19.0	0.120	7	−78.4	37.0	0.072				
Unionidae					11	−93.1	7.2	<0.001	5	−90.4	19.4	0.010

Note: While dreissenid effects are reported as percentage change, statistical analyses were conducted using a two-tailed *t* test on the population of log response ratio values for each parameter (see *Methods*).

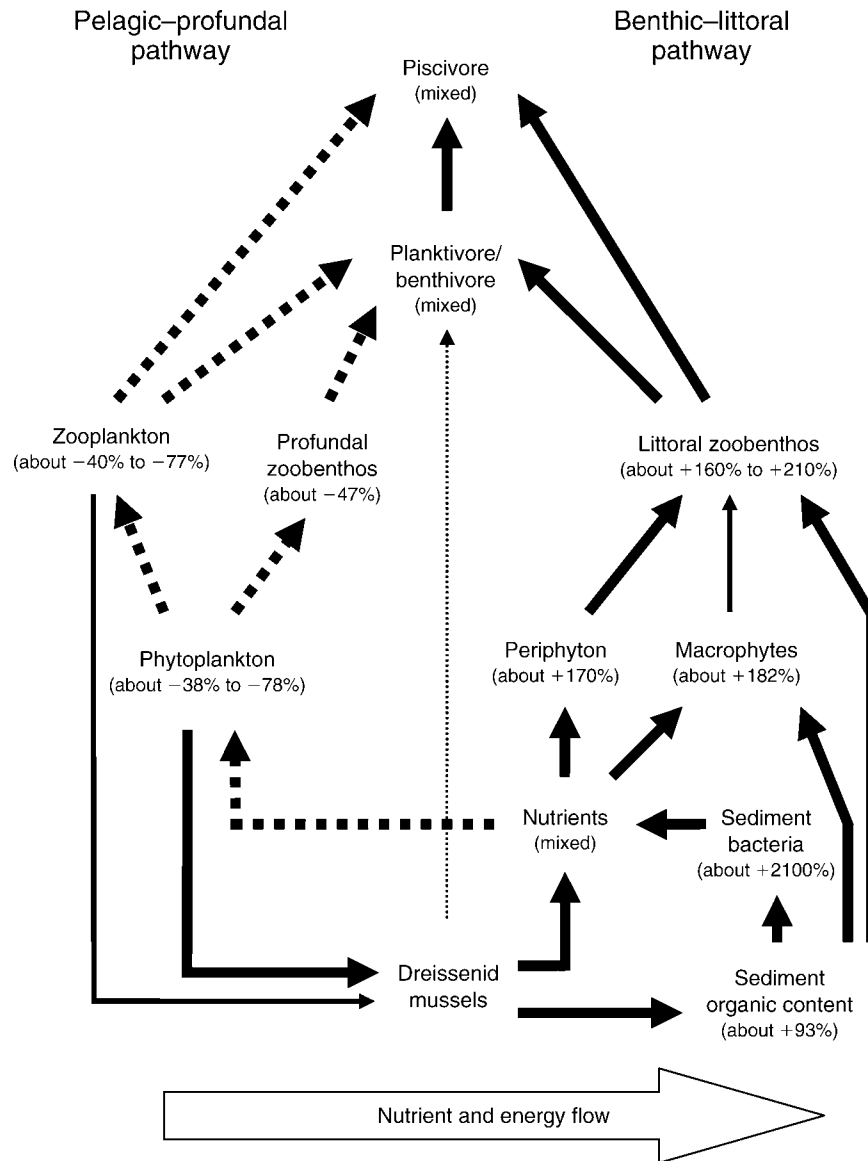


FIG. 8. Dreissenid-induced shifts in the dominant energy pathways of freshwater ecosystems. Arrows represent the direction of energy flow. Solid lines represent increased abundance following dreissenid invasion, while dashed lines represent decreased abundance. The values given represent the mean percentage change in parameter values for different broad groups or organisms between pre- and post-dreissenid invasion periods, based on values in Table 2.

represents a fundamental restructuring of freshwater ecosystems. Our results indicate that dreissenid-induced changes in the resource base of freshwater ecosystems lead to significant and ecologically relevant impacts on higher trophic levels in both pelagic-profundal and benthic-littoral energy pathways (Fig. 8). The magnitude and direction of these impacts on abiotic factors and native flora and fauna were context dependent, with habitat and respective energy pathway and filtration capacity as important explanatory variables.

Dreissenid impacts were structured across two dominant energy pathways (Fig. 8). The first was a pelagic-profundal pathway, where energy fixed by phytoplank-

ton was channeled to one or more trophic guilds of zooplankton, or as detritus to profundal zoobenthos. Biota associated with this pathway broadly declined following dreissenid invasion (Fig. 8). The second was a littoral-benthic pathway, where detritus and energy fixed by benthic autotrophs was channeled to zoobenthos. Biota associated with this littoral-benthic energy pathway generally increased following dreissenid invasion (Fig. 8).

The coupling of benthic and pelagic habitats by bivalves is not unique to dreissenids. Indeed, native freshwater mussels perform a similar ecological function (Strayer et al. 1999). However, dreissenids are capable of

achieving filtration pressures (Fig. 6) several orders of magnitude higher than most native freshwater mussel communities (Strayer et al. 1999). The increased consumption of organic matter from the plankton, coupled with increased deposition to the benthos, has increased littoral benthic invertebrate biomass in invaded ecosystems (Karatayev et al. 1997, Mayer et al. 2002, Hecky et al. 2004, Burkalova et al. 2005). Perhaps the best analogs for dreissenid-invaded ecosystems are dense populations of suspension-feeding bivalves within coastal marine systems. These shallow-water marine bivalve communities have been intensively studied, and descriptions of their ecological effects, including their roles in benthic–pelagic coupling and nutrient cycling, are often indistinguishable from those for invasive dreissenid mussels (Dame 1993, Frechette et al. 1993, Newell 2004). While the ecological implications of these marine bivalves and dreissenids are in many ways similar, there are also fundamental differences that relate to ecosystem size. Suspension-feeding marine bivalves inhabit relatively “open” systems. Their food source (i.e., phytoplankton) is continuously or periodically replenished, and soluble excretory products are carried away through mixing with offshore waters. It has been postulated that the long-term persistence of these bivalve communities and the trophic guilds they support are ultimately dependent on this “openness” (Herman 1993). In contrast, freshwater ecosystems are “closed” by comparison, and the availability of food is controlled by in situ productivity rather than replenishment from an adjacent environment. Though the interannual variability of dreissenid densities was found to decrease with lake size and lake trophic status (Ramcharan et al. 1992), the temporal variation in ecological impacts caused by dreissenids remains largely unexplored (Strayer et al. 2006).

Nutrients and light

Nutrients and light determine the potential autotrophic productivity within freshwater ecosystems. Enclosure experiments have demonstrated that filtration and excretion processes of dreissenids can significantly reduce particulate-bound nutrients and increase the availability of soluble nutrients (Table 2). Overall, dreissenids removed significant quantities of phosphorus, usually considered the limiting nutrient for freshwater ecosystems, from the water column of lakes, though not rivers (Table 2). In rivers, the reduction of particulate phosphorus was offset by large increases in soluble phosphorus concentrations. The accumulation of soluble phosphorus in the water column of rivers suggests that increases in benthic autotrophic productivity following dreissenid invasions do not fully compensate for reductions in phytoplankton productivity, and that P does not limit autotrophic production. In most lakes, soluble P did not increase in the water column despite large reductions in phytoplankton and zooplankton biomass, suggesting that benthic biota

compensated with increased P uptake and storage. Enclosure experiments also demonstrated an accumulation of soluble N species in the water column in the presence of dreissenid mussels (Table 2); however, such increases were not common in dreissenid-invaded lakes or rivers.

Water clarity (Secchi depth) is a common indicator of ecosystem condition, determines the depth of the littoral zone, and is an important factor controlling rates of primary production and the distribution of that production between benthic and pelagic habitats (Vadeboncoeur et al. 2008). Dreissenid invasions increased water clarity in nearly all invaded ecosystems (Fig. 2b) by reducing phytoplankton and other suspended particulate matter that would otherwise attenuate downwelling irradiance. Such changes in water clarity also have large implications for the heat budgets of lakes, deepening of the mixed layer, nutrient regeneration, and reductions in deepwater habitat for cool-water fish species (Fee et al. 1996, Schindler 2001). We are aware of only a single study that has directly examined dreissenid impacts on stratification. This study (Yu and Culver 2000) indicated that increases in mixing depths within a small (59-ha) reservoir were directly proportional to dreissenid-induced increases in Secchi depth (about 1 m).

In order to understand and anticipate dreissenid effects on water clarity for any particular ecosystem, it is important to consider the nonlinear relationship between SS and water clarity (Fig. 3). This relationship indicates that for highly turbid ecosystems, dreissenid invasions may not increase water clarity despite large reductions in suspended solids (SS) (Fig. 3). In contrast, dreissenid-induced increases in water clarity, littoral depth, and benthic primary production were highest in ecosystems where turbidity was relatively low prior to dreissenid invasion (i.e., near or below 2–3 mg/L; Fig. 3). In addition to their effects on water clarity, elevated SS concentrations are an important cause of environmental degradation in many aquatic ecosystems (Bilotta and Brazier 2008). Thus, the large declines in SS within dreissenid-invaded ecosystems (–40% to –70%; Table 2) that were formerly degraded by high SS may result in some improvements in the condition of native flora and fauna (Bilotta and Brazier 2008).

Pelagic–profundal energy pathway

The magnitude of dreissenid impacts on biota within the pelagic energy pathway (Fig. 8) for any individual ecosystem was, in large part, dependent on the filtration pressure exerted by the dreissenids. In the range of filtration pressures experienced within most natural ecosystems (Fig. 6, inset), the response of phytoplankton ranged from about +20% to –95% of pre-dreissenid values (Fig. 6). While dreissenid densities and the filtration pressure were unknown for most invaded ecosystems, our results clearly demonstrated that dreissenid impacts were both common and dramatic

across large gradients of ecosystem size and trophic status (Table 2). The magnitude of impacts was generally higher in shallow, nonstratified lakes and rivers than in deeper, stratified (pelagic) habitats (Table 2). However, pelagic habitats within some of the largest freshwater ecosystems in the world were not immune to the impacts of dreissenids. In these ecosystems, dreissenid invasions led to significant changes in water column transparency (Budd et al. 2001, Binding et al. 2007), dissolved and particulate nutrient concentrations (Markawicz et al. 2000, Rockwell et al. 2005), and phytoplankton productivity (Mills et al. 2003).

Several authors have commented that the excretion of soluble nutrients or the selection of smaller and faster-growing taxa might stimulate phytoplankton productivity, even though biomass had been reduced due to grazing (Fahnenstiel et al. 1995, Heath et al. 1995, Caraco et al. 1997). These claims are supported by a mean increase (+16%) in the maximum photosynthetic rate of phytoplankton, when normalized to biomass, following dreissenid invasion (Table 3). However, changes in areal photosynthetic rates over the dreissenid invasion period, which integrated both the photosynthetic response and the change in biomass, declined by nearly one-half (Table 3). So, while the post-dreissenid phytoplankton community was capable of achieving higher photosynthetic rates, these were generally not sufficient to overcome the dramatic loss in biomass, and the total productivity of pelagic autotrophs declined substantially following dreissenid invasions. Some exceptions to this general pattern of decreasing areal production did occur. For example, declines in phytoplankton biomass were offset by increases in water clarity in eutrophic Oneida Lake, and areal production remained similar between pre- and post-invasion periods (Idrisi et al. 2001).

Dreissenid impact on zooplankton biomass was context dependent. As with phytoplankton, the strongest impacts on zooplankton biomass were in rivers and littoral habitats of lakes (Table 2). In pelagic habitats of lakes, mean declines in zooplankton, though large (−40%), were highly variable among lakes (Fig. 5b) and not significant. The direct consumption of small zooplankton (e.g., rotifers and copepod nauplii) has been demonstrated in numerous controlled experiments (MacIsaac et al. 1995, Thorp and Casper 2002, Wong et al. 2003, Wong and Levinton 2006). Declines in rotifer abundance were noted in at least two ecosystems where declines in phytoplankton biomass were negligible (data not shown), suggesting direct predation on small zooplankton in at least some natural habitats. However, our results do not differentiate whether declines in these taxa occurred through direct predation or competition.

Benthic–littoral energy pathway

In contrast to the negative impacts of dreissenids on biota within pelagic–profundal energy pathways, biota within benthic–littoral pathways generally increased or

remained unchanged following dreissenid invasions (Table 5, Fig. 8). Improvements in water clarity, and cross-habitat subsidies associated with the consumption of phytoplankton and excretion of nutrients at the sediment–water interface, provided resources (solar energy, fixed energy in the form of feces and pseudofeces, and soluble nutrients) that benefited a number of native floral and faunal groups associated with benthic–littoral habitats (Table 5, Fig. 8). The facilitation of native species by invasives is not commonly addressed in the scientific literature (Rodriguez 2006). However, it is clear that facilitation is extremely important for many taxa within the benthic–littoral pathways of dreissenid-invaded ecosystems (Stewart and Haynes 1994, Ricciardi et al. 1997, Bially and MacIsaac 2000, Mills et al. 2003), and for higher trophic levels (e.g., planktivorous and piscivorous fish) that are capable of utilizing organisms from the benthic–littoral energy pathway (Strayer et al. 2004).

Since the majority of available data on individual macroinvertebrate groups was based on abundance rather than biomass, we did not attempt to assess how dreissenid invasions impacted the relative importance of functional feeding groups. Previous studies have documented that, with the exception of native filter feeders, the response of other functional feeding guilds are generally positive or neutral in littoral habitats (Strayer and Smith 1996, Karatayev et al. 1997, Ricciardi et al. 1997, Ward and Ricciardi 2007). Studies in the former Soviet Union (Karatayev et al. 1997) indicated that dreissenid invasions were associated with a relative increase in large-bodied taxa such as leeches, amphipods, and gastropods. Our results are in broad agreement with these findings, with leeches, amphipods, and gastropods increasing by 0.5 to 1.25 orders of magnitude following dreissenid invasion (Table 5). While the total biomass of native macroinvertebrates in the littoral habitats of lakes and rivers generally increased following dreissenid invasions, the mean biomass of dreissenid mussels was an order of magnitude higher than all other taxa combined and comprised 95% of the total macroinvertebrate biomass (Fig. 7).

The majority of studies examining the response of littoral zoobenthic communities (including those used in our analysis) to dreissenid invasion have been within, or in close proximity to, dreissenid mussel colonies (Stewart and Haynes 1994, Ricciardi et al. 1997, Stewart et al. 1998, Horvath et al. 1999). Thus, our results on the littoral zoobenthic community (and the literature in general) may capture a localized response of the zoobenthic community that likely overestimates the impacts of dreissenids on shallow littoral communities. The degree to which these localized responses reflect those throughout the littoral zone depends on the proportion of littoral zone colonized by dreissenids and on changes in communities in uncolonized habitats. A comprehensive study of the response of the Hudson River zoobenthic community to dreissenid invasion

found that within shallow littoral sites with low densities of dreissenids, the total zoobenthic biomass increased by about 10% (Strayer and Smith 2001). The study by Strayer and Smith (2001) also found that some taxa (e.g., Annelida, Ceratopogonidae, and Sphaeriidae) responded quite differently to dreissenid invasion depending on habitat type (shallow vegetated sites vs. zebra mussel beds). Our results indicated a widespread increase in macrophytes and macroalgae (Table 2) in lakes following dreissenid invasions, suggesting that changes in the biomass and community structure of the zoobenthos outside of the localized areas around dreissenid colonies are likely occurring.

Fish

How do fish communities respond to such dramatic shifts in their forage base? The majority of fish species obtain their energy from both pelagic and benthic energy pathways (Hecky and Hesslein 1995, Vander Zanden and Vadeboncoeur 2002). The ability to utilize pelagic or benthic resources would buffer individual species from the dramatic impacts of dreissenid invasions on lower trophic levels. In contrast, the inability of some fish species (e.g., obligate planktivores or deepwater benthic fish) to fully utilize benthic–littoral energy pathways may result in declines in individual body condition, reproduction, and recruitment (Mills et al. 2003, Pothoven and Madenjian 2008, Rennie et al. 2009). Thus, the responses of fish communities to dreissenid invasions (e.g., Fig. 8) would be dependent on the magnitude of ecological changes, and the ability of fishes to respond to such changes.

Qualitatively, reports of dreissenid effects on indicators of individual fish health, population dynamics, and community structure generally supported our expectation that obligate planktivore or deepwater benthivore species would be impacted negatively and benthic–littoral species would have neutral or positive impacts. In a particularly well-documented study on fish communities in the Hudson River, pelagic species declined in abundance by 28%, with a 17% decline in growth rates, and littoral species increased in abundance by 97%, with a 12% increase in growth rates (Strayer et al. 2004). In several of the Laurentian Great Lakes, the expansion of *D. bugensis* into profundal habitats was accompanied by large declines, or extirpations, of the profundal benthic amphipod *Diporeia* spp. (Dermott and Kerec 1997, Nalepa et al. 2007, 2009, Hoyle et al. 2008). *Diporeia* spp. were an important high-energy food source for several important planktivores, including bloaters (*Coregonus hoyi*) and lake whitefish (*Coregonus clupeaformis*) during pre-dreissenid years. Declines in *Diporeia* were associated with declines in the body condition and growth of lake whitefish in Lake Michigan (Pothoven et al. 2001, Pothoven and Madenjian 2008), Lake Ontario (Hoyle et al. 2008), and Lake Huron (Rennie et al. 2009). Some of these planktivorous and deepwater benthivorous species also served as forage for predators

such as Pacific salmon (*Oncorhynchus* spp.). In Lake Huron, populations of both planktivores and their predators collapsed following dreissenid invasion (Riley et al. 2008). However, it is not well understood if the dreissenid-induced collapse of *Diporeia*, top-down pressure of a large wild population of Pacific salmon, or a combination of factors caused the collapse of the planktivore community (Riley et al. 2008). In either case, there is little debate that the recovery of these pelagic planktivores and their predators, and the multimillion dollar fishery, is severely inhibited by the dreissenid-induced declines in zooplankton and the collapse of *Diporeia* (LHBP 2008, Rennie et al. 2009).

There are at least 38 species of fish, 14 in North America and 27 in Europe (three common to both), and several species of waterfowl that are known to feed on dreissenids (Molloy et al. 1997). However, for many of these reported cases, predation on dreissenids appears to be occasional rather than common, and the importance of dreissenids to fish or waterfowl is not known (Molloy et al. 1997). Some studies have reported that shifts to dreissenid-based diets resulted in declines in fish growth or condition (French and Bur 1996, Hoyle et al. 2008). Their shells offer sufficient protection that dreissenids are, for most fish species, a food source of last resort. The importance of predation on dreissenid population densities appears highly variable. In some cases, fish and waterfowl have reduced dreissenid densities or altered population structure (Hamilton et al. 1994, Petrie and Knapton 1999, Bartsch et al. 2005, Lederer et al. 2006). However, in most cases predation does not appear capable of substantially reducing whole-ecosystem densities (Stanczkowska and Lewandowski 1993, Patterson et al. 2005). While dreissenid veligers are a common dietary item for juveniles of many planktonic and benthic fish species after dreissenid spawning events, their ability to reduce veliger densities and affect dreissenid recruitment is largely unknown (Molloy et al. 1997).

Exceptions

While the broad impacts of dreissenids on biota within benthic and pelagic energy pathways were generally consistent with changes in the autotrophic base of those pathways, some important exceptions occurred. The first was the positive response by some individual phytoplankton taxa within the broadly declining pelagic–profundal pathway, and the second was the large negative response by native filter-feeding organisms.

Our results clearly demonstrate that, at the division level, phytoplankton groups (including cyanobacteria) either decline in biomass or remain unchanged following dreissenid invasions in the vast majority of ecosystems (Table 3). However, a growing body of evidence indicates that even while these broad declines are occurring, a few individual cyanobacterial species increase in abundance in some, but not all, ecosystems.

These studies describe a pattern of increasing biomass of *Microcystis aeruginosa*, *Aphanizomenon* spp., or *Anabaena* spp., following dreissenid invasions in some lakes (Vanderploeg et al. 2001, Raikow 2004, Knoll et al. 2008). Each of these species is capable of forming buoyant chains or colonies, and at least one (*M. aeruginosa*) has been shown to remain viable after being selectively rejected in pseudofeces or passing through the dreissenid digestive tract (Vanderploeg et al. 2001). The success of these species is a troubling phenomenon because these species are capable of producing algal toxins, and because blooms may occur in otherwise oligotrophic systems (Raikow et al. 2004, Knoll et al. 2008). Why these species increase their abundance in some dreissenid-invaded ecosystems but not others is not fully understood, although authors have cited large variations in dreissenid filtration capacity (Vanderploeg et al. 2001), trophic status (Raikow et al. 2004, Knoll et al. 2008), or stoichiometric nutrient ratios (Vanderploeg et al. 2001) of invaded ecosystems as potential reasons. Due to their potentially harmful effects, the mechanisms leading to increases in these troublesome species in invaded ecosystems require further elucidation.

Strong declines in the abundance of native benthic filter feeders have been documented in a growing number of dreissenid-invaded ecosystems (Nalepa et al. 1996, Ricciardi et al. 1996, 1997, 1998, Schloesser et al. 1996, Strayer and Smith 1996, 2001, Karatayev et al. 1997, Strayer and Malcom 2007, Ward and Ricciardi 2007). The negative interaction between dreissenid and unionid mussels manifests in two ways. First, many studies (Gillis and Mackie 1994, Ricciardi et al. 1996) have documented the physical fouling of living unionids by dreissenid mussels. The dreissenid colonies overgrew and smothered individual unionids, restricted filtration and movement, reduced fitness, and led to high rates of mortality, and in some cases local extinction (Haag et al. 1993, Ricciardi et al. 1997). Second, even when physical fouling did not occur, unionid abundance declined due to the large reductions in phytoplankton (Strayer and Smith 1996, Strayer and Malcom 2007). These large declines in unionid abundance and diversity (Lucy et al. 2005, Schloesser et al. 2006) are troubling, since unionids, already impacted by over-harvesting and habitat loss or degradation, are among the most imperiled faunal groups in North America (Ricciardi et al. 1998). Within their native home range dreissenids have successfully coexisted with some unionid and sphaeriid taxa, and it remains to be seen if, over the long term, unionids and sphaeriids (and other filter-feeding organisms) can re-colonize habitats if dreissenid densities decline (Strayer and Malcom 2007).

CONCLUSION

Our results demonstrate that biotic exchange, even the addition of a single species into ecosystems with complex food webs, can result in a profound transformation of the structure and function of whole ecosystems. In

addition to the devastating “top-down” impacts that introduced predators can have on ecosystems, our results demonstrate that species that modulate the cycling of nutrients and energy within ecosystems can induce dramatic “bottom-up” effects that cascade to all trophic levels. As ecosystem engineers and couplers of benthic and pelagic habitats (Crooks 2002, Karatayev et al. 2002), dreissenids restructure energy and nutrient fluxes through ecosystems, producing fundamental changes in food web structure. The impacts of dreissenids on invaded ecosystems were context dependent, with habitat type, filtration capacity, and energy pathway determining the magnitude and direction of impact. Our meta-analysis approach provided a powerful tool for moving beyond individual case studies, and subsequently drawing broad generalizations regarding the ecological impacts of dreissenid mussels in freshwater ecosystems. This approach may also hold promise for characterizing the impacts of other well-studied invasive species.

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APPENDIX

Ecosystems and references used in meta-analysis to assess dreissenid impacts (*Ecological Archives* M080-006-A1).