

Dominance of the noxious cyanobacterium *Microcystis aeruginosa* in low-nutrient lakes is associated with exotic zebra mussels

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Abstract

To examine the hypothesis that invasion by zebra mussels (*Dreissena polymorpha*) promotes phytoplankton dominance by the noxious cyanobacterium *Microcystis aeruginosa*, 61 Michigan lakes of varying nutrient levels that contain or lack zebra mussels were surveyed during late summer. After accounting for variation in total phosphorus (TP) concentrations, lakes with *Dreissena* had lower total phytoplankton biomass, as measured by chlorophyll *a* and algal cell biovolume. Phytoplankton biomass increased with TP in both sets of lakes, although the elevations of the relationship differed. The percentage of the total phytoplankton comprised by cyanobacteria increased with TP in lakes without *Dreissena* ($R^2 = 0.21$, $P = 0.025$) but not in lakes with *Dreissena* ($P = 0.79$). Surprisingly, there was a positive influence of *Dreissena* invasion on *Microcystis* dominance in lakes with TP < $25 \mu\text{g L}^{-1}$ ($P = 0.0018$) but not in lakes with TP > $25 \mu\text{g L}^{-1}$ ($P = 0.86$). The finding that *Microcystis*, a relatively grazing-resistant component of the phytoplankton, was favored by *Dreissena* in low- but not in high-nutrient lakes is somewhat counterintuitive, but predator-prey models make this prediction in certain cases when the cost for the prey of being consumption resistant is a low maximum population growth rate. This *Dreissena*-cyanobacteria interaction contradicts well-established patterns of increasing cyanobacteria with nutrient enrichment in north-temperate lakes and suggests that the monitoring and abatement of nutrient inputs to lakes may not be sufficient to predict and control cyanobacterial dominance of *Dreissena*-invaded lakes.

Decades of limnological research have firmly established the paradigm that cyanobacteria increasingly dominate summer phytoplankton communities as lakes are enriched with nutrients (Trimbee and Prepas 1987; Paerl 1988; Watson et al. 1997; Downing et al. 2001). This paradigm drives eco-

system management policies and is a basis for large societal investments into wastewater treatment and non-point-source pollution control to reduce nutrient inputs to lakes (Tiessen 1995). Much of the research on this topic has been carried out in lakes in temperate North America. The rapid spread of a potent new algal grazer in these lakes—the zebra mussel (*Dreissena polymorpha*)—may alter the fundamental controls on algal abundance and community composition. Introduced to North America during the mid-1980s, the zebra mussel now flourishes in the Laurentian Great Lakes and Mississippi River system and is currently invading inland lakes at a rapid rate (Fig. 1). The most dramatic ecological effects of zebra mussels reported to date have been reductions in phytoplankton biomass and turbidity and local extirpations of native mussel populations (Strayer et al. 1999).

Recent studies of phytoplankton community structure after the invasion of the zebra mussel into coastal habitats in the Great Lakes have reported intense blooms of *Microcystis aeruginosa*, a colonial cyanobacterium that is known for its tendency to produce surface scums as well as its potential toxicity (Vanderploeg et al. 2001; Nicholls et al. 2002). Current empirical models of phytoplankton community structure predict a strong positive relationship between cyanobacterial dominance (i.e., the percentage of summer phytoplankton biomass) and total phosphorus (TP), with dominance reaching 90–100% in lakes with TP concentrations of 50–100 μg

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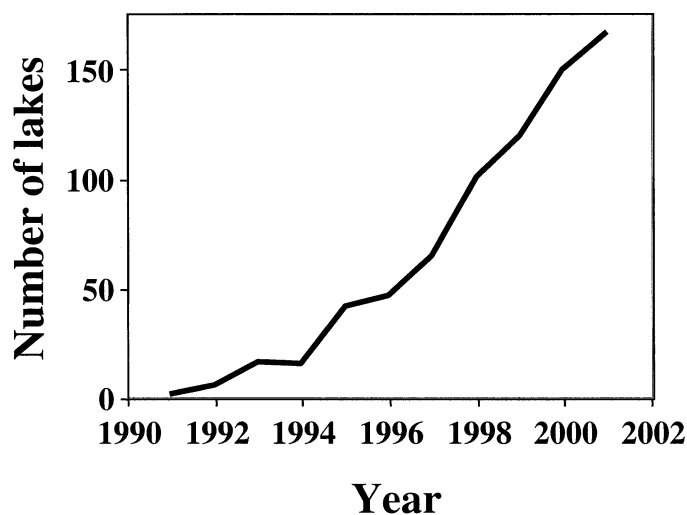


Fig. 1. Rate of zebra mussel invasion of inland lakes in Michigan. Data compiled by the Michigan Sea Grant.

L^{-1} (Trimbee and Prepas 1987; Downing et al. 2001). Cyanobacterial blooms in the Great Lakes are thus a surprise, given decades-long reductions in anthropogenic phosphorus inputs that have reduced TP to mesotrophic levels (20–25 $\mu\text{g L}^{-1}$) (Nicholls and Hopkins 1993). Zebra mussels are suspected to be a cause of these *Microcystis* blooms, but the evidence is difficult to interpret because of the confounding factors of multiple biological invasions, food-web manipulations, and other disturbances in the Great Lakes (Vanderploeg et al. 2001).

Observational evidence for or against the effects of *Dreissena* on cyanobacterial dominance has so far been limited to uncontrolled before-and-after comparisons of single ecosystems undergoing invasion (Smith et al. 1998; Idrisi et al. 2001; Nicholls et al. 2002). Experiments to examine the effects of *Dreissena* on overall phytoplankton community structure have yielded conflicting results. For example, diatoms were more heavily reduced, whereas cyanobacteria were relatively unaffected by zebra mussels in a short-mesocosm experiment in Lake Huron (Heath et al. 1995). In contrast, cyanobacteria were suppressed at high zebra mussel densities, and diatoms were promoted at midlevel densities in an in situ experiment on the Ohio River (Jack and Thorp 2000). Bastviken et al. (1998) demonstrated filtering of all algae from the water column (gross clearance) by zebra mussels in microcosms and an alteration of phytoplankton community composition upon the resuspension of biodeposited material (net clearance), including an increase in the relative abundance of *Microcystis* colonies. However, the relative abundance of *Microcystis* declined sharply in the Hudson River after the invasion of *Dreissena* (Smith et al. 1998), and Baker et al. (1998) demonstrated a preferential ingestion of *Microcystis* by Hudson River zebra mussels. Vanderploeg et al. (2001) showed that *Dreissena* rejected *Microcystis* as pseudofeces when the particular algal strains produced the toxin microcystin, which could explain some of the variable results found in the studies described above.

The ongoing invasion of inland lakes of the midwestern United States provides a unique opportunity to examine the

hypothesis that zebra mussels alter phytoplankton communities by a promoting dominance of cyanobacteria, particularly by *M. aeruginosa*. We focused on *M. aeruginosa* because existing evidence points to this species as being the most likely to respond positively to an invasion by *Dreissena* (Vanderploeg et al. 2001; Nicholls et al. 2002). We present empirical evidence that the exotic zebra mussel may be altering the limnological paradigm of increasing cyanobacterial dominance with increasing nutrient enrichment by fostering dominance by *Microcystis* in lakes with relatively low TP. Our results suggest negative consequences of *Dreissena* invasion for water quality in lakes with low to moderate levels of nutrients.

Materials and methods

During 1998 and 1999, we conducted synoptic limnological surveys of lakes with and without *Dreissena* in Michigan, the state that currently has the greatest number of invaded lakes. Historical data on TP concentrations were obtained from the Michigan Department of Environmental Quality. Lakes to be sampled were then chosen to represent the range of TP concentrations common in Michigan Lakes but only included lakes with pH and calcium concentrations suitable for zebra mussels (Ramcharan et al. 1992). Data on maximum depth and surface area were used to find lakes of roughly similar morphometries with and without *Dreissena*. Most lakes were located in southern third of the Lower Peninsula of Michigan (Raikow 2002).

Samples were collected from a single station in each lake during late summer, when cyanobacteria are seasonally most abundant and most of the lakes were thermally stratified. A vertical profile of temperature, oxygen, pH, and specific conductance was measured using a YSI multisensor. Phytoplankton were collected with an integrating tube sampler from the water surface to the thermocline, thoroughly mixed, preserved in 1% Lugol's fixative, and enumerated using the Utermohl technique. Biovolume was estimated from cell counts and measurements of cell dimensions, then converted to biomass on a dry weight basis under the assumption of a density of 1.0 g cm^{-3} and a wet:dry weight ratio of 10. Soluble reactive phosphorus (SRP) and ammonium (NH_4^+) were measured colorimetrically using long-pathlength spectrophotometry, and nitrate (NO_3^-) was measured by ion chromatography (Raikow 2002). Total dissolved phosphorus (TDP) and TP were measured by persulfate digestion of filtered and unfiltered water, followed by colorimetric analysis of SRP (Raikow 2002). All data were log-transformed before performing statistical analyses. Analysis of covariance (ANCOVA) was used with log-transformed TP concentration as the covariate to examine the effect of zebra mussels across a broad range of nutrient levels.

Cyanobacterial and *Microcystis* dominance (as the percentage of total phytoplankton biomass) in lakes with and without zebra mussels were compared using indices of relative abundance, which were computed as $\ln[\%X/(100 - \%X)]$, where %X is the percentage of either total cyanobacteria or *M. aeruginosa* (Trimbee and Prepas 1987; Downing et al. 2001). Given that cyanobacterial dominance has been

found to increase sharply above TP concentrations of 20–30 $\mu\text{g L}^{-1}$ (Downing et al. 2001), we subdivided the data set into lakes with TP < 25 $\mu\text{g L}^{-1}$ and >25 $\mu\text{g L}^{-1}$, to increase the statistical power of detecting a specific influence of *Dreissena* on *M. aeruginosa*.

The present study was specifically designed to evaluate the relationship between zebra mussels and *Microcystis*, but multivariate statistical analyses were also done a posteriori to look for differences in other elements of the phytoplankton community that might correspond with zebra mussel invasion. Principal-components analysis (PCA), correspondence analysis (CA), and multidimensional scaling (MDS, using Euclidean distances) were used to ordinate patterns in phytoplankton biovolume and relative abundance at the levels of division and genus. Simple linear discriminant analysis (LDA) using phytoplankton biovolume and relative abundance served to summarize differences in algal community composition between the two predefined groups of lakes (i.e., with and without zebra mussels). Rare genera (<5% of total biovolume in any lake or present in only one lake) were removed from the data set used for ordination and classification. Analyses were conducted with SAS for Windows version 8 (ANCOVA, PCA, and CA), SYSTAT version 9 (MDS), and SPSS version 10 (LDA).

Results

TP in the 61 surveyed lakes ranged 11–117 $\mu\text{g L}^{-1}$ and did not differ between lakes with and without zebra mussels (Kolmogorov-Smirnov test, $D = 0.135$, $P = 0.94$). Similarly, the presence of *Dreissena* was not associated with significant differences in the concentrations of TDP, NH_4^+ , NO_3^- , or the sum of NH_4^+ and NO_3^- , although concentrations of NO_3^- were often below our detection limit of $\sim 10 \mu\text{g N L}^{-1}$. In contrast, SRP concentrations were higher in lakes with zebra mussels (mean SRP = 4.05 vs. 2.14 $\mu\text{g P L}^{-1}$, $P = 0.008$). Given the above results for available nutrients, it was not surprising that the $\text{NH}_4^+:\text{SRP}$ ratio was lower in lakes with mussels (mean $\text{NH}_4^+:\text{SRP} = 15.2$ vs. 28.0, $P = 0.047$). No other nutrient ratios were influenced by the presence of mussels. These relationships suggest that *Dreissena* may affect nutrient availability by enhancing the available P relative to available N concentrations.

Compared with lakes lacking zebra mussels, lakes with mussels had lower total phytoplankton biomass, as indicated by both chlorophyll *a* (Fig. 2A, ANCOVA, effect of zebra mussels, $P = 0.0028$) and dry-weight biomass estimated from total algal biovolume (Fig. 2B, ANCOVA, effect of zebra mussels, $P = 0.048$). Total cyanobacterial dominance increased with increasing TP in lakes without *Dreissena* (least-squares regression, $P = 0.026$) but not in lakes with *Dreissena* (Fig. 2C, least-squares regression, $P = 0.79$). Total algal biomass was a better predictor of cyanobacterial dominance than TP (Downing et al. 2001), and, again, the relationship was weaker for lakes with *Dreissena* than lakes without (cyanobacteria index vs. log chlorophyll slope = 2.00, $R^2 = 0.10$, $P = 0.23$ for lakes with mussels and slope = 4.41, $R^2 = 0.28$, $P = 0.008$ for lakes without mussels; cyanobacteria index vs. log total biovolume: slope = 1.46,

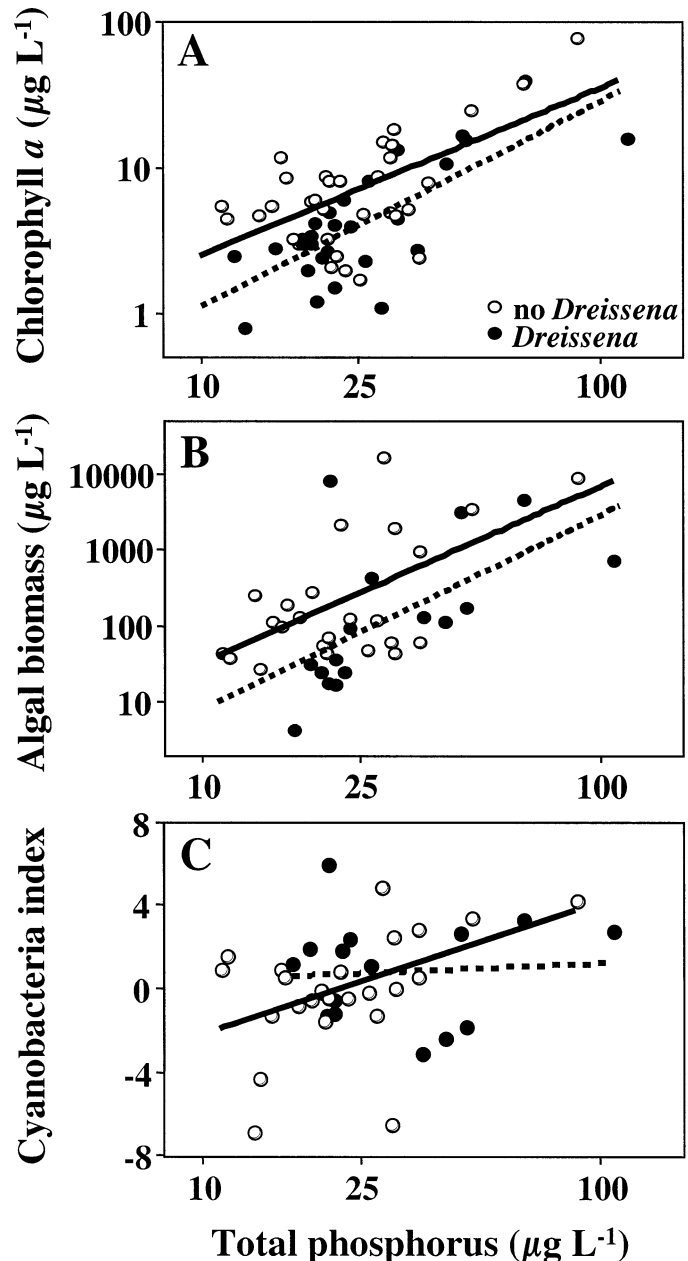


Fig. 2. Effect of zebra mussels on (A) Chl *a* concentration, (B) total algal biomass (dry weight), and (C) total cyanobacterial dominance, expressed as a relative abundance index (Trimbee and Prepas 1987; Downing et al. 2001) (see text). Lines are least-squares regressions, for which statistics are as follows: (A) chlorophyll in lakes without zebra mussels (solid lines): $y = 1.1482x - 0.762$, $R^2 = 0.355$, $P < 0.001$; chlorophyll in lakes with zebra mussels (dashed lines): $y = 1.4071x - 1.3522$, $R^2 = 0.56$, $P < 0.0001$; (B) biomass in lakes without zebra mussels: $y = 2.329x + 3.161$, $P = 0.0021$; biomass in lakes with zebra mussels: $y = 2.554x + 2.361$, $P = 0.0142$; (C) cyanobacteria index in lakes without zebra mussels, $y = 6.338x - 8.6594$, $R^2 = 0.21$, $P = 0.026$; and cyanobacteria index in lakes with zebra mussels, not significant ($P = 0.79$).

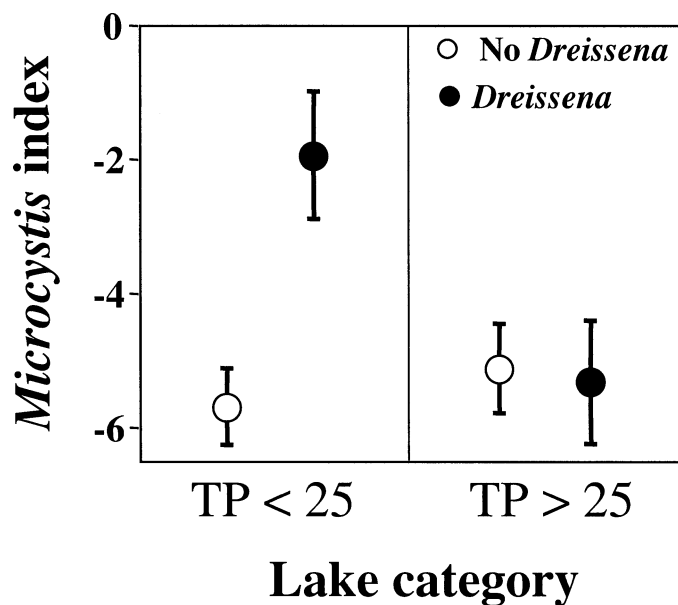


Fig. 3. Influence of zebra mussels on *M. aeruginosa* dominance at low and high TP concentrations. *Microcystis* dominance is expressed as a relative abundance index (Trimbee and Prepas 1987; Downing et al. 2001) (see text). Bars are SEs.

$R^2 = 0.33$, $P = 0.02$ for lakes with mussels and slope = 2.26, $R^2 = 0.38$, $P = 0.001$ for lakes without mussels). However, any analysis of the effect of *Dreissena* on the latter relationships is problematic because the predictor variables (*Dreissena* presence or absence and total algal biomass) are not independent of each other (Fig. 2A,B). We therefore based our conclusions about the influence of *Dreissena* on cyanobacterial dominance on the relationship with TP, because TP was independent of the presence of *Dreissena*.

After dividing the lakes into low- and high-TP groups using $25 \mu\text{g L}^{-1}$ as the boundary, two-way ANOVA revealed a significant *Dreissena* \times TP interaction on *M. aeruginosa* dominance ($P = 0.016$, Fig. 3) but no effects of *Dreissena* on total cyanobacterial dominance ($P = 0.25$). The presence of *Dreissena* had a strong positive influence on *M. aeruginosa* in lakes with $\text{TP} < 25 \mu\text{g L}^{-1}$ (mean \pm SE of the percentage of *M. aeruginosa* in lakes with and without *Dreissena*, respectively, 29.7 ± 9.9 and 5.1 ± 4.7 , significantly different via F test at $P = 0.0018$) but had no influence on *M. aeruginosa* in lakes with $\text{TP} > 25 \mu\text{g L}^{-1}$ ($P = 0.86$; Fig. 3). The positive influence of *Dreissena* on *M. aeruginosa* dominance at low TP was not an artifact of the somewhat lower range of TP in lakes without *Dreissena* in our data set; excluding the five lakes with the lowest TP (all of which lacked *Dreissena*) from the analysis resulted in both a lower mean and SE of the *Microcystis* index for lakes without *Dreissena*, and did not affect the statistical significance of the *Dreissena* \times TP interaction ($P < 0.01$).

Multivariate statistical analyses revealed that there were few differences in algal communities beyond the *Microcystis* results described above (Raikow 2002). Ordination using PCA, CA, or MDS did not distinguish between lakes with and without zebra mussels. LDA using biovolume and relative abundance of algal divisions did not classify lakes with

and without zebra mussels (Wilk's $\lambda = 0.919$, $df = 5$, $P = 0.701$ and Wilk's $\lambda = 0.914$, $df = 5$, $P = 0.669$, respectively), although lakes were successfully classified by LDA on the basis of biovolume and relative abundance of genera (Wilk's $\lambda = 0.188$, $df = 23$, $P = 0.005$ and Wilk's $\lambda = 0.226$, $df = 23$, $P = 0.018$, respectively), with *Microcystis* as one of several genera contributing to the discriminant function (Raikow 2002).

Discussion

The results of the synoptic surveys of Michigan lakes suggest that zebra mussels may be altering the well-established limnological paradigm that cyanobacterial dominance increases with TP (Trimbee and Prepas 1987; Downing et al. 2001). In accordance with the results of previous studies, we found a positive relationship between TP and the relative abundance of total cyanobacteria in lakes without zebra mussels (Fig. 2C). The amount of variation explained by TP in our data set was lower than that in previous studies, but this is likely a result of the smaller range of concentrations in our data set and the fact that our data consist of one-time estimates from each lake rather than seasonal averages (Trimbee and Prepas 1987; Downing et al. 2001). In contrast, there was no relationship between cyanobacterial dominance and TP in lakes with zebra mussels (Fig. 2C).

Most of the lakes we surveyed were deep enough to be thermally stratified during the summer and therefore would have a substantial fraction of the epilimnetic area that is not underlain by benthic habitat, which would possibly reduce benthic grazing pressure compared with well-mixed larger lakes and rivers where the effect of zebra mussels has been most studied (Nicholls and Hopkins 1993; Smith et al. 1998; Idrisi et al. 2001; Vanderploeg et al. 2001; Nicholls et al. 2002). Nevertheless, the lower total phytoplankton biomass in lakes with zebra mussels in our survey is in concordance with the results of previous reports of declines in phytoplankton biomass after the invasion of zebra mussels into relatively well-mixed water bodies, which underscores the efficacy of this exotic grazer in affecting phytoplankton.

The promotion of *Microcystis* dominance by zebra mussels in lakes with lower TP, but not in lakes with higher TP (Fig. 2C), is surprising, given the general tendency for bloom-forming cyanobacteria to be favored by high TP concentrations. However, this observation is consistent with the results of previous studies in the Great Lakes, where *Microcystis* blooms have been reported in waters with TP concentrations $\leq 25 \mu\text{g L}^{-1}$ (Holland et al. 1995; Vanderploeg et al. 2001; Nicholls et al. 2002). According to the current paradigm, *Microcystis* blooms in these habitats would not be expected, considering their moderate TP concentrations.

The mechanisms underlying the unique relationships that we report between *Dreissena* and *Microcystis* cannot be determined from our data, but we can comment on alternative hypotheses that could explain the variable influence of *Dreissena* on *Microcystis* dominance. These hypotheses are not mutually exclusive and can be categorized into those that involve grazing mortality and those that involve grazer-mediated nutrient recycling. *Microcystis* is typically regarded

as being relatively resistant to consumption by most herbivores, including zebra mussels (Lampert 1987; Vanderploeg et al. 2001). Theoretical studies of consumer effects on communities of competing prey usually predict a shift in dominance from prey species that are more vulnerable to consumption to dominance by species that are less vulnerable to consumption (such as *Microcystis*) as nutrient input increases (Leibold 1996), which is a direct consequence of an increase in grazing pressure with enrichment in such models. This prediction is not congruent with our observations. However, the opposite prediction is also possible if prey species trade the ability to resist predation against the ability to grow rapidly at high resource levels (Armstrong 1979; Chase et al. 2000). There is empirical support for key assumptions of these simple models, including an increase in *Dreissena* grazing pressure with enrichment (Wilson and Sarnelle 2002), greater resource availability (SRP) at higher TP (our survey data, ANOVA F test, $P < 0.0001$), and an adaptive tradeoff among phytoplankton species between consumption resistance and resource-saturated population growth rate (Agrawal 1998). The latter assumption is crucial to the counterintuitive prediction that grazers may favor dominance by grazing-resistant species at low, but not high, levels of enrichment. Although counterintuitive, herbivore suppression of grazing-resistant cyanobacteria has been commonly reported in eutrophic lakes during periods of high *Daphnia* abundance (Sarnelle 1993). *Dreissena* and *Daphnia* populations both have relatively broad diets and high filtering rates, which may partially explain their ability to control relatively resistant cyanobacteria.

Alternatively, the promotion by *Dreissena* of *Microcystis* dominance may be related to changes in the supply of available N and P to the phytoplankton subsequent to invasion. We found lower $\text{NH}_4^+:\text{SRP}$ ratios in lakes with mussels, which is consistent with low N:P ratios of excretion for *Dreissena* in Lake Erie (Arnott and Vanni 1996) and suggests that nutrients supplied by mussels may favor phytoplankton species that are better competitors for N. In general, cyanobacteria tend to be poor competitors for P but good competitors for N (Smith 1983). However, more recent data from Saginaw Bay have suggested that the N:P ratio of mussel excretion may be dependent on the level of P loading to the system, with the ratio increasing as P loading decreases (Vanderploeg et al. 2002). This suggests that the competitive advantage gained by good N competitors from mussel recycling may decrease as TP decreases. As a consequence, the pattern that we report of *Microcystis* promotion by mussels only in low-TP lakes is difficult to reconcile with a hypothesis that is solely based on the N:P ratio of mussel excretion. In our data set, there was a significant negative correlation between the $(\text{NO}_3^- + \text{NH}_4^+):\text{SRP}$ ratio and cyanobacterial dominance in mussel-free lakes ($P = 0.041$) but not in mussel-infested lakes ($P = 0.85$). Thus, we found some evidence for the role of ratios of available N:P as a mechanism underlying cyanobacterial dominance but not in lakes containing *Dreissena*.

The above discussion is not intended to explain the observed pattern of zebra mussel influence on *Microcystis*, but it does provide a set of preliminary hypotheses for future testing. Large-scale experimental manipulations of zebra

mussel densities across a range of nutrient availability are needed to demonstrate the causal link between mussel invasion and *Microcystis* dominance and to understand the mechanisms underlying this complex interaction. We will report the results of such experiments in a subsequent article.

Our results illustrate the potentially negative and often unpredictable consequences of biological invasions. Our data support the hypothesis, first posed in studies of the Great Lakes, that zebra mussels promote the dominance of phytoplankton communities by *Microcystis* in lakes with relatively low TP ($<25 \mu\text{g L}^{-1}$). This influence may be at least partly responsible for the lack of increase in total cyanobacterial dominance with increasing TP in *Dreissena*-infested lakes (Fig. 2C). Lakes with relatively low TP are very common in north-temperate glacial regions; $\sim 80\%$ of Michigan lakes and $\sim 43\%$ of inland lakes in the states that border the Laurentian Great Lakes have TP concentrations $<25 \mu\text{g L}^{-1}$ (Nutrient Criteria Database, U.S. E.P.A. STORET waterbody ID 4; data retrieved for Minnesota, Wisconsin, Indiana, Illinois, Michigan, Ohio, Pennsylvania, and New York; $n = 210$ for Michigan and 1,534 for all states). Most lakes in this region also have suitable calcium concentrations to support zebra mussels ($>20 \text{ mg L}^{-1}$; Ramcharan et al. 1992). Once they become colonized by zebra mussels, our analysis suggests that these oligomesotrophic lakes are more likely to be dominated by *Microcystis*. By promoting *M. aeruginosa*, one of the most notorious species that produces harmful algal blooms, zebra mussels may thus be degrading water quality in low-nutrient lakes. As zebra mussels continue to spread into North American waters, monitoring of nutrient levels (particularly TP) may no longer be sufficient to evaluate the risk of dominance of lake phytoplankton by highly undesirable cyanobacteria.

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