

The effect of dreissenid invasions on chlorophyll and the chlorophyll:total phosphorus ratio in north-temperate lakes

S.N. Higgins, M.J. Vander Zanden, L.N. Joppa, and Y. Vadeboncoeur

Abstract: We investigated the effects of dreissenid mussel (*Dreissena polymorpha* and *D. rostriformis bugensis*) invasions on the concentrations of chlorophyll *a* (Chl) and total phosphorus (TP), and the Chl:TP ratio within 27 north-temperate lakes that spanned large gradients in lake size and trophic status, using two approaches: (i) regression analysis and (ii) hierarchical modeling. Overall, Chl declined by 40%–45% after dreissenid invasion and the magnitude of effect was structured by epilimnetic volume within stratified, but not nonstratified (mixed) lakes. Declines in TP over the invasion period were significant only for stratified systems and were smaller (~16% reduction from pre-invasion values) than for Chl. Across the complete trophic gradient (i.e., among lakes) the regression approach (analysis of covariance) indicated a significant decline in the intercept of the Chl:TP, but not the slope. In contrast, hierarchical modeling indicated a decline in the slope of Chl:TP among lakes between pre- and post-invasion periods. As with Chl, the effect of dreissenids on Chl:TP declined with increases in epilimnetic volume in stratified, but not nonstratified lakes. Dreissenid effects on Chl were prolonged, with no indication of diminishing within 7–10 years of invasion.

Résumé : Nous étudions les effets des invasions de moules dreissenidées (*Dreissena polymorpha* et *D. rostriformis bugensis*) sur la chlorophylle *a* (Chl), le phosphore total (TP) et la relation Chl:TP dans 27 lacs tempérés nordiques qui couvrent de vastes gradients de tailles et de statuts trophiques lacustres au moyen de deux méthodes, l'analyse de régression et la modélisation hiérarchique. Globalement, la Chl diminue de 40–45 % après l'invasion des dreissenidés et l'importance de l'effet est conditionnée par le volume de l'épilimnion dans les lacs stratifiés, mais non dans les lacs non stratifiés (à brassage intégral). Les déclinés du TP durant la période d'invasion ne sont significatifs que dans les systèmes stratifiés et sont moins importants (~16 % de réduction par rapport aux valeurs d'avant l'invasion) que dans le cas de la Chl. Sur l'ensemble du gradient trophique (c'est-à-dire entre les lacs), la méthode de régression (analyse de covariance) indique une réduction significative de l'ordonnée à l'origine, mais non de la pente, dans la relation Chl:TP. En revanche, la modélisation hiérarchique montre un déclin de la pente de la relation Chl:TP entre les lacs entre les périodes qui précèdent et qui suivent l'invasion. Comme dans le cas de la Chl, l'effet des dreissenidés sur la relation Chl:TP diminue en fonction de l'augmentation du volume de l'épilimnion dans les lacs stratifiés, mais non dans les lacs non stratifiés. Les effets des dreissenidés sur la Chl sont prolongés, sans indication de diminution 7–10 ans après l'invasion.

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Introduction

Invasive species are among the most important drivers of global change and biodiversity loss for freshwater ecosystems (Sala et al. 2000; Lodge et al. 2006). A handful of invaders, including the zebra mussel (*Dreissena polymorpha*) and the quagga mussel (*D. rostriformis bugensis*) have had disproportionately large economic and ecological effects, owing to their propensity for rapid dispersal within and

across continents and ability to transform nutrient processing and food webs of invaded ecosystems (Strayer 2009).

In lakes, the importance of nutrient control (bottom-up control) over the phytoplankton standing crop has been extensively described using empirical relationships between the concentrations of chlorophyll *a* (Chl) and total phosphorus (TP) (Sakamoto 1966; Dillon and Rigler 1974; Peters 1986). Significant declines in the Chl:TP ratio by grazers

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(top-down control) have been previously documented in studies comparing lakes or mesocosm experiments with and without large-bodied zooplankton (Sarnelle 1992; Mazumder 1994a, 1994c). These studies demonstrated that grazers can suppress Chl yields well below their potential (based on phosphorus availability) and introduce considerable variance into the Chl:TP ratio (Sarnelle 1992; Mazumder 1994a, 1994c). However, grazer-induced changes in the Chl:TP ratio can underestimate or overestimate effects on Chl if they do not account for grazer-induced shifts in TP (Mellina et al. 1995). Studies that compare lakes with and without large bodied zooplankton cannot resolve grazer effects on TP. Accounting for these effects at appropriate spatial and temporal scales requires whole-ecosystem manipulations or careful long-term observational studies. However, such studies are costly, require considerable investments in time and effort, and have not been conducted over complete gradients of lake size or trophic status.

Perturbations of ecosystems by invasive species, such as those caused by dreissenid mussels, can be viewed as non-intentional whole-ecosystem manipulations. In addition to the improved understanding of invader effects, the careful study of these invasions in natural ecosystems can reveal insights into ecological processes that are otherwise difficult to obtain (Sax et al. 2007). Here, we examine the effects of invasive dreissenid mussels on the Chl, TP, and the Chl:TP ratio within 27 north-temperate lakes spanning large gradients in lake size and trophic status. Our primary objective was to determine whether grazing pressure by dreissenids suppressed Chl and altered the Chl yield per unit TP in lakes, and whether these effects scaled with gradients of grazer efficiency and trophic status. The importance of dreissenid grazer efficiency, which has been assessed using estimates of their filtration capacity (FC) (i.e., the proportion of the water column that can be filtered in one day), has been demonstrated previously (Vanderploeg et al. 2002; Higgins and Vander Zanden 2010). However, whole ecosystem estimates of dreissenid density, which are required for estimating FC, can vary by orders of magnitude over space (e.g., Patterson et al. 2005) and time (e.g., Howell et al. 1996) and are unknown for most invaded ecosystems. Since FC is also a function of ecosystem size (volume of water to be filtered) and hydrodynamics (horizontal and vertical mixing), dreissenid effects on phytoplankton might be expected to scale with epilimnetic volume, lake size, and degree of mixing. Empirical relationships between effect sizes and these variables could be useful for predicting dreissenid effects on phytoplankton and higher trophic levels for lakes where dreissenid densities and FC are unknown. Dreissenids have also invaded lakes across a wide gradient of trophic status. It is widely recognized that TP concentrations are an important driver of phytoplankton biomass and Chl across most north-temperate lakes. However, whether the magnitude of dreissenid effects on Chl (top-down effect) varies with trophic status is not well understood. Our specific objectives were (i) to determine the effect of dreissenid invasions on Chl, TP, and the Chl:TP ratio in lake ecosystems; and (ii) to determine how the magnitude of the effect is influenced by ecosystem size, trophic status, and mixing status (seasonally stratified vs. nonstratified).

Materials and methods

Data compilation

Data on chlorophyll *a* and total phosphorus (TP) during the period May–October were compiled from the literature, several online databases, and governmental reports for north-temperate lakes invaded by dreissenid mussels (a complete listing of lakes and data sources is available in Appendix A, Table A1). Data on Chl and TP for each lake represent samples collected within the mixed layer at one or more pelagic zone stations. For long-term monitoring datasets, Chl and TP data were collected from a single station in the pelagic zone. For datasets from the literature, Chl and TP values represent that reported by the authors of the respective studies. For larger lakes, such as the Laurentian Great Lakes, the data represent multiple pelagic zone stations that were averaged for each season by the authors of each particular study (Appendix A, Table A1). The categorization of lakes as “mixed” or “stratified” was based on mixing depths reported in the literature or estimated based on lake surface area (Hanna 1990). Lakes were categorized as mixed if $\geq 80\%$ of lake area was above the mixing depth (Higgins and Vander Zanden 2010). Epilimnetic volume was calculated from estimates of lake shape derived from the mean and maximum depth, and depth of the mixed layer (Carpenter 1983). The timing of dreissenid invasion was recorded (Appendix A, Table A1) as reported in the literature or, for long-term monitoring datasets, by the responsible agency. For regression analyses (see below) we followed Mazumder (1994a, 1994b) and treated data from each lake and year (May–October) as a “lake year,” and coded lake years for pre- and post-invasion periods. In total we identified 27 lakes for which sufficient data were available to test effects of dreissenid mussels on TP and Chl, including 120 lake years of data pre-invasion and 96 lake-years of data post-invasion (Table 1). The number of annual data points for each individual lake was variable, ranging from 1–10 data points (years) in each of the pre- and post-invasion periods (Appendix A, Table A1). Data were excluded from the analysis for the following reasons: (i) data were unavailable for both pre- and post-invasion periods, (ii) data were from years >15 years before or after invasion, (iii) individual data points in long-term datasets were outside of two standard deviations of the seasonal mean value, and (iv) fewer than three data points were available in the period May–October of a given year with which to estimate a seasonal mean value.

The differences in timing of data collection within a season, number of data points per season and per invasion period, and the number of stations within each lake are sources of sampling error in our dataset and will confound our ability to detect changes over the invasion period and relationships between dreissenid effects and other factors (e.g., ecosystem size, mixing status, trophic status). For these reasons, our identification of significant changes between pre- and post-invasion period, and the relationships between these changes and these other factors, are expected to be conservative.

Statistical analysis

The effect of dreissenid invasions on TP and Chl for the entire 27-lake dataset was assessed using annual mean val-

Table 1. Total phosphorus (TP, mg·m⁻³) and chlorophyll *a* (Chl, mg·m⁻³) in 27 lakes during pre- and post-invasion periods.

	Pre-invasion		Post-invasion	
	TP	Chl	TP	Chl
<i>N</i>	120	120	96	96
Min.	7.1	1.7	7.7	0.9
Max.	141.8	103.0	142.3	43.7
Mean	39.0	16.2	34.3	8.9
SD	30.0	18.8	29.5	9.5

Note: Data are for multiple lake years. *N*, number of samples; Min., minimum; Max., maximum; SD, standard deviation.

ues from pre- and post-invasion periods for each lake and a *t* test on the unweighted log response ratio (LR) values (Gurevitch and Hedges 1999; Higgins and Vander Zanden 2010). Briefly, the LR ratio is defined as

$$(1) \quad \text{LR} = \ln(X_{+ZM}/X_{-ZM})$$

where X_{-ZM} and X_{+ZM} are the mean values of TP or Chl in the absence of (pre-invasion) or presence of (post-invasion) dreissenid mussels, respectively. The natural logarithm of X_{+ZM}/X_{-ZM} was taken to normalize the distribution of LR values and a two-tailed *t* test was conducted to test whether the population of LR values significantly differs from zero (i.e., a significant effect). Whereas significance tests for changes in TP and Chl over the invasion period were conducted on LR values, absolute or percent changes are presented in the majority of our tables and figures to facilitate interpretation. Where time-series data for Chl and TP are presented, they were standardized using *Z* scores. *Z* scores were calculated from each lake independently using the mean value of Chl and TP within the pre-invasion period.

Owing to heteroscedasticity, the Chl:TP ratio is most often described using log₁₀ transformed values of both Chl and TP to normalize the variance across large ranges in values. However, log–log relationships can obscure the absolute variation in response variables, and the display of untransformed relationships is also recommended (Shapiro et al. 1982; Mazumder 1994a). Therefore, we display the Chl:TP ratios of both untransformed and log₁₀ transformed data. The Chl:TP ratio was examined using least squares regressions of log₁₀ transformed values of Chl and TP. Potential changes in the Chl:TP ratio between pre- and post-invasion periods were evaluated using an analysis of covariance (ANCOVA) with one factor (invasion status) and two levels (pre, post). As noted by Mazumder (1994a) the inclusion of multiple years of data from a lake inflates the degrees of freedom; however, in many lakes TP and Chl were highly variable and averaging the data would have obscured the natural variation in Chl (Mazumder 1994a). To assess whether the use of lake years affected our conclusions, we compared the ANCOVA results using all lake years (unpooled) with the results of an ANCOVA using mean TP and Chl values for each of the pre- and post-invasion periods for each lake ($N_{\text{pre}} = 27$, $N_{\text{post}} = 27$) (pooled). The use of TP and Chl from unpooled lake years, rather than the pooled data, reduced the variance but did not affect the significance of statistical tests at the $\alpha = 0.05$ level.

While the ANCOVA approach examines potential effects on the Chl:TP between pre- and post-invasion periods across

all lakes and years, we were also interested in examining whether the Chl:TP ratio was altered within individual lakes. As our data followed a clear hierarchical structure (years nested in lakes) we utilized a multilevel (ML), or hierarchical, modeling approach that corrected for degrees of freedom (Gelman and Hill 2007). We used a stepwise approach to constructing the ML model, beginning with an unconditional model including only Chl and TP, and adding in INVASION status, an interaction term (between INVASION and TP), and epilimnetic volume sequentially. Model selection was based on deviance information criteria (DIC) applicable to ML models (Gelman and Hill 2007). The selected ML model was defined as

$$(2) \quad \log_{10}\text{Chl} = \text{INVASION} \times \log_{10}\text{TP} + (1 + \text{INVASION} \mid \text{Lake})$$

Equation 2 indicates that log₁₀Chl varies as a function of INVASION (as a binary variable with pre-invasion = 0 and post-invasion = 1), log₁₀TP, and an interaction between INVASION and log₁₀TP. Parameters within the brackets of eq. 2 describe the multilevel component of the model, indicating that the intercepts and slopes were allowed to vary with INVASION and that observations were grouped by lake. ANCOVA and hierarchical modeling were conducted using the statistical software R (version 2.10.0) with individual packages available from Comprehensive R Archive Network. In addition to the preloaded packages used for ANCOVA, the “lme4” and “arm” packages were used for hierarchical modeling.

Results

Grazer effects on total phosphorus and chlorophyll

The 27 lakes in this study had mean TP concentrations ranging from 7.1 mg P·m⁻³ to 142 mg P·m⁻³ in pre-invasion years, and 7.7 mg P·m⁻³ to 142 mg P·m⁻³ (Table 1; Fig. 1a) in post-invasion years. Few lake years had TP concentrations below 10 mg P·m⁻³ (10, pre-invasion; 2, post-invasion), or over 100 mg P·m⁻³ (7, pre-invasion; 5, post-invasion). In shallow nonstratified lakes, TP averaged 48.8 ± 29.8 mg P·m⁻³ across all lake years pre-invasion and 47.2 ± 31.6 mg P·m⁻³ across all lake-years post-invasion years. There was no significant difference in TP between pre- and post-invasion periods for nonstratified lakes (Table 2; Fig. 1a). For stratified lakes, TP concentrations declined significantly, from 18.6 ± 11.1 mg P·m⁻³ across all lake-years pre-invasion years to 14.6 ± 5.8 mg P·m⁻³ across all lake years post-invasion years (Fig. 1a). The concentration of chlorophyll *a* showed dramatic declines following dreissenid invasion (Fig. 1b), which were significant in stratified and nonstratified lakes (Table 2). The effect of dreissenids on Chl and the Chl yield per unit TP (Chl:TP) declined with epilimnetic volume in stratified, but not nonstratified lakes (Fig. 2). The effect of lake size on Chl LR in stratified lakes,

$$(3) \quad \text{Chl LR} = -0.65 \pm 0.08 \pm 0.14 \times \text{lake area (km}^2)$$

($N = 14$, $r^2 = 0.48$, $F = 13.4$, $p = 0.003$); and the Chl:TP ratio in stratified lakes,

Fig. 1. Time series of standardized total phosphorus (TP) and chlorophyll (Chl) concentration values before and after dreissenid invasion in stratified (filled circles) and nonstratified (open circles) lakes. Z scores for each lake and year were calculated based on the mean and standard deviation of pre-invasion TP or Chl values for each lake. Broken horizontal lines represent the mean value during the pre-invasion period.

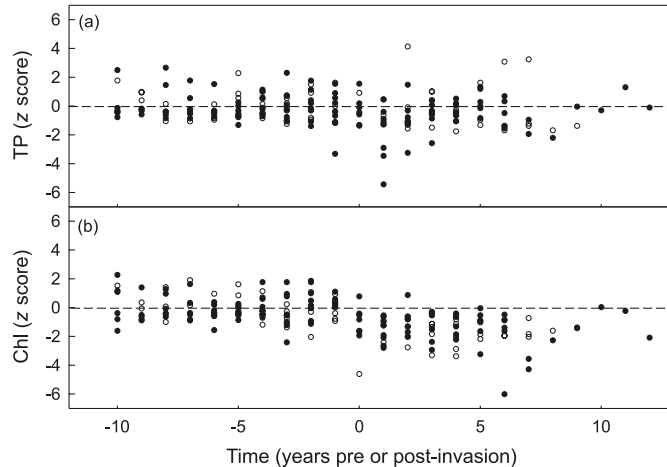


Table 2. Changes in concentrations of phosphorus and chlorophyll *a* between pre- and post-dreissenid mussel invasion periods in 27 lake ecosystems.

Parameter	<i>N</i>	Mean change ± SD (%)	<i>p</i>
Total phosphorus			
All	27	-8.4 ± 33.4	0.02
Stratified	14	-21.2 ± 33.8	0.02
Mixed	13	-3.2 ± 30.4	0.32
Chlorophyll			
All	27	-40.6 ± 67.1	<0.0001
Stratified	14	-43.1 ± 46.1	<0.0001
Mixed	13	-40.0 ± 54.9	<0.0001

Note: *N*, number of samples. Mean percent changes calculated based on absolute values of Chl and TP, while *p* values were calculated from a *t* test of LR ratios.

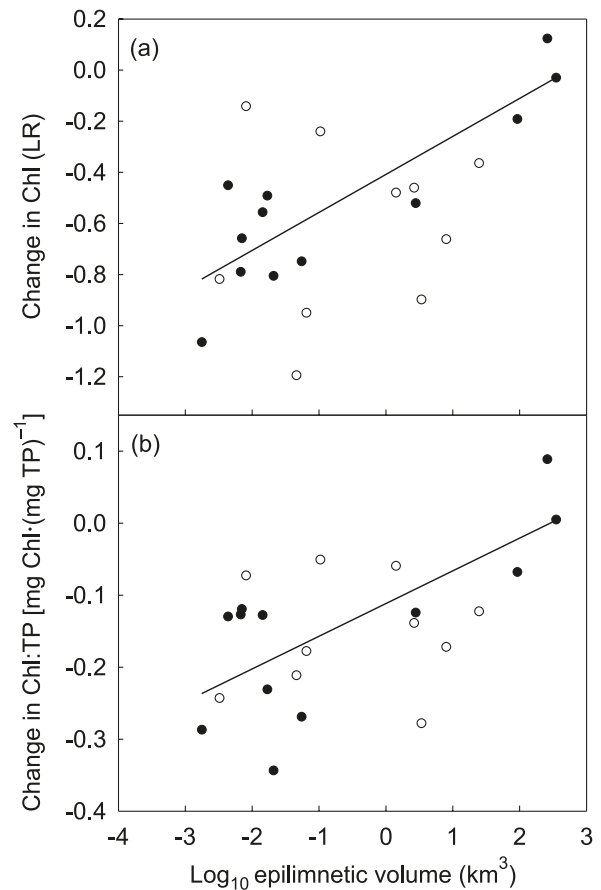
$$(4) \quad \text{Chl LR} = [(-0.20 \pm 0.03) + (0.05 \pm 0.01)] \times \text{lake area (km}^2)$$

($N = 14$, $r^2 = 0.44$, $F = 11.4$, $p = 0.006$), was similar to that reported for epilimnetic volume (Fig. 2). As with epilimnetic volume, lake area was not significantly correlated ($p > 0.05$) with Chl LR or Chl:TP in nonstratified lakes.

Grazing effects on the ratio of chlorophyll *a* : total phosphorus

Some authors have described the transformed Chl:TP ratio as sigmoidal, with deviations from linearity occurring at TP concentrations below 5 mg P·m⁻³ and above 300–500 mg P·m⁻³ (McCauley et al. 1989; Prairie et al. 1989; Watson et al. 1992). Total phosphorus in our study lakes fell exclusively between 5 mg P·m⁻³ and 300 mg P·m⁻³ for all years (Table 1), and the relationship between log₁₀ transformed values of Chl and TP was linear. However, a visual inspection of the residuals in the transformed Chl:TP ratio

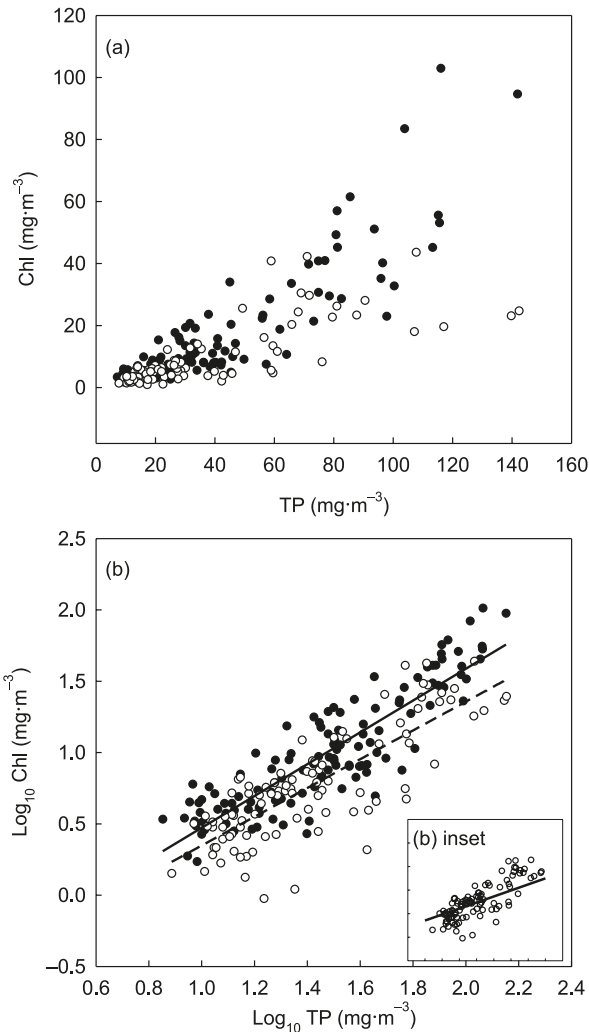
Fig. 2. The effect of epilimnetic volume and mixing status on the magnitude of dreissenid effects on (a) chlorophyll *a* concentration (Chl), and (b) the ratio of Chl to total phosphorus (TP) in lakes. Significant relationships ($p < 0.05$, unbroken lines) were found for stratified systems (filled circles), but not mixed (open circles) systems. Least squares regression equation between log₁₀ epilimnetic volume and (a) changes in Chl(LR) ($y = -0.41 \pm 0.06 + 0.15 \pm 0.03x$, $N = 14$, $r^2 = 0.72$, $F = 29.6$, $p = 0.0003$), and (b) changes in Chl:TP ratio ($y = -0.11 \pm 0.03 + 0.05 \pm 0.01x$, $N = 14$, $r^2 = 0.49$, $F = 11.7$, $p = 0.007$) between pre- and post-invasion periods in stratified lakes. Error values in equations are standard errors.



during pre-invasion years (Fig. 3b) indicated that Chl may be under-predicted at TP values near or <10 mg P·m⁻³. No evidence for deviations from linearity was apparent during post-invasion years, or at higher TP values, although all our values were well < 300 mg P·m⁻³ in pre- and post-invasion years (Table 1, Fig. 3a).

The least squares regression relationship between log₁₀ transformed values of Chl and TP was highly significant for the pre-invasion and post-invasion periods (Fig. 3b). Further, the results of the ANCOVA (Table 3) indicated both TP and invasion status as significant. The inclusion of invasion status as a categorical variable (pre-invasion = 0, post-invasion = 1) reduced the unexplained variance from models that did not consider invasion status ($R^2 = 0.70$, $p < 0.001$). There was no significant difference between the slopes of pre- and post-regression equations ($F = 1.37$, $p = 0.24$), but a significant decline in the *Y*-intercept by 0.17 ± 0.03 log units post-invasion (analysis of variance (ANOVA), $p <$

Fig. 3. Chlorophyll *a* vs. total phosphorus concentration before (filled circles) and after (open circles) zebra mussel invasion. (a) Chl:TP ratio using untransformed data from lakes before zebra mussel invasion. (b) Chl:TP ratio for \log_{10} transformed data from lakes pre-invasion ($y = -0.64 \pm 0.08 + 1.12 \pm 0.05x$; $N = 120$, $r^2 = 0.78$, $F = 419$, $P < 0.0001$) and post-invasion ($y = -0.66 \pm 0.11 + 1.01 \pm 0.08x$; $N = 96$, $r^2 = 0.65$, $F = 178$, $P < 0.0001$). Inset in panel (b) displays the fit of the multilevel model (excluding error term) and raw data during the post invasion period (units and scale identical to panel b). Error values in equations are standard errors.



0.001, Fig. 3b). However, this analysis did not assess dreissenid-induced shifts in TP when estimating the magnitude of Chl declines over the invasion period. Whereas changes in the Chl:TP ratio between invasion periods may appear vertical (e.g., Fig. 3b), most changes in the Chl:TP ratio were not solely vertical, and involved changes in both Chl and TP (Fig. 4).

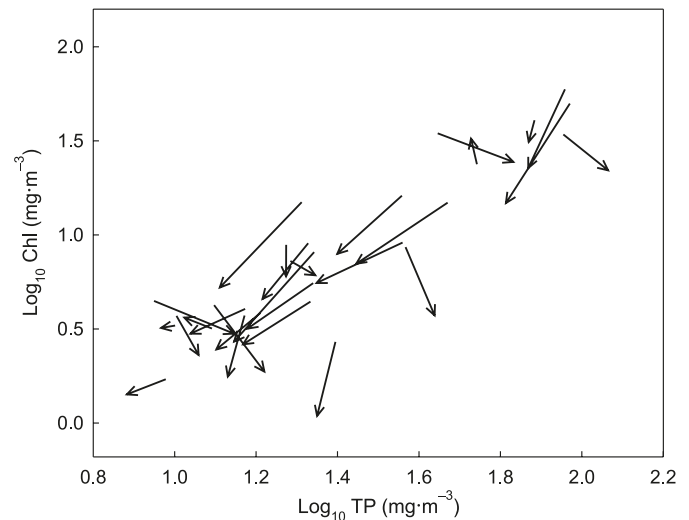
Grazing effects assessed using a multilevel model

Deviance information criteria (DIC, Gelman and Hill 2007) selected for a ML model including an interaction term between INVASION and \log_{10} TP (eq. 2, DIC = -135.4) over an identical model without the interaction term (DIC = -123.1) and an unconditional model where Chl varied solely as a function of TP (DIC = -59.7). The selection of a model with

Table 3. Analysis of covariance (ANCOVA) of dreissenid grazing effects on \log_{10} chlorophyll concentrations with \log_{10} total phosphorus (TP) as a covariate.

Model	df	F (partial)	P (partial)
Dreissenids	1	65.3	<0.0001
Log ₁₀ TP	1	562	<0.0001
Error	213		
$R^2 = 0.74$			

Fig. 4. The effect of dreissenid invasion on the Chl:TP ratio for 27 individual lake ecosystems. Vectors represent the direction and magnitude of change of the Chl:TP ratio from pre- to post-invasion.



an interaction term (Table 4) indicated an improved model fit when allowing the slope of the Chl:TP ratio to vary between pre- and post-invasion periods. The addition of epilimnetic volume as a covariate in the model, evaluated at the fixed effects level, did not significantly improve model performance (DIC values decreased from -119.2 to -120.2).

The selected ML model (eq. 2) provided a similar Chl:TP response as the ANCOVA model during the pre-invasion period (data not shown). However, in contrast with the ANCOVA results, for the post-invasion period, the ML model revealed a significant decline in the slope of the Chl:TP ratio (Fig. 3b, inset). This occurred due to the influence of within-lake responses in the ML model, which were not included in the regression based approach. Whereas the ANCOVA indicated no significant change in the slope of the Chl:TP ratio across the broad range in Chl and TP among lakes, the ML model revealed general declines in the slope of the Chl:TP ratio across individual lakes (Table 4; Fig. 5).

Discussion

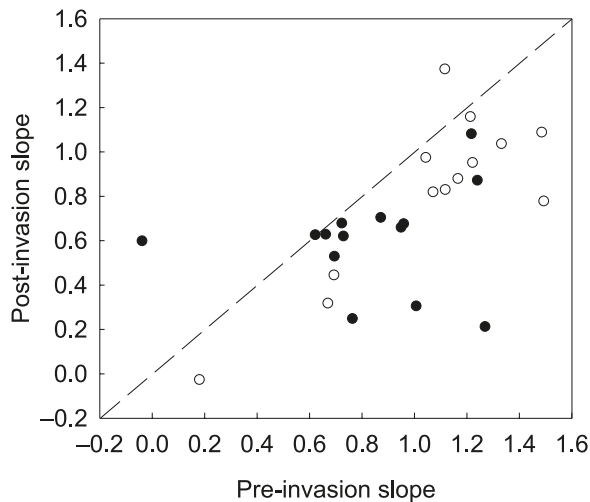
Our results indicate large and significant differences in Chl and the Chl:TP ratio between pre- and post-dreissenid invasion periods for 27 north-temperate lake ecosystems. Since the invasions of these lakes were uncontrolled natural experiments we cannot statistically attribute causality for any differences between periods to dreissenid mussels. Instead, we rely on the current understanding of dreissenid mussel ecology and the likelihood that other factors were re-

Table 4. Evaluation of a multilevel model to assessing the importance of total phosphorus (TP) and dreissenid invasion on chlorophyll *a* concentrations in 27 north temperate lakes.

Model details		Random effects			Fixed effects			
Sampled unit	<i>N</i>	Parameter	SD	Correlation	Coefficient parameter	Coefficient estimate	Coefficient SE	<i>t</i> value
Level 1								
Lake year	216	Residual	0.16		Intercept	-0.43	0.10	-4.39
Level 2								
Lake	27	Intercept	0.15	0.53	Invasion	0.27	0.14	1.98
		Pre-Post	0.13		TP	0.98	0.06	15.24
					Interaction	-0.34	0.10	-3.49

Note: Model selection was based on deviance information criteria (DIC) and results are based on fitting the ML model (eq. 2) to Chl and TP data from 27 north temperate lakes including 120 lake-years of data pre- and 96 lake-years of data post-dreissenid mussel invasion. Pre-Post, before and after invasion; *N*, number of samples.

Fig. 5. Effect of dreissenid mussel invasion on the slope of the Chl:TP ratio in 27 north-temperate lakes. Slopes in stratified (filled circles) and mixed (open circles) lakes were calculated using a hierarchical modeling approach (see Materials and methods). Values below the 1:1 line (broken line) indicate a decline in slope between the pre- and post-invasion period, while values above the line indicate an increase. Regression equations (eqs. 2 and 3) predicted a slope near 1 during pre- and post-invasion periods when all data points (i.e., lake years) were considered independently.



responsible for the differences to assess causality. First, the responses of Chl, TP, and the Chl:TP ratio in the study lakes were consistent with the ecology of dreissenid mussels as reported in controlled experiments (e.g., Mellina et al. 1995; Miller and Watzin 2007) and with the effects of other filter feeders on Chl and the Chl:TP ratio (e.g., Sarnelle 1992; Mazumder 1994a). Second, the lakes spanned large gradients in trophic status and ecosystem size, represented seasonally stratified and nonstratified systems, were geographically dispersed, and were invaded over a 16 year period (1986–2002) with post-invasion years in some lakes overlapping with pre-invasion years in others (Appendix A, Table A1). We do not argue that other factors were unimportant in influencing TP, Chl, and the Chl:TP ratio during pre- and post-invasion periods within individual lakes. For example, the decline in epilimnetic Chl (~40%) in Lake

Como, Italy (Binelli et al. 1997; Appendix A, Table A1), or increases in TP in Lake Winnebago, Wisconsin (Appendix A, Table A1) between invasion periods may have been caused, or partially caused, by other factors. However, owing to their variation among lakes and variability in the timing of invasion, these factors (i.e., nondreissenid effects) would act to confound our ability to detect significant effects of dreissenid invasion. Thus, the inclusion of 27 independent natural experiments (dreissenid invaded lakes) provided a means to overcome the idiosyncrasies of any individual system and compelling evidence that dreissenids were responsible for the statistical differences found between pre- and post-invasion periods.

Our results indicate that dreissenid mussels can exert a strong and prolonged structuring force on the autotrophic community of lakes, significantly reducing Chl and significantly altering the relationship between phytoplankton and limiting nutrients. On average, grazing by dreissenid mussels reduced Chl by 40%–45% in the 27 north-temperate lakes in this study. Although Chl is often used to represent phytoplankton biomass, the relationship between the two variables can vary considerably. However, a recent meta-analysis of dreissenid effects has indicated that declines in phytoplankton assessed using cell counting methods were similar to those assessed using Chl (Higgins and Vander Zanden 2010). The long-term effects of invaders have important implications for ecosystem responses and management, yet remain largely unreported (Strayer et al. 2006). Our results also indicated that dreissenid effects on Chl were prolonged, with no evidence of diminishing within 7–10 years of invasion.

The degree to which dreissenid mussels suppress Chl varies as a function of the filtration capacity (FC) of the mussel community (Vanderploeg et al. 2002; Higgins and Vander Zanden 2010). Unfortunately, there are few whole-ecosystem estimates of dreissenid mussel density, and FC cannot be estimated for most invaded ecosystems. Further, it should be expected that dreissenid FC can vary spatially in lakes, owing to spatial variations in dreissenid densities and hydrodynamics. As a result, the magnitude of dreissenid influence over water column constituents are hypothesized to be greatest in nearshore areas of large stratified lakes (Hecky et al. 2004). Our results were restricted to the off-

shore pelagic zones of lakes, where data are more generally available and factors such as lake size and mixing status broadly reflect the influence of dreissenid FC. Our results were consistent with the expectation that mussel FC, and the associated effects on Chl and Chl:TP in the pelagic zone, would decline with epilimnetic volume in stratified systems. In the Laurentian Great Lakes, which are amongst the largest freshwater systems in the world, dreissenid effects on phytoplankton in pelagic waters (Johannsson et al. 1998; Makarewicz et al. 1999; Mills et al. 2003) were relatively small by comparison with those in smaller lakes. However, the filtration pressure exerted by dreissenids in nearshore waters, embayments, and nonstratified basins of large lakes is presumably much higher. Effects on phytoplankton biomass (Nicholls 2001; Hecky et al. 2004; Depew et al. 2006), and the Chl:TP ratio (Nicholls et al. 1999) in these nearshore regions can be similar in magnitude to declines found in small lakes. Thus, while dreissenid effects on phytoplankton in offshore pelagic zones decrease with epilimnetic volume, strong nearshore–offshore gradients in effects within larger lakes can occur. Recent evidence, however, suggests that increases in lake size may not entirely buffer dreissenid effects on phytoplankton in pelagic zones. Recent studies on Lake Michigan, the world's sixth largest lake by area, have demonstrated significant reductions in phytoplankton and nutrients caused by dreissenid grazing during the spring isothermal period at stations with water depths of 30–50 m, resulting in lake wide reductions in phytoplankton biomass and production (Fahnenstiel et al. 2010; Vanderploeg et al. 2010). In nonstratified and smaller stratified lakes the effects of dreissenid grazing on Chl were quite variable and not well predicted by epilimnetic volume. We expect that in these systems FC was more strongly controlled by variations in dreissenid density. We therefore encourage more rigorous monitoring and experiments designed for assessing the drivers of spatial and temporal variations in whole-ecosystem dreissenid mussel densities.

In contrast with the large effects of dreissenids on Chl, effects on TP were minor and highly variable. Dreissenid effects on TP were only significant for stratified systems, and were not significantly correlated with epilimnetic volume or lake area in nonstratified or stratified systems ($p > 0.05$). Since dreissenid consumption of phytoplankton would presumably remove Chl and TP proportionately, their differential response to the presence of dreissenids indicates that much of the P consumed by dreissenids is recycled to the water column.

Consistent with studies evaluating the effect of grazing activity by large zooplankton (Sarnelle 1992; Mazumder 1994a, 1994b), our results indicated broad declines in Chl yield per unit TP across a large trophic gradient as a result of dreissenid mussel grazing. As a result, regression equations developed pre-invasion systematically over-predict Chl after invasion. Our regression-based approach indicated that Chl was highly correlated with TP both before and after invasion and the slope of the Chl:TP ratio was unaffected. In contrast, our ML approach indicated a decline in the slope of the Chl:TP ratio in 24 of 27 lakes after invasion. The difference between methods occurred because the ML model was strongly influenced by within-lake responses that were not included in the regression-based approach. Within many individual lakes, dreissenid invasions disrupted the Chl:TP

relationship entirely. Thus, the conclusions reached from the two different approaches were unique and insightful. The regression approach allowed estimation of broad-scale (among lake) patterns in the Chl:TP ratio across large trophic gradients. This approach indicated that both top-down (grazing) and bottom-up (TP) are important in structuring Chl across large trophic gradients. The ML approach indicated that within lakes the top-down pressure exerted by dreissenid grazing suppressed Chl to an extent that annual variations in TP had little influence on Chl.

Management implications

The Chl:TP ratio is a fundamental relationship in limnology, and has served as an underlying principle governing the use of P-abatement programs to control eutrophication (Dillon and Rigler 1974; Peters 1986; Carpenter et al. 1999). At first glance, our results suggest that dreissenid mussel invasion controls eutrophication, and that strict nutrient loading limits could be relaxed in invaded lakes. However, this view is reliant on assumptions that Chl alone is the appropriate unit of management, and that other consequences are of relatively minor importance. Broader assessments of the effects of dreissenid mussels on lake and river ecosystems have indicated the often dramatic ability of these mussels to transform food webs (Strayer et al. 1999), increase blooms of benthic filamentous algae (Higgins et al. 2008; Malkin et al. 2008), and shift phytoplankton communities toward toxin-producing cyanobacteria (Vanderploeg et al. 2001; Sarnelle et al. 2005; Knoll et al. 2008). In other words, the top-down suppression of phytoplankton and the fertilization of shallow benthic habitats by dreissenid mussels have led to a number of negative ecosystem-level effects that are likely to be reinforced by a relaxation of nutrient controls.

Ecological implications

In addition to their global effects on the biodiversity (Sala et al. 2000) and integrity of ecosystems (Simberloff 1996; Vitousek et al. 1997), biological invasions can reveal a great many insights into ecological relationships and processes (Sax et al. 2007).

Dreissenid invasions are no exception to this general principle. For example, there has been a history of heated debate on the importance of top-down and bottom-up controls on food web structure, including the ability of grazers and trophic cascades to suppress the autotrophic base of food webs (e.g., Polis and Strong 1996; Brett and Goldman 1997; Carpenter et al. 1999). A noted difficulty in resolving these debates has been the lack of data originating from appropriate spatial and temporal scales in natural ecosystems (Power 1992). Our results, from 27 natural lake ecosystems, provide compelling evidence that grazers do indeed have a remarkable ability to suppress autotrophic production (top-down effect) and alter the response of phytoplankton to limiting nutrients (bottom-up effect). Evidence from other studies has indicated that dreissenid induced shifts in the autotrophic base of pelagic food webs have induced a cascading series of effects that that propagate to higher trophic levels in pelagic zones (Strayer et al. 1999; Strayer 2009; Higgins and Vander Zanden 2010) and that habitat coupling by dreissenids has altered energy and nutrient fluxes to littoral

habitats stimulating benthic primary and secondary production (Ward and Ricciardi 2007; Higgins and Vander Zanden 2010). Thus, evidence from dreissenid invaded ecosystems provides strong empirical support for ecological theories indicating that top-down and bottom-up control of food webs occur simultaneously in natural ecosystems (Hunter and Price 1992; Power 1992).

Food web theories that incorporate both top-down and bottom-up mechanisms predict that top-down control is weakened by reductions in consumer efficiency (Power 1992). As predicted by these theories, our results indicated that top-down control over phytoplankton broadly declined with increases in ecosystem size (epilimnetic volume, lake area) for stratified lakes. A complementary study (Higgins and Vander Zanden 2010) indicated that dreissenid effects on major zooplankton groups (rotifers, cladocerans, and copepods) were generally proportional to effects on Chl. Thus, variations in ecosystem size will influence the degree to which dreissenid effects are propagated through food webs. Our results also indicated that the relative importance of top-down and bottom-up control may appear different depending on the scale of interest. Across broad trophic gradients, such as those that occur among lakes, bottom-up and top-down mechanisms both appear as important drivers of Chl in lakes. However, within lakes, where ranges of TP were smaller, top-down control of phytoplankton by dreissenid grazers was more readily observed.

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Appendix A

Table A1. Lakes and data sources utilized to assess the impact of dreissenids on phytoplankton biomass (Chl) and the Chl:TP ratio.

Lake	Location	Year invaded ^a	Mixing status	No. years pre-invasion ^b	No. years post-invasion ^b	Area (km ²)	Mean depth (m)
Beulah	Wisconsin, USA	1999	Stratified	2	3	3.38	5.1
Butte Des Morts	Wisconsin, USA	1999	Mixed	3	3	35.8	1.8
Como	Italy	2000	Stratified	1	1	46.7	161
Crystal	Wisconsin, USA	2001	Stratified	10	7	0.6	6.1
Elizabeth	Wisconsin, USA	2001	Stratified	7	6	2.6	3.4
Erie, central basin	Canada, USA	1989	Stratified	6	10	16184	18.3
Erie, east basin	Canada, USA	1990	Stratified	7	9	6156	24.0
Erie, west basin	Canada, USA	1986	Mixed	6	10	3340	7.4
Ford	Michigan, USA	2003	Mixed	1	2	3.9	NR
Huron, Saginaw Bay	USA	1990	Mixed	1	2	1554	5.1
Long	Wisconsin, USA	2001	Stratified	10	6	1.7	6.7
Long	Michigan, USA	1998	Mixed	1	1	0.6	NR
Machinakee	Wisconsin, USA	2002	Mixed	8	5	1.8	1.8
Metonga	Wisconsin, USA	2001	Stratified	3	5	8.7	7.6
Nagawicka	Wisconsin, USA	1998	Stratified	9	2	3.7	11.0
Oconomowoc	Wisconsin, USA	1999	Stratified	6	4	3.1	9.8
Oneida	New York, USA	1991	Mixed	10	10	207	6.8
Ontario	Canada, USA	1989	Stratified	5	5	18960	86.0
Pleasant	Michigan, USA	1995	Stratified	1	1	1.1	4.3
Poygon	Wisconsin, USA	2000	Mixed	1	4	57.1	1.8
Silver	Wisconsin, USA	1994	Stratified	10	7	1.9	4.8
St. Clair	Canada, USA	1988	Mixed	3	2	1100	3.0
Twin South	Michigan, USA	1998	Stratified	1	1	0.2	NR
Union	Michigan, USA	1999	Mixed	1	1	2.2	NR
Upper Nemahbin	Wisconsin, USA	2001	Stratified	6	4	1.2	9.0
Veluwe	Netherlands	1993	Mixed	7	6	30.5	1.5
Winnebago	Wisconsin, USA	1999	Mixed	6	5	557	4.7

Note: TP, total phosphorus concentration; pre., pre-invasion by zebra mussels; post., post-invasion by zebra mussels; epi-volume, volume of epilimnion;

^aInvasion year was as reported by literature sources or appropriate management agency. For Lake Veluwe the lake was invaded prior to 1965; however,

^bPre-invasion and post-invasion years are provided by literature sources or long term datasets.

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Log epi-volume (km ³)	Mean TP-pre. (mg·m ⁻³)	Mean TP-post. (mg·m ⁻³)	Mean Chl-pre. (mg·m ⁻³)	Mean Chl-post. (mg·m ⁻³)	References
-1.84	22.1	15.1	5.5	3.2	USEPA 2008
-1.19	91.9	75.1	59.4	23.0	USEPA 2008
0.45	21.7	14.8	4.4	2.6	Binelli et al. 1997
-2.76	22.2	14.1	8.0	2.8	USEPA 2008
-2.09	19.4	21.9	7.3	6.2	USEPA 2008
2.41	12.4	10.3	3.2	3.6	Barbiero and Tuchman 2004; Rockwell et al. 2005
1.97	9.6	7.4	1.7	2.0	Barbiero and Tuchman 2004
1.39	19.0	24.5	8.9	4.6	Barbiero and Tuchman 2004
NR	56.1	53.9	23.3	32.3	Michigan Department of Environmental Quality 2009
0.90	21.4	16.7	8.9	4.6	Fahnenstiel et al. 1995; Johengen et al. 1995
-2.16	36.3	25.5	15.7	8.1	USEPA 2008
NR	21.0	13.0	15.4	5.2	Michigan Department of Environmental Quality 2009
-2.49	37.0	43.8	8.6	3.8	USEPA 2008
-1.26	15.0	13.6	3.7	1.8	USEPA 2008
-1.68	12.6	16.7	4.2	1.9	USEPA 2008
-1.77	10.1	11.5	3.8	2.3	USEPA 2008
0.15	36.5	22.5	9.0	5.6	Idrisi et al. 2001
2.54	11.2	10.4	3.5	3.2	Johannsson et al. 1998
NR	15.0	11.0	4.0	3.0	Michigan Department of Environmental Quality 2009
-0.98	77.0	75.1	41.0	32.2	USEPA 2008
-2.17	47.3	28.2	15.3	7.0	USEPA 2008
0.53	25.0	22.5	2.7	1.1	Mellina et al. 1995
NR	9.0	14.0	4.5	3.0	Michigan Department of Environmental Quality 2009
NR	45.0	68.0	34.0	24.4	Michigan Department of Environmental Quality 2009
-2.36	16.4	12.8	3.9	2.5	USEPA 2008
-1.34	94.1	65.5	48.9	14.8	Ibelings et al. 2007
0.42	90.7	116	34.3	21.6	USEPA 2008

Chl, chlorophyll *a* concentration; NR, data were not reported or could not be estimated..

densities declined to 0 between 1975 and 1990, and the re-establishment year (1991) was used as the year of invasion.