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Lake Characteristics, Population Properties and Invasion History Determine Impact of Invasive Bivalves on Lake Nutrient Dynamics

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Abstract

Invasive species can have large impacts on ecosystems, including the cycling and distribution of nutrients. To determine the whole-ecosystem effects of invasive zebra mussels on lake nutrient dynamics, we sampled 10 invaded Minnesota lakes spanning a broad trophic status gradient. We conducted N and P excretion and biodeposition rate measurements and determined the C, N and P composition of dreissenid soft tissues and shell material in the study lakes. We also estimated the whole-lake biomass of live dreissenid mussels and their dead shell material, constructing comprehensive nutrient budgets for dreissenid populations in the study lakes. We used the results of our measurements and published data to estimate the contribution of dreissenids to P budgets in 24 additional lakes in Europe and North America. Results show that nutrient cycling rates and composition of soft tissues and shells vary with mussel size and lake trophic status. Zebra mussels made variable, but often large, contributions to cycling and storage of water column standing stocks of POC, PON and TP in the study and literature lakes. In some lakes, the effects of zebra mussels on P dynamics were also considerable in the context of estimated P external and internal loading, sediment sequestration and effects of other biota. We show that the impact of zebra mussels on whole-lake nutrient budgets depends on lake properties, dreissenid population characteristics and invasion history. This information can be used by ecosystem managers to prioritize invasion prevention efforts toward lakes likely to be most strongly impacted by zebra mussel invasions.

Key words: dreissenid mussels; invasive species; nutrient cycling; benthic-pelagic coupling; nutrient budgets; ecological stoichiometry.

Highlights

- Zebra mussel nutrient excretion and composition depends on mussel size and lake trophic status.
- Impacts of zebra mussels on lake C, N and P budgets are variable among lakes but can be large.
- Effects of zebra mussels on nutrient budgets depend on lake and mussel population properties.

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Author Contributions FW conducted field and lab work, analyzed samples and data, wrote manuscript. TO conceived study, conducted field work, analyzed data, wrote manuscript.

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Introduction

Dreissenid (zebra and quagga) mussels are among the most widely distributed and recognized aquatic invasive species in Europe and North America. Dreissenids exert large effects on invaded ecosystems in part because of the high densities they can attain—often overwhelmingly dominating benthic invertebrate biomass—and their high filter feeding rates. By filtering particles from the water column and directing them toward the benthos, dreissenids increase water clarity, strengthen benthic-pelagic coupling processes and change the way energy and nutrients are distributed in aquatic systems (Gergs and others 2009; Higgins and Vander Zanden 2010; Ozersky and others 2015). Dreissenid establishment in lakes is frequently accompanied by large changes to ecosystem properties, including changes to the abundances and community composition of pelagic and benthic primary producers and consumers, ecosystem metabolism and food web structure (Higgins and Vander Zanden 2010; Ozersky and others 2012; Tyner and others 2015). Dreissenid invasions have also impacted ecosystem services, increasing the prevalence of cyanobacterial and benthic algal blooms, negatively impacting fisheries and causing the extirpation of native species (Schloesser and Nalepa 1994; Vanderploeg and others 2001; Hecky and others 2004; Fera and others 2017).

Many of the ecosystem effects of dreissenids are related to their impacts on carbon and nutrient cycling. Particulate carbon and nutrients that are removed from the water column by mussel filtration have four fates (Nalepa and others 1991). Some material will be deposited on the lake bottom as solid feces and pseudofeces (particles that have been filtered from the water but not ingested). Another fraction will be released into the water column as dissolved metabolic wastes (PO_4, NH_4 or CO_2). A third fraction will be incorporated into soft tissues and a final portion will be incorporated into shell material. Studies have shown that nutrient biodeposition, remineralization and storage by dreissenids can be large compared to other fluxes and pools. For example, Gergs and others (2009) found that dreissenids approximately doubled sedimentation rates in Lake Constance, increasing the flux of C and nutrients to the benthos. Other researchers have shown that dreissenid P excretion can be comparable with cycling by non-dreissenid biota in Lake Erie (Arnott and Vanni 1996) and can be sufficient to support nuisance levels of benthic algal growth in Lake Ontario (Ozersky and others 2009). The amount of carbon and nutrients stored in soft tissues of dreissenids can, in some cases, comprise a large portion of the total nutrient and carbon budget of a lake (Stańczykowska and Planter 1985; Goedkoop and others 2011).

Although several studies have examined the effects of dreissenids on nutrient dynamics, important knowledge gaps remain. First, most studies of dreissenid impacts on nutrients focus on a single lake, making it difficult to say how and why dreissenids impacts on nutrient dynamics and budgets vary among systems. Second, most studies focus on one or two aspects of dreissenid impacts on nutrients (e.g., biodeposition, excretion or storage in tissues); this narrow focus has precluded the construction of complete nutrient budgets for dreissenid populations and the understanding of their impacts in a whole-ecosystem context. Finally, very few studies examined the role of live and dead dreissenid shell in nutrient and carbon storage. Dreissenids produce copious amounts of shell material and, unlike soft tissues which become remineralized rapidly after death, the dissolution of shell material is slow (Strayer and Malcom 2007; Ozersky and others 2015); thus, shell material may represent a hitherto underappreciated compartment in the elemental dynamics of dreissenid-invaded systems.

Our study aims to address the above knowledge gaps and contribute to a more comprehensive understanding of dreissenid impacts on nutrient cycles in lakes. We sampled dreissenids in 10 Minnesota lakes spanning a large gradient of trophic status and invasion history. We measured the rates of dreissenid excretion of dissolved N and P and biodeposition of C, N and P in feces and pseudofeces, as well as the C, N and P composition of their tissues and shells. We also collected samples to estimate the whole-lake mass of living dreissenids and dead shell material stored in sediments of study lakes. Additionally, we compiled literature information on dreissenid biomass in 24 European and North American lakes and used our elemental composition and cycling rate results to estimate the effect of dreissenids on P budgets in those lakes. Our objectives were threefold: (1) examine variation in rates of nutrient excretion and biodeposition and the composition of tissue and shell for dreissenids in lakes of different trophic status; (2) combine whole-lake dreissenid biomass estimates with measured nutrient composition and turnover rates to examine the contribution of dreissenids to whole-lake nutrient dynamics in different lakes; (3) determine what types of systems are especially susceptible to dreissenid-mediated impacts on whole-lake nutrient dynamics.

Methods

Study Sites and Sampling Design

We sampled 10 lakes across Minnesota (Table 1; Figure S1). Lakes spanned a range of trophic status, size and mussel invasion history. All lakes were colonized by zebra mussels (*Dreissena polymorpha*); quagga mussels (*D. rostriformis bugensis*) were not detected in any of the study lakes. Most lakes were visited twice, once in June 2015 and once in July 2016. In 2015 we collected water quality samples and benthic samples to characterize the biomass of live mussels and their dead shell material. We also collected mussel samples for analysis of shell C, N and P composition. In 2016 we performed experimental incubations to determine excretion rates of dissolved N and P and biodeposition rates of C, N and P and collected samples for analysis of soft tissue C, N and P composition.

Water Chemistry Sampling and Analysis

Water samples were collected at 1 m below surface at the deepest point of each lake except for Lake Mille Lacs, where water samples were collected only at a nearshore site. We collected samples for measurement of total phosphorus (TP), chlorophyll a (chl. a), particulate organic carbon and nitrogen (POC and PON). TP samples were not filtered. Chl. a, POC and PON samples were filtered onto pre-combusted GF/F filters. TP samples were analyzed spectrophotometrically on a Shimadzu 1800 UV–Vis spectrophotometer using the molybdovanadate method and a persulfate digestion (at 100°C for 60 min). Particulate carbon and nitrogen were analyzed on a Finnigan Delta Plus XP elemental analyzer-isotope ratio mass spectrometer (EA-IRMS). Chl. a sample filters were extracted into 90% acetone for 24 h, centrifuged and measured on Turner 10AU fluorometer. A YSI EXO2 multi-parameter sonde was used to measure temperature, conductivity, pH, and dissolved oxygen in the field.

Nutrient Excretion and Biodeposition Rate Measurements

Excretion rate measurements were performed in 2016 on mussels collected by snorkeling at near-shore sites (ca. 1.5–2 m depth) in each study lake. Immediately after collection mussels were gently removed from benthic substrates, separated into three size classes (small: 4–11 mm, medium: 12–18 mm, large: 19–28 mm) and gently cleaned with a soft toothbrush to remove silt and attached algae. Following cleaning, mussels for use in nutrient excretion measurements were placed into acid-washed 50 mL centrifuge tubes filled with 45 mL of low-nutrient culture media (NOPN medium; Lehman 1980). The number of individuals per incubation tube varied with size class: 3 large, 4 medium or 5 small mussels were used. Three replicate incubations were used per size class as well as three control incubations containing only NOPN medium, for a total of 12 samples per lake. Incubation tubes with partially open caps (to avoid hypoxic conditions during incubations) were placed in test tube racks and into plastic coolers filled with lake water two-thirds of the way to the top of the incubation tubes (forming a water bath). Temperature in the coolers was maintained at 17 ± 2°C for the duration of the 3-h incubation period by adding small quantities of ice to the water in the coolers. This temperature was chosen because it was close to average in situ temperatures at all the sampling sites. At the end of the incubation period the media from each incubation tube was

Table 1. Study Lake Information

Lake	Latitude	Longitude	Year infested	Lake area (km^2)	Depth (m)	Secchi (m)	Chl-a (μg/L)	TP (μg/L)	POC (μg/L)	PON (μg/L)
Carlos	45°58.65N	95°21.46W	2009	10.5	50	9.1	0.76	1.33	244.1	31.31
Crystal	46°37.33N	95°57.27W	2009	5.7	17	4.7	1.86	7.04	498.8	81.04
Duluth Harbor	46°43.31N	92°03.81W	1998	519	10	0.5	4.55	24.20	1384	70.36
Lizzie	46°38.16N	96°00.45W	2009	7.7	20	5.9	1.69	5.26	1083	166.97
Mille Lacs	46°17.25N	93° 49.20W	2006	519	13	2.8	0.85	10.19	460.8	49.44
Pelican	46°32.90N	94°11.46W	2012	33.9	32	8.6	0.85	1.43	287.7	39.94
Pepin	44°26.46N	92°14.73W	1994	102	18	1.1	13.69	59.96	1487	246.96
Pike	46°51.97N	92°18.02W	2009	2.0	18	7	1.39	3.02	375.4	50.76
Round	46°27.12N	94°16.83W	2010	6.7	16	6.3	1.51	5.11	449.8	78.22
Zumbro	44°12.57N	92°28.57W	2000	2.9	13	1.7	8.26	40.61	1502	83.28

syringe-filtered through a 0.22 μm nuclepore filter into acid-washed 50 mL centrifuge tubes and frozen until analysis. Mussels were retained and frozen for soft tissue nutrient content analysis (see below). Filtered samples were analyzed for NH_4^+-N and PO_4^{3-}-P on an AQ400 nutrient auto-analyzer (Seal Analytical) following standard methods. N and P excretion was determined as the change in NH_4^+ and PO_4^{3-} content in the NONP media during incubations with mussels relative to controls without mussels. N and P excretion rates were expressed as μg N or P excreted per g mussel shell free dry mass (SFDM) per hour.

Biodeposition rate measurements were performed at the same time as excretion rate measurements. Mussels were collected and cleaned following the same method as for excretion rate measurements, but biodeposition rate measurements were done only on medium-sized mussels because it was difficult to collect enough small or large mussels for this experiment. 45 mussels in the medium size class (12–18 mm) were divided into 3 groups of 15 mussels and placed in acid-cleaned 50 mL centrifuge tubes with 45 mL NOPN medium and incubated along with the excretion rate experiment. After 3 h, mussels were removed from the containers and the water sample with biodeposits was frozen for later processing. Thawed samples were vigorously stirred, evenly divided into two equal portions and then filtered through 2 separate pre-weighed and pre-combusted GF/F filters. Filters were dried and weighed to assess total biodeposition rate. After weighing, one filter was used for C and N analysis using the same method as for seston PON and POC analysis (EA-IRMS); the second filter was used for P analysis using same method as water TP analysis. The rate of C, N and P biodeposition was expressed as mg element egested per g mussel SFDM per hour.

Tissue and Shell C, N and P Analysis

Soft tissue composition was determined on mussels collected in 2016; shell elemental composition was determined on samples collected from the same locations in 2015. For soft tissue elemental composition determination, the mussels from the excretion rate measurements were thawed and their soft tissues were removed from the shell (taking care to discard byssal threads). For shell elemental composition measurements, mussels from all study lakes were separated into the same three size classes used in other measurements, their shells were thoroughly cleaned with a toothbrush and a kimwipe and the soft tissues removed and discarded. After tissue removal, shells were thoroughly cleaned with deionized water. Tissue and shell samples were dried at 60°C for 48 h or until completely dry and ground into fine powder using a mortar and pestle. Triplicate samples of shell and tissue material were analyzed for each mussel size category in each lake. C and N content were determined by EA-IRMS; P content was determined spectrophotometrically using the molybdovanadate method following combustion (4 h at 450°C) and persulfate digestion (at 100°C for 60 min) of samples.

Whole-Lake Mussel Biomass and Nutrient Budget Estimation

Samples for estimation of whole-lake mussel biomass were collected in 2015 in 9 of the 10 study lakes. A petite ponar sampler was used to collect benthic grabs along a single depth transect in each lake. Samples were collected at about 1, 2, 4, 6 and 10 m depths along each transect, with 5 replicate samples per depth. Ponar samples were sieved in the field through a 500 μm screen and the retained material was frozen until processing. In the lab, samples were thawed and separated into live mussels and dead shell material. Dead shell material was cleaned, dried at 60°C until dry and weighed. Live mussels were measured using electronic calipers to the nearest 0.1 mm along the longest shell axis and lake-specific shell length–weight regressions were used to estimate total shell free dry tissue mass and shell mass for all mussels in the sample. Shell length–weight regressions of the form $W = aL^b$ were determined for each lake by selecting 50 mussels of different sizes from each lake, measuring their shell lengths, drying at 60°C until dry and weighing the soft tissues and shells separately. Depth-specific values of live soft tissue, live shell and dead shell mass were expressed on a per m^2 basis and extrapolated to the entire lake based on the total area of each depth interval (0–1 m, 1–3 m, 3–5 m, 5–8 m, > 10 m) in each lake. It is important to note that these whole-lake biomass estimates are based on data from a single depth transect and should thus be treated as first-order approximations.

The exception to the above-described approach was for Lake Mille Lacs, where we did not collect ponar samples for biomass estimation. Instead, data collected by the Minnesota Department of Natural

Resources was used to estimate lake-wide soft tissue and live shell biomass (Thomas Jones, MN DNR, unpublished data). For this, we used data on average lake-wide mussel densities for 2015, DNR-collected information about mussel size frequency distributions for 2010 (the last year of available data on size distributions) and our Mille Lacs-specific length–weight regressions. We did not have the necessary information to estimate dead shell mass in Lake Mille Lacs. No live mussels were present in Duluth Harbour samples, where almost all living mussels are associated with artificial substrata such as riprap and boat docks. We therefore only include dead shell material in the dreissenid nutrient budget for Duluth Harbor.

Whole-lake biomass estimates and information about the size distribution of live mussels in each lake was combined with lake-specific measurements of C, N and P excretion and biodeposition rates and tissue and shell composition to estimate the contribution of zebra mussels to whole-lake nutrient cycles. To examine the role of dreissenid in nutrient budgets of study lakes, we compared the C, N and P stored or cycled by dreissenids to water column standing stocks of TP, POC and PON which were estimated by multiplying results of our TP, POC and PON analyses by lake volume. We note that these estimates are based on a single water column sample and should be considered as approximations.

Literature Data

To assess the effect of dreissenids on nutrient budgets in a wider array of lakes than studied here, we compiled published data on dreissenid biomass and nutrient standing stocks in 24 European and North American lakes (Table S1; Wilson and Sarnelle 2002; Patterson and others 2005; Rudstam 2010; Rowe and others 2017; Ginn and others 2018). We restricted our analysis to TP budgets because TP concentrations were much more commonly reported alongside dreissenid biomass than water column C and N concentrations. Water column TP concentrations and lake volume were used to estimate water column TP standing stocks. We used published areal shell free dry biomass results and lake size to estimate total mussel biomass. Because we had no data on size distributions of mussels in the literature lakes, we combined the size distributions from all our study lakes and applied this combined (average) size distribution to all literature lakes. We used the average ratio between dry tissue and live shell biomass in our study lakes to estimate live shell mass in the literature lakes. P excretion rates and soft tissue and shell P content in the different lakes were estimated based on multiple regressions derived from data in our study lakes linking P excretion and composition to mussel size and water column TP. Because P biodeposition rates were not clearly correlated to lake trophic status and are probably less well constrained than measurements of P excretion or composition (see results), we did not include biodeposition in the P budgets of literature lakes.

Statistical Analysis

We used multiple linear regression to examine factors affecting the N and P excretion and C, N and P composition of soft tissues and shell material. For N and P excretion models, we included mussel size, lake trophic status (as chl. a concentration) and tissue N or P composition (for N and P excretion models, respectively), as well as all interactions between the predictor variables. For tissue and shell C, N and P composition, we used only mussel size, lake trophic status (as chl. a) and their interaction as predictor variables. Large outliers were present in some of the response variables, and we repeated analyses with and without the outliers, reporting results for both. Data were transformed as needed to approximate normality and equal variance and details on transformations are shown in the results section; normality and equal variance were diagnosed by inspecting q–q and residual plots. Models were parametrized with all potential predictor variables and simplified by sequentially removing the least significant terms until all remaining terms contributed significantly to the model. Because biodeposition rates were not measured for different size classes and were clearly not linearly related to any descriptor of lake trophic status, we used non-parametric Siegel regression to assess the relationship between deposition rate and lake trophic status. We used analysis of covariance (ANCOVA) to compare shell length-tissue weight and shell length-shell weight regressions from different lakes, $\log_{10}$ transforming length and weight. All analyses were performed in the R statistical computing environment.

Results

Excretion Rates

Across all lakes and mussel size classes, NH_4 and SRP excretion rates averaged 65.66 (± 41.52 SD) and 14.10 (± 10.80 SD) µg/g SFDM/h, respectively (Figure 1; Table S2). Log of NH_4 excretion was significantly and negatively related log of mussel

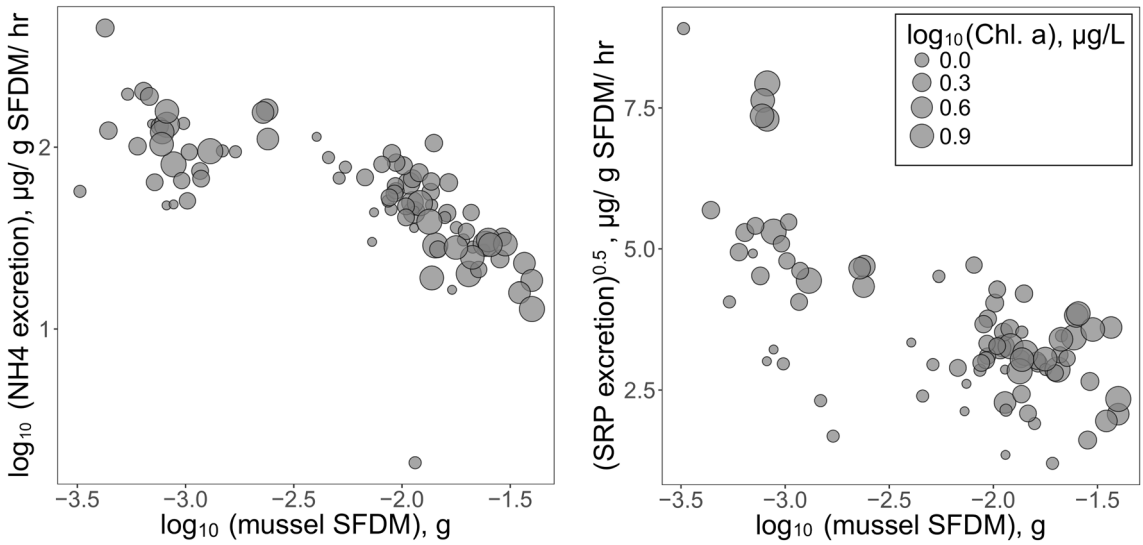

Figure 1. NH_4 and SRP excretion rates of zebra mussels of different sizes in 10 Minnesota lakes of different trophic status (measured as water column chl. a).

weight and positively related to tissue N content, with a significant interaction between log of weight and tissue N content (Table 2). When 3 extreme outliers were removed from the NH_4 data, the terms in the best model changed. There was still a strong negative effect of log of weight, but log of chl. a became a significant predictor (negative coefficient) with a significant weight-chl. a-tissue N interaction. The outlier-included and outlier-excluded models explained 61% and 62% of variation in log-transformed NH_4 excretion. Square root-transformed SRP excretion was also strongly and negatively related to log of mussel weight (Table 2). The outlier-included and outlier-excluded models both contained log of mussel weight as the main predictor, with a log of mussel weight by log of chl. a interaction as the second significant predictor. The outlier-included and outlier-excluded models, respectively, explained 60% and 59% of the variation in square root-transformed SRP excretion.

Biodeposition Rates

Biodeposition rates of total solids averaged 3.00 (± 1.99 SD) mg/g SFDM/hr across all replicates. C, N and P deposition rates averaged 0.70 (± 0.49 SD), 0.10 (± 0.06 SD) and 0.085 (± 0.08 SD) mg/g SFDM/h, respectively (Table S3). Total solids biodeposition was strongly correlated with rates of C and N biodeposition (Pearson's $r = 0.82$ and 0.72 with $p < 0.0001$ for C and N), but not with biodeposition of P (Pearson's $r = -0.03$, $p = 0.85$). Total and element-specific biodeposition rates were related to various indicators of lake trophic status (chl. a, TP, POC and PON). Regardless of productivity metric used, average deposition rates were higher (but also more variable) in less productive lakes, decreasing with lake trophic status (Figure 2). Non-parametric Siegel regression showed a significant decrease in total biodeposition with lake chl. a ($p = 0.0004$).

Tissue and Shell Composition

Across all lakes and mussel size classes, soft tissue C, N and P composition averaged 476.3 (± 21.41 SD), 112.6 (± 8.00 SD) and 20.5 (± 4.83 SD) mg/g SFDM (Figure 3; Table S4). Tissue C data included 6 large outliers that precluded transformations to normality and equal variance and results of the outlier-included analysis should be interpreted with caution. The outlier-excluded analysis showed a weak negative relationship between tissue C and the interaction between log of mussel weight and log of lake chl. a (Table 2). Tissue N also included 6 large outliers (for same samples as the C results) that prevented the assumptions of multiple linear regression from being met (Figure 3). Analysis on outlier-excluded data showed a significant but weak relationship with log of mussel weight (Table 2). Tissue P content data did not contain outliers, and a model containing log of chl. a, log of mussel weight and their interaction explained 54% of the variation in tissue P, with a positive relationship between tissue P and all predictors (Table 2).

Shell C, N and P composition averaged 122.1 (± 1.88 SD), 2.48 (± 0.69 SD) and 0.07 (± 0.04

Table 2. Results of Multiple Regression Models for Predictors of Zebra Mussel N and P Excretion Rates and Tissue and Shell C, N and P Composition

Parameter	*df*	Factor	Coefficient	*t*	R^2	Partial R^2	*p* value
Excretion							
$\log_{10}$(NH4 excretion)	3, 83	$\log_{10}$(SFDW)	− 1.63	− 5.97	0.61	0.30	< 0.0001
		Tissue N	0.033	4.77		0.22	< 0.0001
		$\log_{10}$(SFDW) * tissue N	0.011	4.43		0.19	< 0.0001
No outliers	3, 80	$\log_{10}$(chl. a)	− 0.47	− 2.80	0.62	0.09	0.006
$\log_{10}$(NH4 excretion)		$\log_{10}$(SFDW)	− 0.29	− 7.14		0.39	< 0.0001
		$\log_{10}$(chl. a) * $\log_{10}$(SFDW) * tissue N	− 0.002	− 2.68		0.08	0.009
SRP excretion$^{0.5}$	2, 81	$\log_{10}$(SFDW)	− 1.59	− 9.22	0.60	0.51	< 0.0001
		$\log_{10}$(SFDW) * $\log_{10}$(Chl. a)	− 0.59	− 5.56		0.28	< 0.0001
No outliers							
SRP excretion$^{0.5}$	2, 79	$\log_{10}$(SFDW)	− 1.36	− 8.73	0.59	0.49	< 0.0001
		$\log_{10}$(SFDW) * $\log_{10}$(Chl. a)	− 0.60	− 6.13		0.32	< 0.0001
Tissue composition							
Tissue C	1, 85	$\log_{10}$(SFDW)	0.03	3.26	0.10		0.0016
No outliers							
Tissue C	1, 79	$\log_{10}$(SFDW) * $\log_{10}$(Chl. a)	− 5.10	− 2.14	0.04		0.036
Tissue N	1, 85	$\log_{10}$(SFDW)	9.78	3.92	0.14		0.0002
No outliers							
Tissue N	1, 80	$\log_{10}$(SFDM)	3.61	2.3	0.05		0.024
Tissue P	3, 81	$\log_{10}$(chl. a)	13.39	3.97	0.54	0.16	0.00016
		$\log_{10}$(SFDW)	2.55	2.89		0.09	0.0049
		$\log_{10}$(chl. a) * $\log_{10}$(SFDW)	3.57	2.40		0.07	0.019
Shell composition							
Shell C	No significant relationships						
No outliers							
Shell C	No significant relationships						
Shell N	2, 81	$\log_{10}$(chl. a)	0.20	6.87	0.35	0.37	< 0.0001
		$\log_{10}$(SFDW)	− 0.04	− 2.04		0.05	0.044
$\log_{10}$(shell P)	2, 81	$\log_{10}$(chl. a)	0.30	5.59	0.36	0.28	< 0.0001
		$\log_{10}$(SFDW)	− 0.21	− 5.88		0.30	< 0.0001

SD) mg/g shell (Figure 3; Table S5). Shell C varied very little (once outliers were excluded) and there were no significant predictors of shell C content in our data (Table 2). Shell N and shell P content were both significantly and positively related to log of chl. a and negatively related to log of mussel weight, with these two factors explaining 35% and 36% of the variation in shell N and P content, respectively (Table 2).

Mussel Population Characteristics and Biomass

Mussel populations in different lakes had different size distributions (Figure S2). Length-tissue and shell weight relationships also differed among mussel populations (Figure S3; Table S6). Analysis of covariance ($df = 9, 479$) using log-transformed length and weight showed that shell length-soft tissue weight regressions from different lakes had similar slopes ($F = 1.26$, $p = 0.25$), but different intercepts ($F = 108.9$, $p < 0.0001$). On the other hand, shell length–shell weight regressions ($df = 9, 479$) had both significantly different slopes ($F = 2.86$, $p = 0.0026$) and intercepts ($F = 8.57$, $p < 0.0001$) in different lakes. There was a significant positive relationship between lake trophic status and predicted weight-at-length for both soft tissue and shell (Figure S4), suggesting that mussels from more productive systems have heavier soft tissues and shells at a given length.

Across all lakes and samples, mussel soft tissue, live shell and dead shell biomass averaged 4.8 (± 24.75 SD), 63.3 (± 177.9 SD) and 295.3 (± 937.2 SD) g/m^2, and were highly variable, both between and within lakes (Table 3; Figure S5). Biomass of living mussels and their shells was generally higher at shallow and intermediate

depths in the littoral zone (Figure S5), decreasing with depth. Dead shell mass generally followed the same pattern, but with some exceptions. For example, in Duluth Harbor no live mussels were collected by ponar grab at any depth, but dead shell was present in moderate quantities (average 26.6 g/m^2), especially at intermediate depths. In steep-sided Lake Zumbro, dead shell mass peaked at greater depths than live mussel biomass. When extrapolated to the whole-lake scale, the total biomass of live and dead mussel tissues and their relative quantities were also highly variable among lakes.

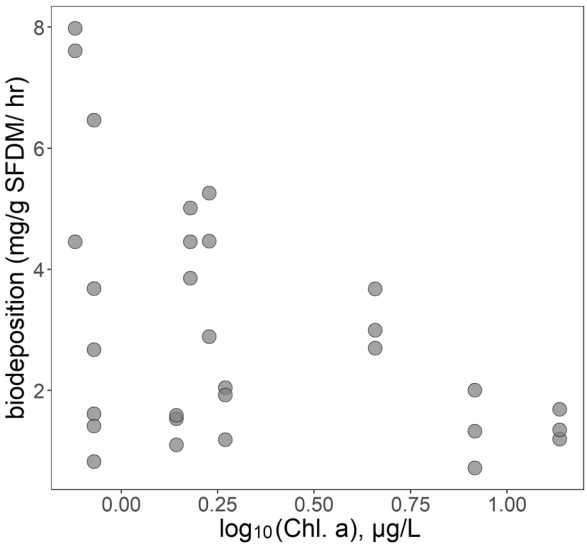

Figure 2. Total solids biodeposition rates of medium-sized (12–18 mm) zebra mussels in 10 Minnesota lakes of different trophic status.

Whole-Lake Nutrient Budgets

Different tissues contributed differently to storage of C, N and P (Figure 4; Table S7). Overall, live and dead shell material stored most of the C associated with dreissenids, whereas soft tissues were more important compartments for N and P storage. The exception to this were Lakes Pepin and Zumbro, where dead shell material accounted for much of the N and P associated with dreissenids; this is because these lakes had very large pools of dead shell material and relatively low densities of live mussels. Similarly, in Duluth Harbor, where no live mussels were collected, dead shell accounted for all the C, N and P associated with dreissenids.

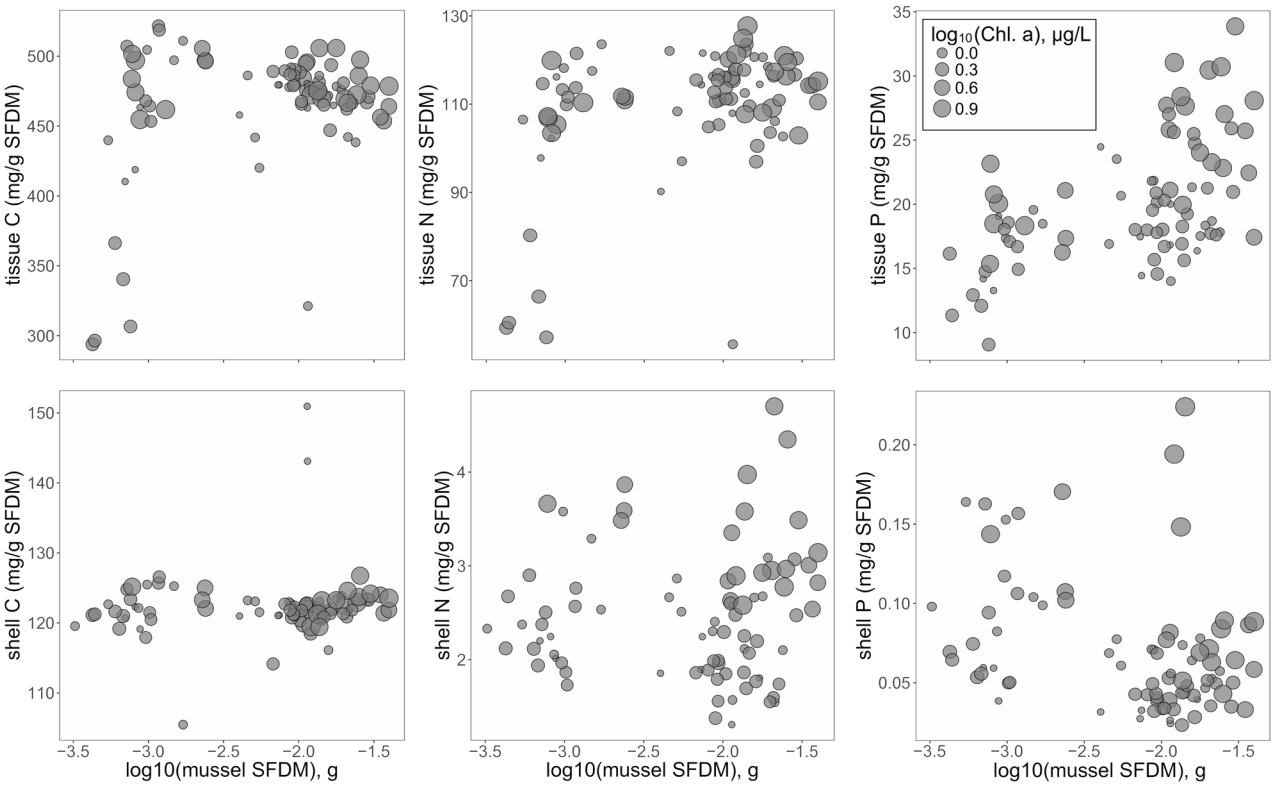

Figure 3. Soft tissue and shell C, N and P composition of zebra mussels of different sizes in 10 Minnesota lakes of different trophic status (measured as water column chl. a).

Table 3. Average Areal Biomass (g/m^2) for Tissue, Shell, Dead Shell in the 10 Minnesota Study Lakes

Lake	Tissue mass, g/m^2 (± SD)	Live shell, g/m^2 (± SD)	Dead shell, g/m^2 (± SD)
Carlos	7.28 (± 2.63)	137.1 (± 54.77)	107.23 (± 40.4)
Pelican	0.61 (± 0.59)	7.4 (± 7.13)	0.19 (± 0.4)
Pike	11.54 (± 5.84)	278.7 (± 145.66)	102.77 (± 66.6)
Round	2.98 (± 1.39)	48.5 (± 15.69)	33.82 (± 13.9)
Lizzie	1.53 (± 0.8)	30.2 (± 15.34)	44.44 (± 14.9)
Crystal	0.3 (± 0.23)	4.1 (± 3.08)	0.49 (± 0.6)
Mille Lacs[a]	78	1300	n/a
Duluth Harbor[b]	0	0	26.64 (± 42.4)
Zumbro	5.57 (± 6.13)	44.7 (± 48.92)	1778 (± 533.2)
Pepin	6.26 (± 9.61)	57.9 (± 91.07)	852.71 (± 607.6)

[a]*Data from Minnesota Department of Natural Resources.*
[b]*No live mussels were collected in ponar samples.*

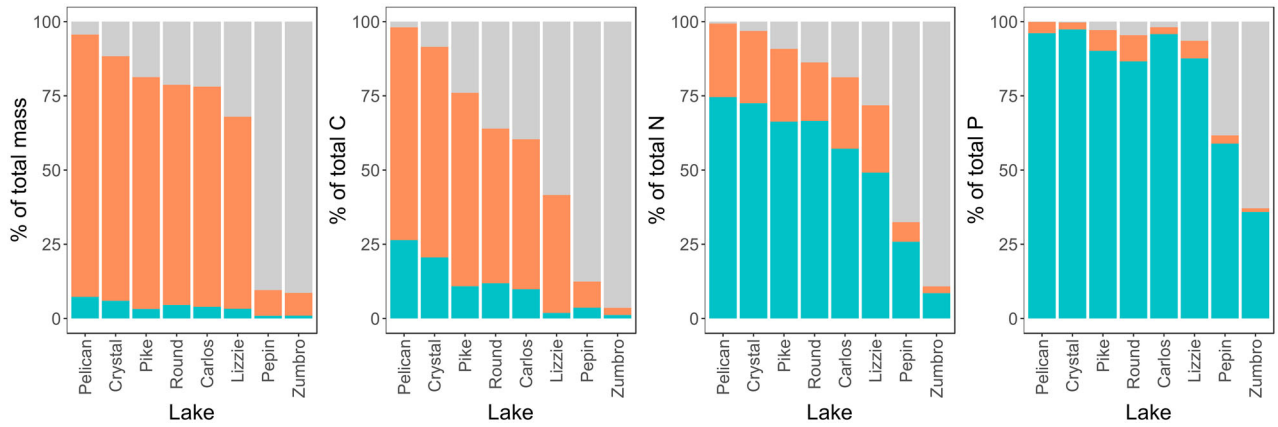

Figure 4. The relative distribution of total zebra mussel biomass and dreissenid-associated C, N and P among dreissenids soft tissue (blue), live shell (orange) and dead shell (gray) material in 8 Minnesota lakes (Color figure online).

Dreissenids populations played variable but often substantial roles in whole-lake elemental budgets (Figure 5, Tables S7, S8). Lake Mille Lacs, which had much higher estimated areal dreissenid biomass than any of the other study or literature lakes, was an outlier in the relative importance of dreissenids to nutrient budgets (Figure 5); in this section we exclude results from Mille Lacs as they do not appear typical of most dreissenid-invaded lakes. On a daily basis, dreissenids in the study lakes excreted an average of 0.4 (± 0.3 SD) % of water column PON; in the study and literature lakes, dreissenids excreted an average of 1.6 (± 2.1 SD) % of water column TP every day. In the study lakes, dreissenids biodeposited an average of 0.6 (± 0.6 SD) %, 0.8 (± 0.9 SD) % and 11.1 (± 15.6 SD) % of water column POC, PON and TP every day.

Across the study and literature lakes (Mille Lacs excluded), dreissenid stored an average of 92 (± 118 SD) % and 5.6 (7.9) % of water column TP standing stocks in their soft tissues and live shell material, respectively. Dead shell material accounted for an average 9.8 (± 19.4 SD) % of water column P in the study lakes (no dead shell mass estimates were available for the literature lakes). Across all study lakes, dreissenids stored 37.0 (± 41.3 SD) %, 12.1 (± 12.6 SD) % and 149.0 (± 400.1 SD) % of water column PON in their live tissues, live shells and dead shell material. Live tissues, live shells and dead shell material accounted for an average of 17.0 (± 15.5 SD) %, 75.6 (± 90.3 SD) % and 322 (± 738 SD) % of lake POC.

Discussion

We studied the role of invasive zebra mussels in the cycling of C, N and P in ten lakes differing in size, trophic status and invasion history and used literature data on dreissenid abundance to assess the effect of dreissenids on P budgets in an additional

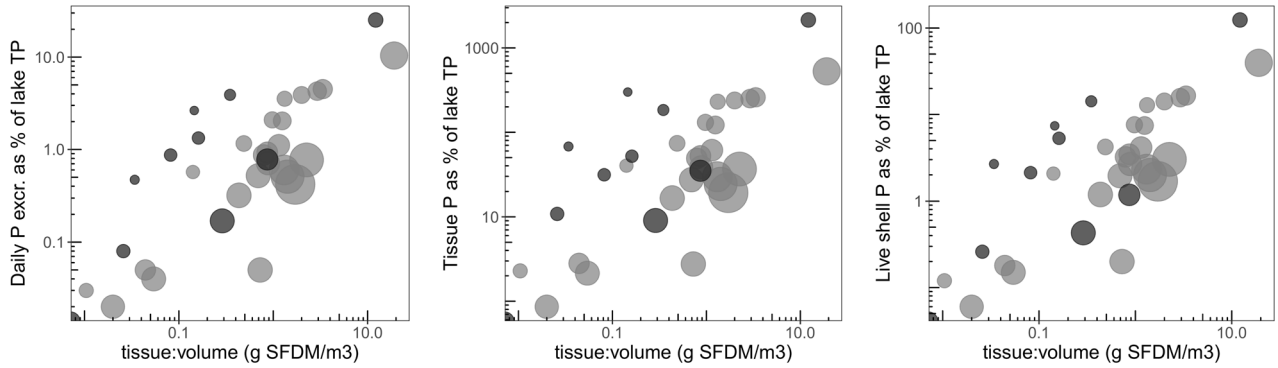

Figure 5. Estimated contribution of P excretion and storage in soft tissues and shells to the cycling of water column total phosphorus in 10 Minnesota lakes (dark gray symbols) and 24 literature lakes (light gray symbols).

24 lakes. This represents the most comprehensive field study of dreissenid impacts on elemental cycling to date. Novel aspects of this study include construction of complete nutrient budgets for multiple dreissenids populations, examination of variation in shell elemental composition and explicit inclusion of live and dead shell material in nutrient budgets. Results show that mussel size and lake trophic status predict aspects of tissue and shell elemental composition and nutrient excretion rates. We show that different processes (excretion, biodeposition, storage in tissue and live and dead shell material) vary in their importance to the cycling of different elements, with large lake-specific differences in the overall role of dreissenids in elemental budgets. Mussel population size, lake size and trophic status are shown to determine the degree of dreissenid impact on lake nutrient cycles.

Excretion, Biodeposition, Composition

The average mass-specific NH_4 and SRP excretion rates measured in our study lakes are close to the mean excretion rates from 13 previous studies (reviewed in Bootsma and Liao 2013; Ozersky and others 2015; Vanderploeg and others 2017). Size was the main predictor of mass-specific N and P excretion rate by zebra mussels in our study. The negative relationship between body size and mass-specific excretion rates is well-established for vertebrates and invertebrates (Vanni 2002; Vanni and McIntyre 2016), including for P excretion in dreissenids (Arnott and Vanni 1996; Conroy and others 2005; Bootsma and Liao 2013; Ozersky and others 2015). Evidence for the effect of size on NH_4 excretion in dreissenids has been equivocal (Bootsma and Liao 2013). Like Ozersky and others (2015), our results show a negative relationship between tissue weight and NH_4 excretion rate. Other studies have shown that N and P excretion rate in dreissenids and other aquatic animals can be affected by system productivity and tissue stoichiometry relationships (Sterner and Elser 2002; Vanni 2002; Morehouse and others 2013; Vanderploeg and others 2017). Lake trophic status (as chl. a) was a significant, positive predictor of SRP excretion, but only for smaller mussels. Tissue composition and lake trophic status were significant predictors of NH_4 excretion rates, but their importance differed depending on whether outliers were included and the nature of their effect on NH_4 excretion rates is difficult to determine from our data. Previous studies have shown different relationships between productivity and nutrient excretion. Arnott and Vanni (1996) saw contrasting correlations between chl. a and N excretion rates in different sized zebra mussels from Lake Erie, and Ozersky and others (2015) saw a negative relationship between chl. a and N excretion, but neither study showed a relationship between chl. a and P excretion. In a lab trial, Morehouse and others (2013) demonstrated a positive relationship between food quality (as C:P) and excretion rates of P and N. In a large mesocosm experiment, Vanderploeg and others (2017) showed a strong positive relationship between water column particulate P, P assimilation and zebra mussel P excretion, but not between PON, N assimilation and N excretion. In that study, P excretion was more closely related to food quality (negative relationship with seston C:P ratio) than total P concentrations. Collectively, these results show that rates of dissolved N and P excretion by zebra mussel populations depend on population size structure, food availability and food quality. We saw greater variability of excretion rates with mussel size than with lake trophic status, supporting the conclusion of Bootsma and Liao (2013) that the size structure of a mussel population will have large effects on its nutrient cycling

rate. For example, for Pike Lake, the estimated lake-wide excretion of N was 2.1 higher and excretion of P was 2.9 times higher for a hypothetical dreissenid population made up of only small versus only large mussels (assuming the same total biomass).

Across all lakes, the average biodeposition rates we measured fall between those measured in oligotrophic Lake Constance (Gergs and others 2009) and in turbid portions of Lake Erie (Klerks and others 1996). Average rates of N and P deposition were also similar to those determined in a mesocosm experiment across a wide range of seston concentrations by Vanderploeg and others (2017). Interestingly, we did not see a positive relationship between water column particle concentrations and biodeposition rates, a common pattern in other studies on freshwater and marine bivalves, including dreissenids (Widdows and others 1979; Klerks and others 1996; Gergs and others 2009). The C:N and N:P ratios of biodeposits (7.9 and 4.2, respectively) in our study are also different (and approximately 2–3 times lower) than those observed by Gergs and others (2009) and Vanderploeg and others (2017). It is possible that these differences are a function of the relatively crude, static approach we used to estimate biodeposition rates and biodeposition is probably the least well-constrained element of zebra mussel nutrient budgets in our study.

In our study, mussel size and lake trophic status were only weakly related to tissue C and N content, but both were positively related with tissue P content. To our knowledge this is the only study to explicitly examine dreissenid tissue composition across a large natural trophic status gradient. Our finding of increased tissue P in more productive systems agrees with results of experimental work on zebra mussels, where tissue P content was shown to be inversely related to food C:P ratios (Morehouse and others 2013) and a survey of 4 Swedish lakes where zebra mussel tissue C:P was lowest in the most productive lake (Naddafi and others 2012). These results suggest that dreissenids are not strictly homeostatic in regards to tissue C:N and C:P ratios, which varied approximately twofold across lakes (within the same size class). The size-tissue composition pattern we saw (positive size-tissue P relationship) contrasts with the findings of Goedkoop and others (2011) who found a significant (positive) relationship only between size and tissue N content and that of Arnott and Vanni (1996) who did not see a significant relationship between size and tissue composition. Relatively few studies have examined shell elemental composition and none across large trophic gradients, although Arnott and Vanni (1996) and Pennuto and others (2012) showed that dreissenid shell composition can vary among sites within a single lake and through the open water season. We found that shell N and P content are positively related to lake trophic status and negatively related to mussel size, meaning the role of shell material in nutrient dynamics will vary with both mussel population size structure and lake trophic status.

The results of this study and other investigations of nutrient relations in dreissenids show that tissue and shell composition is more consistent across systems compared to excretion and biodeposition rates. In this study, the coefficients of variation of excretion and biodeposition rates across all samples were between 60 and 70%; other measurements of excretion and biodeposition rates in both lab and field settings also show large differences in excretion and biodeposition rate between systems and across seasons (Arnott and Vanni 1996; Gergs and others 2009; Ozersky and others 2015; Vanderploeg and others 2017). In contrast, in our study, coefficients of variation for tissue and shell composition were generally much lower across all samples. Tissue and shell C were especially consistent across samples (coefficient of variation of 4.5 and 1.5%, respectively), while shell N and P were more variable (coefficient of variation of 28 and 58%). These results suggest that nutrient storage by dreissenid mussels in different systems is more easily predictable from biomass estimates than biodeposition or excretion, which are more strongly affected by factors such as mussel size frequency distributions, lake trophic status, algal community composition and physiological state of the mussels.

Dreissenid Population Characteristics

Our 10 study lakes differed substantially in dreissenid population characteristics, including size frequency distributions, length–weight relationships and live mussel and dead shell biomass. The dependence of physiological rates on body size means that the size frequency distribution of a dreissenid population can have large effects on the ecological impact of the population (Bootsma and Liao 2013). We saw differences in size frequency distribution and average mussel size in the 8 lakes in which detailed size frequency distributions were constructed, and average body size was positively related to time since infestation, suggesting a shift from small to larger individuals though time, a pattern that has been shown when tracking size

structure of dreissenid populations through time (Nalepa and others 1995). Length–weight relationships also differed among lakes, with heavier soft tissues and shells at a given length for mussels in more productive lakes. Although tissue condition index (the ratio between shell length and tissue weight) has been used to look at the effect of pollutants on zebra mussel condition (Voets and others 2006), differences in condition through time (Naddafi and others 2008) and effect of food quality on condition (Vanderploeg and others 2017), ours is the first study to show a positive relationship between lake productivity and both tissue and shell weight relative to length across a natural productivity gradient. This finding suggests that dreissenids are in better condition and can allocate more energy to tissue growth and shell formation in more productive systems. This may have implications for reproductive output (mussels in more productive environments may be able to allocate more energy to reproduction), survival during unfavorable conditions (mussels in more productive environments may be able to store more energy and thus better survive unfavorable periods) and predator resistance (mussels in more productive environments may be able to allocate more energy to shell formation and better resist predation).

Average estimated lake-wide areal biomass of live mussels differed by more than two orders of magnitude among study lakes (from a low of 0.3 g SFDM/m^2 in Lake Crystal to a high of 78 g SFDM/m^2 in Lake Mille Lacs) and by a similar degree in lakes for which literature data were available (0.2 g SFDM/m^2 in Lake Beldany to 43.2 g SFDM/m^2 in Lake Olow). Dead shell mass was even more variable among our study lakes, differing by almost four orders of magnitude, from a low of 0.19 g/m^2 in Pelican Lake to 1778 g/m^2 in Lake Zumbro. Dead shell mass was correlated with time since invasion, which explained approximately one third of the variation in areal dead shell mass. This means that shell material accumulates over time, potentially making up a large component of surface sediments (up to 10 kg/m^2 in parts of Lake Pepin, which was invaded in 1994). The large variability in dreissenid live biomass and mass of dead shell material indicates that the effects of mussels on invaded ecosystems are variable and will range from negligible to severe, depending on the size of the population.

Although areal biomass was highly variable among lakes, the pattern of depth distribution of live zebra mussels and their shell material was more consistent among lakes, typically peaking at intermediate depths (2–5 m) and dropping off to very low densities by 10 m depth, where bottom substrate became dominated by soft silt and organic matter. It is well known that zebra mussels avoid soft, unstable substrates (fore example, Mellina and Rasmussen 1994) and the decrease in zebra mussel densities with depth has been demonstrated in several systems (e.g., Higgins and others 2008; Ozersky and others 2015). The restriction of zebra mussel populations to the littoral zone has important implications for their effects on ecosystem processes (Hecky and others 2004; Schwalb and others 2013; Ozersky and others 2015), allowing them year-round access to phytoplankton in the mixed epilimnion and meaning that nutrients excreted or biodeposited by dreissenids are available to benthic and pelagic primary producers. In many North American large lakes, zebra mussels have become replaced with quagga mussels (Patterson and others 2005; Nalepa and others 2009; Ginn and others 2018). Quagga mussels are more tolerant of soft substrates, cold temperatures and low food levels than zebra mussels (Karatayev and others 2015), allowing them to expand into the deep profundal zones of lakes. The zebra–quagga replacement likely leads to total increased storage of nutrients in dreissenids (since they can build up larger total populations) while resulting in nearshore-offshore differences in dreissenid-mediated benthic-pelagic fluxes, since profundal quagga mussel populations are ''cut off'' from the surface mixed layer by stratification for portions of the year (e.g., Rowe and others 2017). More work is needed to determine the fate of nutrients processed by profundal dreissenid populations and the effects of the zebra–quagga replacement on whole-lake nutrient dynamics.

Nutrient Budgets for Dreissenid Populations

There was large variation in the importance of dreissenids to nutrient budgets in the study and literature lakes relative to water column standing stocks of TP, POC and PON. Estimates of whole-lake daily excretion and biodeposition rates show that in some lakes dreissenid populations can redirect large portions of water column C, N and P to the littoral benthos and turn over pelagic nutrient pools multiple times a year (e.g., in 20% of the study and literature lakes, dreissenid dissolved P excretion was estimated to turn over the water column TP pool in less than a month). Dreissenid populations were also shown to store variable, but sometimes large quantities of C, N and P in their

tissues and shells relative to water column standing stocks of TP, PON and POC. Published estimates of external and internal P loading and sediment burial efficiency are available for some of our study and literature lakes (Table S9) and the role of dreissenids relative to these processes is variable but can be significant. For example, in Lakes Mille Lacs, Erie, Michigan and Simcoe, dreissenid soft tissue P storage and estimated annual dissolved P excretion exceeded external and internal loading and sediment burial. On the other hand, in eutrophic Lakes St. Clair and Pepin dreissenids played a negligible role in cycling and storage of P relative to external loading and sediment retention.

It is well known that zooplankton, non-dreissenid benthos and fish can contribute significantly to nutrient turnover in lakes (e.g., Lehman 1980; Vanni 2002), and others have compared the role of dreissenids in nutrient recycling and storage to that of other biota. For example, Stańczykowska and Planter (1985) showed that dreissenids and macrophytes stored comparable quantities of P and N in 5 Polish lakes. Arnott and Vanni (1996) and Conroy and others (2005) estimated that dreissenids nutrient release in Lake Erie is comparable to or larger than that from zooplankton or macrophytes. To examine the relative roles of dreissenids and zooplankton in P budgets in the study and literature lakes, we estimated zooplankton biomass (based on an empirical TP versus zooplankton biomass relationship; Hanson and Peters 1984), zooplankton community P content (approximately 1% of dry mass; Andersen and Hessen 1991) and zooplankton community P excretion (145 μg/g DW/h, based on mean crustacean community excretion rates from Oliver and others 2014). Excluding the extreme results from Lake Mille Lacs, across all study and literature lakes, dreissenids stored 21-fold (± 29 SD) more P than zooplankton but excreted only slightly more P (dreissenid:zooplankton ratio of 1.06 ± 1.55 SD). Although our estimates of the biomass and P turnover by zooplankton are very approximate, they suggest that in many invaded lakes dreissenids have at least a comparable role to zooplankton in nutrient cycling. Comparisons to the role of non-dreissenid benthos is more complicated, because no simple empirical relationships for predicting littoral invertebrate biomass are available. The average littoral invertebrate biomass from 21 diverse dreissenid-free lakes in Europe and North America was 4.3 (± 3.8 SD) g DM/m^2 (Rasmussen 1988), compared to average dreissenid biomass of 11.2 g SFDM/m^2 across our study and literature lakes. Higgins and Vander Zanden (2010) found that, in the littoral zone of 7 invaded lakes, dreissenids made up about 95% of total benthic invertebrate biomass. It is thus likely that in most invaded lakes dreissenids play a more important (or at least equivalent) role in nutrient dynamics than native littoral benthic invertebrates.

Dreissenid establishment represents the addition of a new, and in come cases large, element in the nutrient budgets and dynamics of invaded lakes. The rapid recycling of water column nutrients through dreissenid biodeposition and excretion in lake littoral zones has the potential to affect the balance of pelagic and benthic productivity in invaded lakes, contributing to what Mills and others (2003) called ''benthification.'' The nutrients excreted by dreissenids can fuel benthic primary production (Ozersky and others 2009; Depew and others 2018), whereas biodeposited material provides food for benthic macroinvertebrates (Izvekova and Lvova-Katchanova 1972; Gergs and others 2011), leading to increased abundance of littoral biota and changes to the structure of food webs (Botts-Silver and others 1996; Higgins and Vander Zanden 2010; Ozersky and others 2012; Turschak and others 2014; Fera and others 2017). Soft tissues and shell material can store large quantities of carbon and nutrients in some invaded lakes, although the role of these tissues in nutrient dynamics plays out over longer time scales than that of excretion and biodeposition. The difference in the elemental composition of tissue and shell (C:N:P of 60:12:1 vs. 4500:78:1, respectively) and in their environmental persistence means that their roles in nutrient cycles differ. Soft tissues decompose rapidly after death and, as recognized by Mellina and others (1995), represent a net sink for material only while the population is growing, becoming a ''neutral'' compartment when the population stabilizes and potentially a source of nutrients during die-off periods. Shell material, on the other hand, has slow dissolution rates (Strayer and Malcom 2007; Ozersky and others 2015). Although shell has low P content, comparison of P content in dreissenid shells against estimated sediment P burial suggests that, in some cases, shell may represent a significant long-term P sink. For example, living mussel shells contained 17, 8 and 19% of estimated annual P burial in sediments of Lakes Simcoe, Erie and Michigan, respectively.

One of our clearest findings is the very large among-lake variability in the importance of dreissenid populations to whole-lake nutrient budgets. In some lakes dreissenids made a negligible contribution to elemental dynamics, while in others dreissenids moved and stored significant quantities

of nutrients compared to other compartments and fluxes. Two main factors appear to drive this variability: (1) the biomass of the dreissenid population relative to lake volume and (2) the trophic status of the system (Figure 5). Dreissenids played the largest roles in the nutrient budgets of shallow lakes with high areal dreissenid biomass and low water column nutrient concentrations; these types of systems also likely show larger changes to ecosystem processes following dreissenid invasions. Meta-analyses have found that substrate availability, morphometry, water chemistry and system productivity combine to determine dreissenid population biomass (Ramcharan and others 1992; Wilson and Sarnelle 2002; Jones and Ricciardi 2005; Naddafi and others 2011). Information about potential dreissenid population size and our findings could be used by ecosystem managers to prioritize invasion prevention efforts to systems that are likely to see the largest changes to their nutrient dynamics and consequently ecosystem function.

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REFERENCES

Andersen T, Hessen DO. 1991. Carbon, nitrogen, and phosphorus content of freshwater zooplankton. Limnol Oceanogr 36:807–14.

Arnott DL, Vanni MJ. 1996. Nitrogen and phosphorus recycling by the zebra mussel (*Dreissena polymorpha*) in the western basin of Lake Erie. Can J Fish Aquat Sci 53:646–59.

Bootsma HA, Liao Q. 2013. Nutrient cycling by dreissenid mussels: controlling factors and ecosystem response. In: Nalepa TF, Schloesser DW, Eds. Quagga and zebra mussels: biology, impacts, and control. 2nd edn. London: Taylor & Francis. p 555–74.

Botts-Silver P, Patterson BA, Schloesser DW. 1996. Zebra mussel effects on benthic invertebrates: physical or biotic? J N Am Benthol Soc 15:179–84.

Conroy JD, Edwards WJ, Pontius RA, Kane DD, Zhang H, Shea JF, Richey JN, Culver DA. 2005. Soluble nitrogen and phosphorus excretion of exotic freshwater mussels (*Dreissena* spp.): potential impacts for nutrient remineralisation in western Lake Erie. Freshw Biol 50:1146–62.

Depew DC, Koehler G, Hiriart-Baer V. 2018. Phosphorus dynamics and availability in the nearshore of eastern Lake Erie: insights from oxygen isotope ratios of phosphate. Front Mar Sci 5:215. https://doi.org/10.3389/fmars.2018.00215.

Fera SA, Rennie MD, Dunlop ES. 2017. Broad shifts in the resource use of a commercially harvested fish following the invasion of dreissenid mussels. Ecology 98:1681–92.

Gergs R, Grey J, Rothhaupt KO. 2011. Temporal variation in zebra mussel (*Dreissena polymorpha*) density structure the benthic food web and community composition on hard substrates in Lake Constance, Germany. Biol Invasions 13:2727–38.

Gergs R, Rinke K, Rothhaupt KO. 2009. Zebra mussels mediate benthic–pelagic coupling by biodeposition and changing detrital stoichiometry. Freshw Biol 54:1379–91.

Ginn BK, Bolton R, Coulombe D, Fleischaker T, Yerex G. 2018. Quantifying a shift in benthic dominance from zebra (*Dreissena polymorpha*) to quagga (*Dreissena rostriformis bugensis*) mussels in a large, inland lake. J Great Lakes Res 44:271–82.

Goedkoop W, Naddafi R, Grandin U. 2011. Retention of N and P by zebra mussels (*Dreissena polymorpha* Pallas) and its quantitative role in the nutrient budget of eutrophic Lake Ekoln, Sweden. Biol Invasions 13:1077–86.

Hanson JM, Peters RH. 1984. Empirical prediction of crustacean zooplankton biomass and profundal macrobenthos biomass in lakes. Can J Fish Aquat Sci 41:439–45.

Hecky RE, Smith RE, Barton DR, Guildford SJ, Taylor WD, Charlton MN, Howell T. 2004. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Can J Fish Aquat Sci 61:1285–93.

Higgins SN, Vander Zanden MJ. 2010. What a difference a species makes: a meta-analysis of dreissenid mussel impacts on freshwater ecosystems. Ecol Monogr 80:179–96.

Higgins TM, Grennan JM, McCarthy TK. 2008. Effects of recent zebra mussel invasion on water chemistry and phytoplankton production in a small Irish lake. Aquat Invasions 3:14–20.

Izvekova EI, Lvova-Katchanova AA. 1972. Sedimentation of suspended matter by *Dreissena polymorpha* Pallas and its subsequent utilization by Chironomidae larvae. Pol Arch Hydrobiol 19:203–10.

Jones LA, Ricciardi A. 2005. Influence of physicochemical factors on the distribution and biomass of invasive mussels (*Dreissena polymorpha* and *Dreissena bugensis*) in the St. Lawrence River. Can J Fish Aquat Sci 62:1953–62.

Karatayev AY, Burlakova LE, Padilla DK. 2015. Zebra versus quagga mussels: a review of their spread, population dynamics, and ecosystem impacts. Hydrobiologia 746:97–112.

Klerks PL, Fraleigh PC, Lawniczak JE. 1996. Effects of zebra mussel (*Dreissena polymorpha*) on seston levels and sediment deposition in western Lake Erie. Can J Fish Aquat Sci 53:2284–91.

Lehman JT. 1980. Release and cycling of nutrients between planktonic algae and herbivores. Limnol Oceanogr 25:620–32.

Mellina E, Rasmussen JB. 1994. Patterns in the distribution and abundance of zebra mussel (*Dreissena polymorpha*) in rivers

and lakes in relation to substrate and other physicochemical factors. Can J Fish Aquat Sci 51:1024–36.

Mellina E, Rasmussen JB, Mills EL. 1995. Impact of zebra mussel (*Dreissena polymorpha*) on phosphorus cycling and chlorophyll in lakes. Can J Fish Aquat Sci 52:2553–73.

Mills EL, Casselman JM, Dermott R, Fitzsimons JD, Gal G, Holeck KT, Hoyle JA, Johannsson OE, Lantry BF, Makarewicz JC, Millard ES, Munawar IF, Munawar M, O'Gorman R, Owens RW, Rudstam LG, Schaner T, Stewart TJ. 2003. Lake Ontario: food web dynamics in a changing ecosystem (1970–2000). Can J Fish Aquat Sci 60:471–90.

Morehouse RL, Dzialowski AR, Jeyasingh PD. 2013. Impacts of excessive dietary phosphorus on zebra mussels. Hydrobiologia 707:73–80.

Naddafi R, Blenckner T, Eklöv P, Pettersson K. 2011. Physical and chemical properties determine zebra mussel invasion success in lakes. Hydrobiologia 669:227–36.

Naddafi R, Goedkoop W, Grandin U, Eklöv P. 2012. Variation in tissue stoichiometry and condition index of zebra mussels in invaded Swedish lakes. Biol Invasions 14:2117–31.

Naddafi R, Pettersson K, Eklöv P. 2008. Effects of the zebra mussel, an exotic freshwater species, on seston stoichiometry. Limnol Oceanogr 53:1973–87.

Nalepa TF, Fanslow DL, Lang GA. 2009. Transformation of the offshore benthic community in Lake Michigan: recent shift from the native amphipod *Diporeia* spp. to the invasive mussel *Dreissena rostriformis bugensis*. Freshw Biol 54:466–79.

Nalepa TF, Gardner WS, Malczyk JM. 1991. Phosphorus cycling by mussels (Unionidae: Bivalvia) in Lake St. Clair. Hydrobiologia 219:239–50.

Nalepa TF, Wojcik JA, Fanslow DL, Lang GA. 1995. Initial colonization of the zebra mussel (*Dreissena polymorpha*) in Saginaw Bay, Lake Huron: population recruitment, density, and size structure. J Great Lakes Res 21:417–34.

Oliver SK, Branstrator DK, Hrabik TR, Guildford SJ, Hecky RE. 2014. Nutrient excretion by crustacean zooplankton in the deep chlorophyll layer of Lake Superior. Can J Fish Aquat Sci 72:390–9.

Ozersky T, Evans DO, Barton DR. 2012. Invasive mussels alter the littoral food web of a large lake: stable isotopes reveal drastic shifts in sources and flow of energy. PLoS ONE 7(12):e51249. https://doi.org/10.1371/journal.pone.0051249.

Ozersky T, Evans DO, Ginn BK. 2015. Invasive mussels modify the cycling, storage and distribution of nutrients and carbon in a large lake. Freshw Biol 60:827–43.

Ozersky T, Malkin SY, Barton DR, Hecky RE. 2009. Dreissenid phosphorus excretion can sustain *C. glomerata* growth along a portion of Lake Ontario shoreline. J Great Lakes Res 35:321–8.

Patterson MW, Ciborowski JJ, Barton DR. 2005. The distribution and abundance of *Dreissena* species (Dreissenidae) in Lake Erie, 2002. J Great Lakes Res 31:223–37.

Pennuto CM, Howell ET, Lewis TW, Makarewicz JC. 2012. *Dreissena* population status in nearshore Lake Ontario. J Great Lakes Res 38:161–70.

Ramcharan CW, Padilla DK, Dodson SI. 1992. Models to predict potential occurrence and density of the zebra mussel, Dreissena polymorpha. Can J Fish Aquat Sci 49:2611–20.

Rasmussen JB. 1988. Littoral zoobenthic biomass in lakes, and its relationship to physical, chemical, and trophic factors. Can J Fish Aquat Sci 45:1436–47.

Rowe MD, Anderson EJ, Vanderploeg HA, Pothoven SA, Elgin AK, Wang J, Yousef F. 2017. Influence of invasive quagga mussels, phosphorus loads, and climate on spatial and temporal patterns of productivity in Lake Michigan: a biophysical modeling study. Limnol Oceanogr 62:2629–49.

Rudstam LG. 2010. Lakewide zebra and quagga mussel summary, Oneida Lake, New York, 1992–2009. Online: http://knb.ecoinformatics.org/knb/metacat/kgordon.23.16/knb. Accessed 4 Sep 2018.

Schloesser DW, Nalepa TF. 1994. Dramatic decline of unionid bivalves in offshore waters of western Lake Erie after infestation by the zebra mussel, *Dreissena polymorpha*. Can J Fish Aquat Sci 51:2234–42.

Schwalb AN, Bouffard D, Ozersky T, Boegman L, Smith RE. 2013. Impacts of hydrodynamics and benthic communities on phytoplankton distributions in a large, dreissenid-colonized lake (Lake Simcoe, Ontario, Canada). Inland Waters 3:269–84.

Stańczykowska A, Planter M. 1985. Factors affecting nutrient budget in lakes of the R. Jorka watershed (Masurian Lakeland, Poland): X. Role of the mussel *Dreissena Polymorpha* (Pall.) in N and P cycles in a lake ecosystem. Ekol Pol 33:345–56.

Sterner RW, Elser JJ. 2002. Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton: Princeton University Press.

Strayer DL, Malcom HM. 2007. Shell decay rates of native and alien freshwater bivalves and implications for habitat engineering. Freshw Biol 52:1611–17.

Turschak BA, Bunnell D, Czesny S, Höök TO, Janssen J, Warner D, Bootsma HA. 2014. Nearshore energy subsidies support Lake Michigan fishes and invertebrates following major changes in food web structure. Ecology 95:1243–52.

Tyner EH, Bootsma HA, Lafrancois BM. 2015. Dreissenid metabolism and ecosystem-scale effects as revealed by oxygen consumption. J Great Lakes Res 41:27–37.

Vanderploeg HA, Liebig JR, Carmichael WW, Agy MA, Johengen TH, Fahnenstiel GL, Nalepa TF. 2001. Zebra mussel (*Dreissena polymorpha*) selective filtration promoted toxic Microcystis blooms in Saginaw Bay (Lake Huron) and Lake Erie. Can J Fish Aquat Sci 58:1208–21.

Vanderploeg HA, Sarnelle O, Liebig JR, Morehead NR, Robinson SD, Johengen TH, Horst GP. 2017. Seston quality drives feeding, stoichiometry and excretion of zebra mussels. Freshw Biol 62:664–80.

Vanni MJ. 2002. Nutrient cycling by animals in freshwater ecosystems. Annu Rev Ecol Syst 33:341–70.

Vanni MJ, McIntyre PB. 2016. Predicting nutrient excretion of aquatic animals with metabolic ecology and ecological stoichiometry: a global synthesis. Ecology 97:3460–71.

Voets J, Talloen W, de Tender T, Van Dongen S, Covaci A, Blust R, Bervoets L. 2006. Microcontaminant accumulation, physiological condition and bilateral asymmetry in zebra mussels (*Dreissena polymorpha*) from clean and contaminated surface waters. Aquat Toxicol 79:213–25.

Widdows J, Fieth P, Worrall CM. 1979. Relationships between seston, available food and feeding activity in the common mussel *Mytilus edulis*. Mar Biol 50:195–207.

Wilson AE, Sarnelle O. 2002. Relationship between zebra mussel biomass and total phosphorus in European and North American lakes. Arch Hydrobiol 153:339–51.