

# Impacts of dreissenid mussel invasions on chlorophyll and total phosphorus in 25 lakes in the USA

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## SUMMARY

1. Invasions of zebra and quagga mussels have had long-term, large-scale impacts on lake ecosystems in the USA as characterised by high abundance, broad-scale spread and effective adaptation to new environmental conditions. Due to their high filtering capacity, decreases in chlorophyll *a* (Chl) and total phosphorus (TP) concentrations have been reported in many affected lakes.

2. In 25 US lakes, we analysed the effects of dreissenid invasions on changes in Chl and TP concentrations, measured as the probability of a concentration decrease in the post-invasion period and changes in Chl–TP relationships using Bayesian hierarchical regressions. We also examined whether changes in Chl and TP concentrations and in the Chl–TP relationship differed according to lake hydromorphology, such as mean depth or mixing status (mixed versus stratified lakes).

3. Our results showed that dreissenid invasions were often, but not always, associated with subsequent TP and Chl declines. Dreissenid effects on Chl and TP may be influenced by lake thermal structure. Decreases in Chl and TP were consistently found in mixed lakes where benthic–pelagic coupling is tight, while the effects were less predictable in stratified lakes. Within stratified lakes, Chl and TP reductions were more clearly discernible in deeper lakes with long water residence times.

4. Regression results demonstrated that a joint increase in slope and decrease in intercept and a tighter correlation of the Chl–TP relationship were likely to occur in dreissenid-invaded lakes; this does not support the idea of a shift from bottom-up to top-down control of primary production. These results have important implications for management, suggesting that a relaxation of TP standards would be unwarranted.

5. Across lakes, the slope of the Chl–TP relationship for mixed lakes was substantially higher than that for stratified lakes before mussel invasion, indicating an important role of light in limiting primary production. The slope differences between mixed and stratified lakes decreased in the post-invasion period, possibly because mussel filtration results in a relaxation of light limitation that is more pronounced in deeper, stratified lakes.

*Keywords:* Bayesian hierarchical modelling, chlorophyll *a*, Chl–TP relationships, dreissenid filtration impacts, total phosphorus

## Introduction

Indigenous to Eastern Europe, dreissenid mussels were first documented in the USA in the mid-late 1980s in Lake St. Clair (Roberts, 1990) and have since dispersed into

many North American lakes. Zebra mussels (*Dreissena polymorpha*) spread quickly into shallow areas of the Laurentian Great Lakes and neighbouring waterbodies, reaching peak dispersal rates in the late 1990s (Johnson, Bossenbroek & Kraft, 2006). Quagga mussels (*Dreissena*

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*rostriformis bugensis*) spread more slowly but have replaced zebra mussels in most nearshore areas and have also colonised cold, offshore areas that were uninhabitable by zebra mussels (Vanderploeg *et al.*, 2002; Nalepa, Fanslow & Pothoven, 2010). Quagga mussels have expanded their distribution south-westward into lakes and reservoirs in Arizona, California, Colorado, Nevada and Utah, with the initial colonisation in the south-west reported in 2007 in Lake Mead (Nevada/Arizona) (Stokstad, 2007; Wong & Gerstenberger, 2011). As of March 2011, zebra and/or quagga mussels have been detected in 612 freshwater lakes, including the five Great Lakes, in 26 states (USGS, 2011). Characterised by high abundance, broad-scale spread and effective adaptation to new environmental conditions, the dreissenid invasion is expected to have long-term, large-scale impacts on these lake ecosystems (Strayer, 2009).

Dreissenid mussels influence lakes by filtering large water volumes and depositing the particulate residue on the bottom sediment as either faeces or pseudofaeces. The filtration capacity, the fraction of the water column filtered per unit time, differs considerably over time and space due to the differences in lake hydromorphology and dreissenid patchiness and density (Vanderploeg *et al.*, 2002). Researchers estimated that the zebra mussels in Saginaw Bay, an embayment of Lake Huron, could filter the entire volume of the inner bay several times a day when their density peaked in 1992. Despite population declines in the following years, the filtration capacity ( $0.2\text{--}0.8\text{ day}^{-1}$ ) was comparable to the estimated phytoplankton growth rate of  $0.20\text{--}0.25\text{ day}^{-1}$ , far exceeding the typical filtration capacity of crustacean zooplankton ( $< 0.03\text{ day}^{-1}$ ) (Fahnenstiel *et al.*, 1995a; Fanslow, Nalepa & Lang, 1995; Vanderploeg *et al.*, 2002).

Following the establishment of zebra mussels, decreases in phytoplankton, chlorophyll *a* (Chl) and total phosphorus (TP) concentrations were reported in many affected lakes, resulting from the high filtration capacity of these invaders. In Hatchery Bay of western Lake Erie, the abundance of planktonic diatoms in April–May was 82–91% lower in post-zebra (1990–1992) than in pre-zebra mussel years (Holland, 1993). Apparent declines in annual mean phytoplankton densities and April–September mean Chl concentrations were found in 1989–1990 contemporaneous with zebra mussel invasion at nearshore sites in western, central and eastern Lake Erie (Nicholls & Hopkins, 1993). In Oneida Lake, New York, water quality data collected during April–November from 1988 to 1997 indicated pronounced declines in phytoplankton biovolume and Chl, but no significant change in TP in the presence of zebra mussels (Idrisi *et al.*, 2001).

Post-zebra mussel reductions in Chl and TP have been particularly noticeable in shallow, well-mixed lakes (Macisaac, 1996) and embayments and nearshore regions of the Great Lakes, such as Saginaw Bay of Lake Huron and the western basin of Lake Erie, whereas offshore regions showed more variable responses (Fahnenstiel *et al.*, 1995b; Makarewicz, Bertram & Lewis, 2000). Initially, these differential decreases reduced the nearshore–offshore nutrient gradients in Lakes Huron (Fahnenstiel *et al.*, 1995b), Erie (Makarewicz *et al.*, 2000), Michigan (Carrick, Barbiero & Tuchman, 2001) and Ontario (Hall *et al.*, 2003). However, the ability of zebra mussels to sequester phosphorus in nearshore areas, limiting offshore transport (Hecky *et al.*, 2004; Cha *et al.* 2011) and the more recent expansion of quaggas into deep, offshore regions are currently leading to reports of offshore declines in Chl and TP. At offshore stations ( $\geq 100\text{ m}$  depth) in southern Lake Michigan, where large populations of quagga mussels established in the mid-2000s, Mida *et al.* (2010) documented large decreases in spring Chl and TP concentrations after 2005. Fahnenstiel *et al.* (2010) emphasised that significant declines in offshore phytoplankton biomass were seen only during an isothermally well-mixed period (January–May) when quagga mussels have full access to the phytoplankton in the water column. These findings were supported by Evans, Fahnenstiel & Scavia (2011), who reported decreases in offshore phytoplankton production indicated by decreasing silica drawdown in Lakes Michigan and Huron since the dispersal of quagga mussel populations into offshore waters of the Great Lakes.

While many researchers have reported post-invasion Chl and TP reductions, Vanderploeg *et al.* (2001) indicated that ‘selective rejection’, the tendency of dreissenids to ‘spit out’ less desirable phytoplankton such as cyanobacteria, promotes *Microcystis aeruginosa* growth and relatively high Chl concentrations in Saginaw Bay, Lake Huron. Significant Chl increases and a shift in phytoplankton community towards dominance by cyanobacteria have also been reported in Green Bay, Lake Michigan, in the post-invasion period (De Stasio *et al.*, 2008). Several studies have reported differential dreissenid effects on *Microcystis* with increases occurring at low phosphorus levels and decreases at high phosphorus concentrations (Sarnelle *et al.*, 2005, 2012).

In addition to Chl and TP changes associated with post-dreissenid filtration capacity increases, changes in the Chl–TP relationship have also been noted. Empirical correlations between Chl and TP have been used to examine the factors associated with aquatic ecosystem productivity, infer ‘bottom-up’ control of phytoplankton

growth due to phosphorus limitation and estimate regression parameters (Dillon & Rigler, 1974; Smith & Shapiro, 1981). Mellina *et al.* (1995) examined pre- and post-dreissenid Chl-TP models to differentiate whether phytoplankton decreases resulted primarily from mussel-induced TP reductions or whether the main mussel influence was caused by grazing on phytoplankton. Their rationale was that if the main dreissenid effect was TP removal, then the relationship would be unchanged, but lower TP levels would result in decreased Chl concentrations. However a 'decoupling' of Chl-TP relationship, which they measured as changes from the canonical Dillon and Rigler relationship (1974), would be evidence of mussel grazing. Their conclusions were mixed, with decoupling most likely occurring at high mussel densities and in shallow lakes.

In separate papers, Higgins & Vander Zanden (2010) and Higgins *et al.* (2011) examined Chl and TP concentration changes and changes in the Chl-TP relationship, using cross-sectional lake data. Higgins & Vander Zanden (2010) found that among 42 dreissenid-invaded lakes, TP concentrations decreased by about 18% in the 18 shallow, nearshore areas and well-mixed lakes and by about 21% in offshore regions of the remaining 24 lakes. In contrast, Chl concentrations decreased by about 58% in shallow, nearshore areas and well-mixed lakes and by about 38% in offshore waters. Higgins *et al.* (2011) examined 27 dreissenid-invaded lakes in Europe and North America and estimated dreissenid-induced Chl decreases to be about 40% on average and found that the magnitude of the decrease declined with increasing epilimnetic volume in stratified, but not in well-mixed lakes. Post-invasion TP decreases were less pronounced than the Chl decreases and confined to stratified lakes only. Their hierarchical regression model of the Chl-TP relationship estimated a lower slope in the post-invasion as compared to the pre-invasion period, and they expressed concern that this result could be used as a justification to relax phosphorus standards in dreissenid-affected lakes.

Our analysis builds on this previous research and, using a data set of 25 lakes in the United States, examines whether discernible changes occurred in Chl and TP concentrations following the dreissenid invasion and whether these changes were accompanied by a modified Chl-TP relationship. However, because the data for each lake exhibit considerable variability and sample sizes differ substantially among the lakes, we approached these questions probabilistically, using the full sample distribution rather than comparing sample averages as surrogates for the 'true', but unknown, mean values. We examine the relationship of these changes with lake

morphological features (depth, surface area and presence/absence of thermal stratification) that may influence the effective dreissenid filtration capacity. We note that our analytical methods combine elements of both classical (frequentist) and Bayesian statistical inference. Although the limitations of classical 'significance testing' have been proclaimed (Ziliak & McCloskey, 2008), there is still considerable utility in simple methods to discern 'signal from noise' and the two statistical approaches are increasingly used complementarily (Mcgrayne, 2011), taking advantage of useful features of each. Some of our findings differ from those of previous analyses; we discuss the key differences, make inferences about the dreissenid impacts that systematically differ with lake properties and discuss whether the inferences can be supported by existing theories and concepts.

## Methods

### Data description

TP and Chl concentration data availability was checked for all 612 lakes that were reported to be mussel-invaded (by March 2011) using the US Environmental Protection Agency's online legacy and modernised STORET databases. For Oneida Lake, data were provided by Cornell University Library DataStaR database. Saginaw Bay data were obtained from STORET (1969–2005), the Michigan Department of Environmental Quality (2006–2007), Bierman *et al.* (1984) (1974–1980) and the National Oceanic and Atmospheric Administration Great Lakes Environmental Research Laboratory (1991–1996 and 2008–2009). The information on the year of dreissenid discovery was obtained from personal contact (Amy Benson at US Geological Survey).

We constrained the data collection to include TP and Chl concentrations sampled during the growing season (April–November) within a surface mixed layer at one or more sites in a lake. To avoid the confounding effects of decreased P loading to lakes during the pre-invasion period, we excluded years that showed consistent decreases in TP or Chl concentrations that could reflect ongoing processes unrelated to the mussel invasion. Subsequent to the screening, we removed the lakes with data spanning fewer than 3 years either before or after the invasion, or that had fewer than five observations in each of the pre- and post-invasion periods. Consequently, 25 US lakes were included in our analysis (Table 1). Note that a number of lakes that have been invaded recently (e.g. Lake Le Homme Dieu, MN, where mussels were first detected in 2009) had to be excluded from the analysis

**Table 1** Lake description and comparison of mean annual Chl ( $\mu\text{g L}^{-1}$ ) and TP ( $\mu\text{g L}^{-1}$ ) concentrations, and Chl–TP relationship in terms of intercept ( $\pm 1$  standard error) and slope in pre- and post-invasion periods. When  $\text{Pr-X} > 0.5$ , it is more likely that Chl (or TP) has decreased since dreissenid invasion and *vice versa*, and \*indicates that the decrease (or increase) is significant ( $P$ -value  $< 0.05$ ).  $P$ -value was calculated from a  $t$ -test of  $X_{\text{pre}}$  and  $X_{\text{post}}$ , which are the vectors of TP or Chl concentrations during the post- and pre-invasion periods, respectively

Lake	State	County	Data availability	Year of discovery	Mean Depth (m)	Surface area (km <sup>2</sup> )	Mixing Status	Pre-invasion		Post-invasion		Pr-Chl	Pr-TP	$\Delta$ Intercept	$\Delta$ Slope
								Chl	TP	Chl	TP				
Big Cedar	WI	Washington	1988–2006	2000	10.4	3.77	Stratified	5.0	14.1	6.6	17.5	0.46	0.39*	-1.04 ( $\pm 0.02$ )	0.36 ( $\pm 0.01$ )
Butte des Morts	WI	Winnebago	1997–2004	1999	1.8	35.84	Mixed	53.7	85.2	43.7	80.7	0.53	0.51	-0.75 ( $\pm 0.03$ )	0.17 ( $\pm 0.01$ )
Champlain	NY, VT	Multiple	1980–2009	1994	19.5	1269	Stratified	8.4	35.6	11.1	36.9	0.44*	0.46*	-0.72 ( $\pm 0.01$ )	0.24 ( $\pm 0.00$ )
Clear	IA	Cerro Gordo	2001–2008	2005	3	15	Mixed	50.8	77.3	38.2	79.2	0.50	0.51	-0.28 ( $\pm 0.03$ )	0.07 ( $\pm 0.01$ )
Crystal	WI	Sheboygan	1988–2006	2001	6.1	0.6	Stratified	2.7	12.1	3.3	12.2	0.40	0.38*	-1.36 ( $\pm 0.02$ )	0.59 ( $\pm 0.01$ )
Dunmore	VT	Addison	1980–2009	1999	33.5	4.197	Stratified	2.3	10.3	3.3	11.8	0.32*	0.42	-0.12 ( $\pm 0.03$ )	0.12 ( $\pm 0.01$ )
Elizabeth	WI	Kenosha	91, 94–06	2001	3.4	2.58	Stratified	6.7	18.6	7.2	23.1	0.43	0.28*	-1.33 ( $\pm 0.03$ )	0.39 ( $\pm 0.01$ )
Ford	MI	Wastenaw	88, 93, 98, 99, 01, 04, 05, 07	2003	4.7	3.95	Mixed	36.1	54.1	20.7	61.0	0.59	0.38	-0.75 ( $\pm 0.03$ )	0.11 ( $\pm 0.01$ )
Geneva	WI	Walworth	88–90, 96, 98–00, 02–06	1995	18.6	21.17	Stratified	4.0	20.0	3.0	11.0	0.73	0.96*	-1.19 ( $\pm 0.03$ )	0.36 ( $\pm 0.01$ )
Hunters	WI	Waukesha	98–00, 02–06	2002	1.5	0.54	Mixed	2.6	16.5	3.3	14.9	0.42	0.55	-1.26 ( $\pm 0.03$ )	0.52 ( $\pm 0.01$ )
Lac La Belle	WI	Waukesha	88–01, 03, 06	1999	3.4	4.71	Stratified	4.4	11.2	4.7	21.0	0.53	0.25*	-1.22 ( $\pm 0.02$ )	0.34 ( $\pm 0.01$ )
Long	WI	Fond du Lac	1988–2006	2001	6.7	1.7	Stratified	6.2	23.1	4.7	20.4	0.62	0.49	-1.51 ( $\pm 0.02$ )	0.44 ( $\pm 0.01$ )
Mary	WI	Kenosha	91, 95–06	2002	2.7	1.2	Stratified	5.0	16.2	8.0	23.4	0.27*	0.20*	-1.51 ( $\pm 0.03$ )	0.53 ( $\pm 0.01$ )
Metonga	WI	Forest	1999–2006	2001	7.6	8.73	Stratified	3.2	14.9	2.3	14.8	0.61	0.52	-1.05 ( $\pm 0.03$ )	0.26 ( $\pm 0.01$ )
Nagawicka	WI	Waukesha	1988–2002	1998	11	3.71	Stratified	4.7	14.7	3.1	15.0	0.72*	0.40	-1.62 ( $\pm 0.03$ )	0.46 ( $\pm 0.01$ )
North	WI	Waukesha	93, 95–06	2003	11.3	1.78	Stratified	9.5	22.1	5.1	20.8	0.66	0.54	-0.46 ( $\pm 0.03$ )	0.03 ( $\pm 0.01$ )
Oconomowoc	WI	Waukesha	88–89, 93–06	1999	9.8	3.1	Stratified	2.7	11.7	2.2	10.8	0.60	0.53	-1.94 ( $\pm 0.03$ )	0.73 ( $\pm 0.01$ )
Oneida	NY	Oneida	1975–2006	1991	6.8	207	Mixed	7.5	27.3	6.1	23.5	0.62*	0.61*	-1.36 ( $\pm 0.01$ )	0.35 ( $\pm 0.00$ )
Pewaukee	WI	Waukesha	1988–2006	2001	4.6	10.09	Stratified	7.7	29.2	10.3	22.5	0.43	0.56	-1.92 ( $\pm 0.03$ )	0.67 ( $\pm 0.01$ )
Poygan	WI	Waushara	1998–2004	2001	2	56.75	Mixed	44.4	76.4	36.1	77.2	0.55	0.47	-0.58 ( $\pm 0.03$ )	0.10 ( $\pm 0.01$ )
Saginaw Bay	MI	Multiple	78–79, 90–09	1991	5	1400	Mixed	11.7	28.6	6.9	19.2	0.69*	0.72*	-0.25 ( $\pm 0.01$ )	0.02 ( $\pm 0.00$ )
Shawano	WI	Shawano	1999–2006	2001	2.7	25	Mixed	9.8	31.4	12.5	31.5	0.47	0.52	-1.26 ( $\pm 0.03$ )	0.40 ( $\pm 0.01$ )
Upper Nemahbin	WI	Waukesha	92, 94, 95, 97–06	1998	9	1.15	Stratified	3.8	30.1	2.5	11.5	0.62	0.55	-2.18 ( $\pm 0.02$ )	0.80 ( $\pm 0.01$ )
Wind	WI	Racine	88–89, 95, 99–06	2003	3.1	3.72	Mixed	15.0	33.5	6.7	37.0	0.85*	0.52	-0.63 ( $\pm 0.03$ )	-0.04 ( $\pm 0.01$ )
Winnebago	WI	Fond du Lac	90–91, 94–06	1999	4.7	557	Mixed	44.3	112.4	28.1	104.7	0.61	0.53	-0.63 ( $\pm 0.02$ )	0.07 ( $\pm 0.01$ )



despite an intensive sampling history; ongoing monitoring in these lakes will help validate the analysis over a broader geographical range.

For each of 25 lakes, mixing status (i.e. mixed or stratified) was indicated by the presence or absence of persistent thermal stratification during summer months as determined through surveying literature (e.g. lake management plan reports or bathymetry maps) that described vertical thermal profile or morphology.

### Statistical analysis

*Comparison of chlorophyll and total phosphorus levels for pre- and post-invasion.* In this analysis, we compare lake-wide differences in Chl and TP concentrations between pre- and post-invasion periods and examine whether the differing responses of Chl and TP concentrations among lakes can be explained by their hydromorphological characteristics. However, Chl and TP levels are highly variable among lakes and sample size varies substantially by lake and period, making it difficult to compare the decrease (or increase) in concentrations for a specific period and lake with that for another period and lake. In addition, our use of point estimates (i.e. mean values over pre- and post-invasion with the standard error of the mean) to summarise the concentration data means we cannot account for the uncertainty originating from differing sample size and variability of concentrations. To address these issues, we assume that the individual measurements of Chl and TP concentration for a given lake and period are approximately log-normally distributed and we compare the full distributions rather than point estimates of the means. The extent to which the post-invasion level differs from the pre-invasion level is expressed as a probability.

For each lake, TP and Chl concentrations are divided into two time groups based on the invasion status as follows:

$$\begin{aligned} X_{\text{pre},j} &= \{X_{\text{pre},1}, \dots, X_{\text{pre},n_j}\} \\ X_{\text{post},j} &= \{X_{\text{post},1}, \dots, X_{\text{post},m_j}\} \end{aligned} \quad (1)$$

where  $X_{\text{pre},j}$  and  $X_{\text{post},j}$  are the vectors of TP or Chl concentrations sampled in the  $j$ th lake (for  $j = 1, \dots, 25$ ) during the post- and pre-invasion periods, respectively, and  $n_j$  and  $m_j$  represent the sample size for the  $j$ th lake during the post- and pre-invasion periods, respectively.

Assuming that  $X_{\text{pre},j}$  and  $X_{\text{post},j}$  are approximately log-normally distributed, log-transforming  $X_{\text{pre},j}$  and  $X_{\text{post},j}$  normalises their separate distributions as well as their ratio ( $X_{\text{pre},j}/X_{\text{post},j}$ ):

$$\begin{aligned} \text{Log}(X_{\text{pre},j}) &\sim N(\mu_{x,\text{pre},j}, \sigma_{x,\text{pre},j}^2) \\ \text{Log}(X_{\text{post},j}) &\sim N(\mu_{x,\text{post},j}, \sigma_{x,\text{post},j}^2) \\ \text{Log}(X_{\text{post},j}/X_{\text{pre},j}) &\sim N(\mu_{x,\text{post},j} - \mu_{x,\text{pre},j}, \sigma_{x,\text{post},j}^2 + \sigma_{x,\text{pre},j}^2) \end{aligned} \quad (2)$$

where  $\mu$  and  $\sigma$  represent the mean and standard deviation of the normal distributions for the given lake and period. Using the normal probability density function, the probability of the post-invasion decrease (Pr-X) in Chl or TP for the lake can be calculated:

$$\text{Pr-X} = \Pr \left\{ \text{Log} \left( \frac{X_{\text{post},j}}{X_{\text{pre},j}} \right) < 0 \right\} \quad (3)$$

Pr-X accounts for both the differences in the sample mean values between pre- and post-invasion periods and the variances of the samples. Thus, as Pr-X approaches one, which is attributable to a discernible decrease in post-invasion mean and a sufficiently low variance, we are more certain that Chl or TP has decreased post-invasion; conversely, as Pr-X approaches zero, we are more certain that Chl or TP has increased post-invasion.

*Comparison of chlorophyll–total phosphorus relationship for pre- and post-invasion.* The objectives of this modelling are to compare Chl–TP relationships before and after dreissenid invasion, evaluate whether any observed changes are significant and determine whether the post-invasion changes are related to lake trophic status or hydromorphological characteristics. On the basis of cross-sectional lake data, many ecological studies have employed complete-pooling modelling in which common regression parameters across lakes are estimated. The complete-pooling model does not allow the parameters to differ by lake, which may be an overly restrictive assumption and lakes with many observations will be weighted more heavily than lakes with fewer observations. An alternative would be to model the Chl–TP relationship lake-by-lake (no-pooling). This approach allows the parameters to differ by lake, but the number and range of observations for many lakes may be limited, and thus, the precision of the estimated parameters will be low (Stow *et al.*, 2009).

In contrast to these two approaches, partial-pooling, using a Bayesian hierarchical framework, accommodates the limited information and variability for individual lakes, while still allowing differences among lakes in the Chl–TP relationships (Gelman & Hill, 2007; Stow *et al.*, 2009). With the data grouped by lakes, a log-log relationship between Chl and TP can be expressed as:

$$\ln(\text{Chl}_i) \sim N\left(\{\alpha_{\text{pre},j|i} + \beta_{\text{pre},j|i} \cdot \ln(\text{TP}_i)\} \cdot I(g_i) + \{\alpha_{\text{post},j|i} + \beta_{\text{post},j|i} \cdot \ln(\text{TP}_i)\} \cdot I(-g_i), \sigma^2\right) \quad (4)$$

for  $i = 1, \dots, n_j$  and  $j = 1, \dots, 25$

where  $\alpha_{\text{pre},j}$  and  $\alpha_{\text{post},j}$  represent the intercept parameters for the  $j$ th lake during the pre- and post-invasions, respectively, while  $\beta_{\text{pre},j}$  and  $\beta_{\text{post},j}$  represent the slope parameters for the  $j$ th lake during pre- and post-invasions, respectively.  $\text{Chl}_i$  and  $\text{TP}_i$  are the  $i$ th sample among total  $n_j$  observations in the  $j$ th lake. In the hierarchical model, model parameters can be further modelled at the lake level as:

$$\begin{aligned} \begin{pmatrix} \alpha_{\text{pre},j} \\ \beta_{\text{pre},j} \end{pmatrix} &\sim N\left(\begin{pmatrix} \mu_{\alpha,\text{pre}} \\ \mu_{\beta,\text{pre}} \end{pmatrix}, \Sigma\right), \\ \text{for } \Sigma &= \begin{pmatrix} \sigma_{\alpha,\text{pre}}^2 & \rho_{\text{pre}}\sigma_{\alpha,\text{pre}}\sigma_{\beta,\text{pre}} \\ \rho_{\text{pre}}\sigma_{\alpha,\text{pre}}\sigma_{\beta,\text{pre}} & \sigma_{\beta,\text{pre}}^2 \end{pmatrix} \\ \begin{pmatrix} \alpha_{\text{post},j} \\ \beta_{\text{post},j} \end{pmatrix} &\sim N\left(\begin{pmatrix} \mu_{\alpha,\text{post}} \\ \mu_{\beta,\text{post}} \end{pmatrix}, \Sigma\right), \\ \text{for } \Sigma &= \begin{pmatrix} \sigma_{\alpha,\text{post}}^2 & \rho_{\text{post}}\sigma_{\alpha,\text{post}}\sigma_{\beta,\text{post}} \\ \rho_{\text{post}}\sigma_{\alpha,\text{post}}\sigma_{\beta,\text{post}} & \sigma_{\beta,\text{post}}^2 \end{pmatrix} \end{aligned} \quad (5)$$

where  $\mu_{\alpha}$  is the overall mean intercept across lakes during the pre- or post-invasion periods,  $\mu_{\beta}$  is the overall mean slope across lakes during the pre- or post-invasion periods,  $\Sigma$  indicates the covariance matrix,  $\sigma_{\alpha}$  and  $\sigma_{\beta}$  represent the standard deviation of  $\alpha_j$  and  $\beta_j$  between lakes, respectively, and  $\rho$  is the correlation between  $\alpha_j$  and  $\beta_j$  during the pre- or post-invasion periods. The hierarchical regression parameters,  $\alpha_j$  and  $\beta_j$ , are estimated as weighted averages of the parameter estimates for individual lakes and overall parameter estimates across lakes (Gelman & Hill, 2007; Stow *et al.*, 2009).

We use eqn (5) as a basic model structure to infer regression parameters ( $\alpha_j$  and  $\beta_j$ ) differed by lakes; however, the variability in  $\beta_j$ s (or  $\alpha_j$ s) can be coupled through the lake-level regression by adding a lake-level predictor (or predictors), and we examine that the different parameters  $\beta_j$ s (or  $\alpha_j$ s) can be explained by lake mean depth with lake-level intercept ( $\gamma$ ) and slope ( $\delta$ ) for both pre- and post-invasion periods:

$$\begin{aligned} \beta_{\text{pre},j} &\sim N(\gamma_{\text{pre}} + \delta_{\text{pre}} \cdot z_j, \sigma_{\beta,\text{pre}}^2) \\ \beta_{\text{post},j} &\sim N(\gamma_{\text{post}} + \delta_{\text{post}} \cdot z_j, \sigma_{\beta,\text{post}}^2) \end{aligned} \quad (6)$$

where  $z_j$  represents the lake mean depth for lake  $j$ . Model parameter posterior distributions were simulated using Markov chain Monte Carlo (MCMC) procedures in

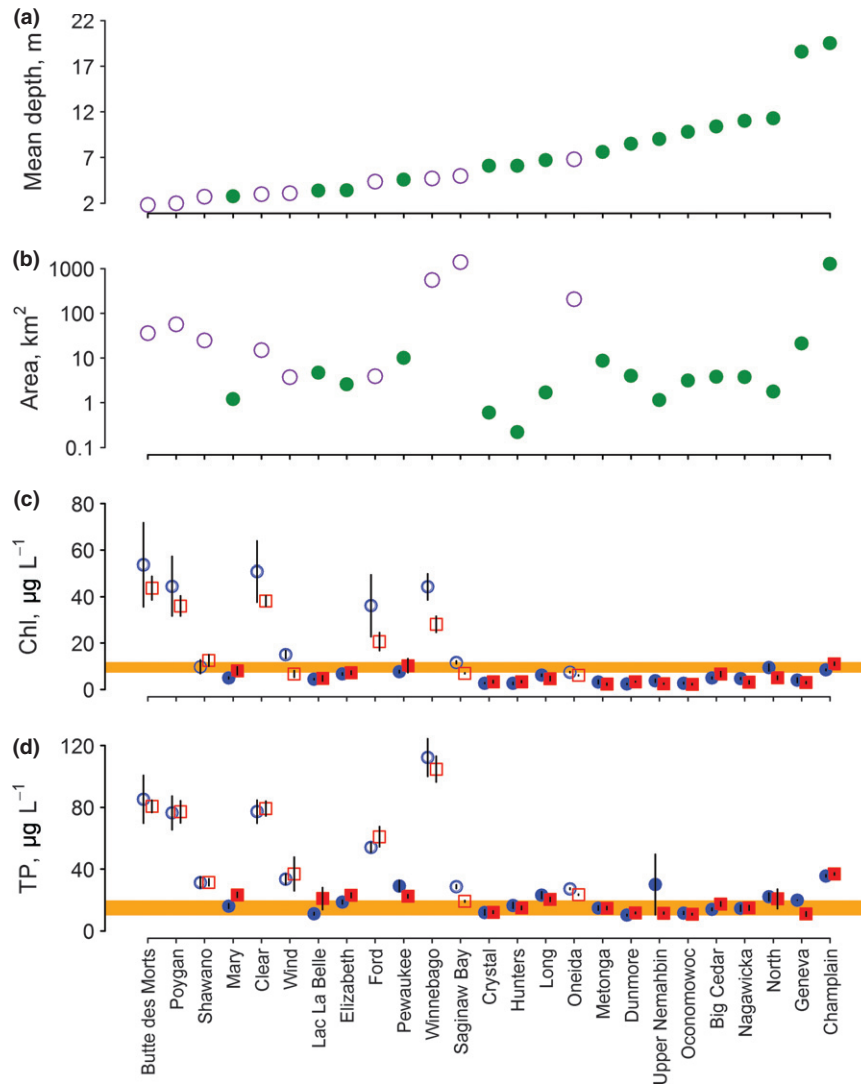
the software program WinBUGS (Lunn *et al.*, 2000). Predictions were made based on the posterior distributions using the R Development Core Team (2011).

### Results

The studied lakes, located in the Midwestern and North-eastern United States, cover a wide range of trophic status, mean depth and surface area and include both stratified and mixed lakes (Fig. 1 and Table 1). The mixed lakes tend to be more eutrophic (mean Chl ranging from 5 to 43  $\mu\text{g L}^{-1}$ ; mean TP ranging from 13 to 109  $\mu\text{g L}^{-1}$ ) than the stratified lakes (mean Chl 2–10  $\mu\text{g L}^{-1}$ ; mean TP 11–36  $\mu\text{g L}^{-1}$ ). The mixed lakes are also generally shallower (mean depth ranging from 1.8 to 6.8 m) and larger (surface area ranging from 3.7 to 1400  $\text{km}^2$ ) than the stratified lakes (mean depth 2.7–19.5 m; area 0.2–1269  $\text{km}^2$ ) (Fig. 1 and Table 1). Within each group of mixed and stratified lakes, mean depth and surface area are positively associated ( $r = 0.43$  and  $r = 0.52$ , respectively).

More than half of the lakes exhibited Chl and TP decreases after the mussel invasion. Based on the calculated Pr-X, the probability of the post-invasion decrease in Chl or TP, post-invasion Chl levels decreased (indicated by  $\text{Pr-Chl} \geq 0.5$ ) in 15 of 25 lakes and TP levels decreased (indicated by  $\text{Pr-TP} \geq 0.5$ ) in 14 lakes (Fig. 2). Clearer post-invasion patterns can be seen when mixed and stratified lakes are separated, with more consistent decreases observable in mixed than in stratified lakes (Fig. 2 and Table 1). Chl and TP levels decreased in seven of nine mixed lakes with Pr-Chl and Pr-TP ranging 0.47–0.85 and 0.39–0.72, respectively. In contrast, the response of stratified lakes showed greater variability, with Chl and TP decreases occurring in only eight and seven of 16 stratified lakes, respectively, and Pr-Chl and Pr-TP ranging 0.27–0.73 and 0.20–0.96, respectively (Fig. 2 and Table 1). Chl and TP concentrations generally changed in the same direction (Fig. 2); in 10 lakes where there were post-invasion Chl decreases, TP concentrations also decreased, and in six lakes where there were post-invasion Chl increases, TP concentrations also increased. In five lakes, however, post-invasion Chl decreases occurred with TP increases, while in four lakes post-invasion Chl increases occurred with TP decreases (See # symbols in Fig. 2).

Positive correlations between Pr-X and mean depth were found in both stratified and mixed lakes, although the correlations were only significant in stratified lakes (Fig. 3a,b). Estimated regression equations for stratified lakes are as follows:



**Fig. 1** (a) Mean depth (m), (b) surface area (km<sup>2</sup>), (c) Chl (µg L<sup>-1</sup>) and (d) TP (µg L<sup>-1</sup>) concentrations in 25 US lakes. In panels (a) and (b), solid green circles represent stratified lakes and open violet circles represent mixed lakes. In panels (c) and (d), blue circles denote pre-invasion means, red squares denote post-invasion means, solid symbols indicate stratified lakes, open symbols indicate mixed lakes, and error bars indicate ± one standard error of the mean. Orange shading represents a concentration range indicative of mesotrophic status (Reckhow & Chapra, 1983). Lakes are listed in order of mean depth.

Pr-Chl = 0.25 (± 1 standard error = 0.11) + 0.13 (± 0.05) · log (mean depth) + ε, R<sup>2</sup> = 0.31, P-value = 0.04 and

Pr-TP = 0.06 (± 0.13) + 0.20 (± 0.06) · log (mean depth) + ε, R<sup>2</sup> = 0.43, P-value < 0.01,

while for mixed lakes the estimated equations are as follows:

Pr-Chl = 0.49 (± 0.12) + 0.09 (± 0.09) · log (mean depth) + ε, R<sup>2</sup> = 0.13, P-value = 0.34 and

Pr-TP = 0.42 (± 0.09) + 0.09 (± 0.07) · log (mean depth) + ε, R<sup>2</sup> = 0.19, P-value = 0.24,

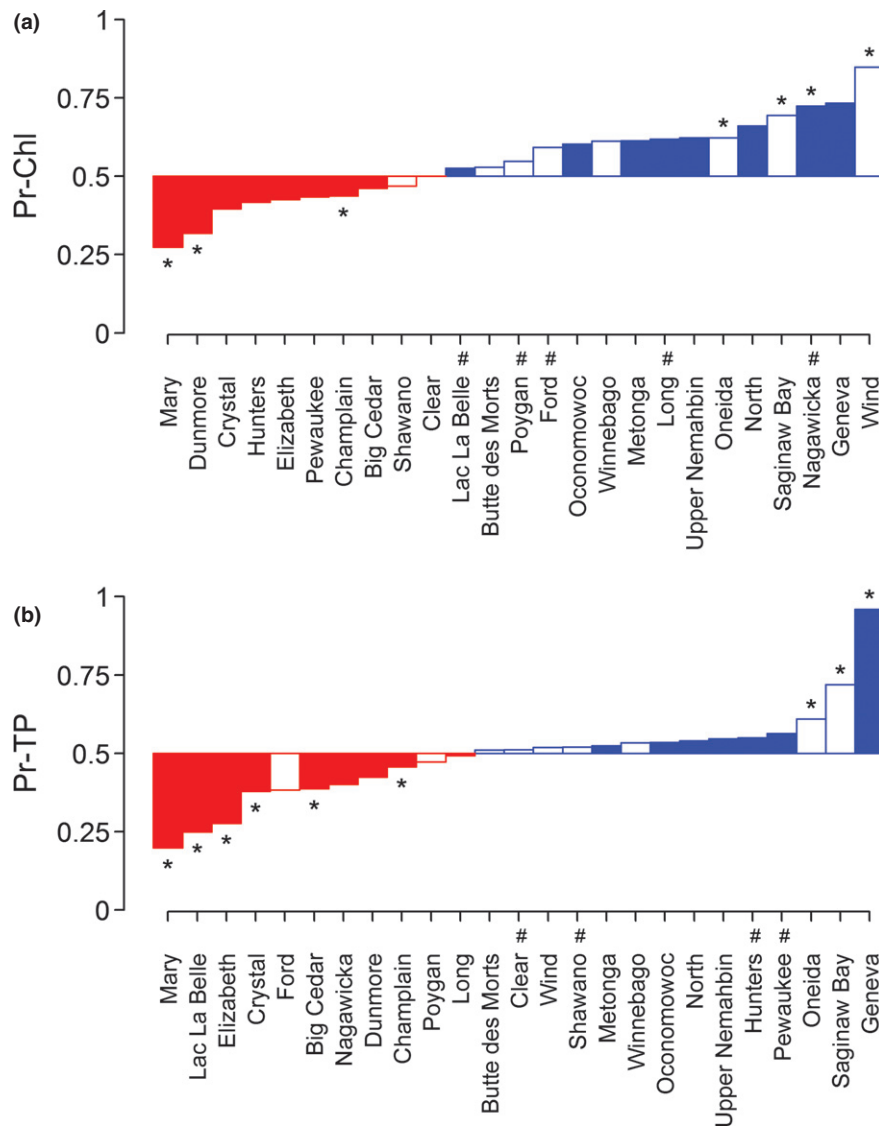
where the distribution for residual errors is assumed normal with the mean zero.

In stratified lakes, the probability of the post-invasion decrease in both Chl and TP concentrations (Pr-Chl and

Pr-TP) increased with mean depth; however, the mixed lakes are shallower and generally showed Pr-Chl and Pr-TP ≥ 0.5; thus, the positive association between Pr-Chl or Pr-TP and mean depth was not as pronounced (Fig. 3a,b).

In contrast to mean depth, lake surface area did not show any discernible relationship with Pr-Chl or Pr-TP in either mixed or stratified lakes (Fig. 3c,d). While the mixed lakes are generally larger and generally exhibited Pr-Chl and Pr-TP values ≥ 0.5, for a given area Pr-Chl and Pr-TP ≥ 0.5 were less likely in stratified lakes (Fig. 3c,d).

The Bayesian hierarchical regression results indicate that after mussel invasion there were slight changes in



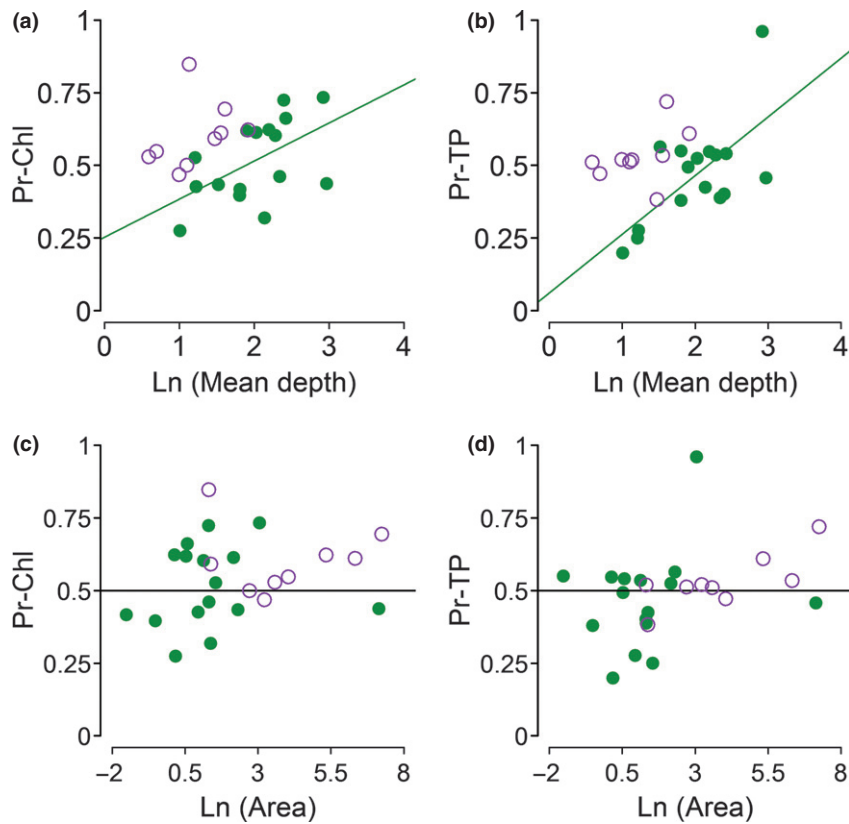
**Fig. 2** (a) Chl and (b) TP concentrations during pre- and post-invasion periods based on Pr-X. Pr-X > 0.5, indicating post-invasion decreases, is coloured blue, while Pr-X < 0.5, indicating post-invasion increases, is coloured red. Open bars represent mixed lakes, and solid bars represent stratified lakes. Filled bars represent Pr-X for stratified lakes, and open bars represent Pr-X for mixed lakes. Statistical significance ( $P$ -value < 0.05) marked with \* at the end of the bar was calculated from a  $t$ -test of  $X_{pre}$  and  $X_{post}$ , which are the vectors of TP or Chl concentrations during the post- and pre-invasion periods, respectively. Symbol # marked at the end of the lake name identifies the lakes that experienced a post-invasion Chl (or TP) decrease, yet a TP (or Chl) increase.

both the intercept and slope of the Chl-TP relationship. Across-lake regression parameters (in contrast to the individual lake parameters) reveal a post-invasion intercept decrease with mean  $\mu_{\alpha,pre} = -0.17$  ( $\pm 1$  standard deviation = 0.25) and mean  $\mu_{\alpha,post} = -1.27$  ( $\pm 0.23$ ), and a slope increase with mean  $\mu_{\beta,pre} = 0.62$  ( $\pm 0.09$ ) and  $\mu_{\beta,post} = 0.95$  ( $\pm 0.08$ ) (eqn 5 and Fig. 4a). When viewed independently, the intercept decrease and slope increase each appear statistically significant, as indicated by the non-overlapping credible intervals (Fig. 4b). However, because the intercept and slope are highly correlated, the

joint pre- and post-invasion parameter sets are statistically indistinguishable, as indicated by the overlap of their joint posterior distributions (Fig. 4b). Thus, these two changes approximately offset one another. Consistent with the pattern across lakes, in all individual lakes the intercept decreased during the post-invasion period and there were post-invasion slope increases in all lakes except for Wind Lake, where the slope decreased slightly by 0.04 from 0.74 to 0.70 (Fig. 5).

Although the observed joint intercept decrease and slope increase would not be judged statistically significant





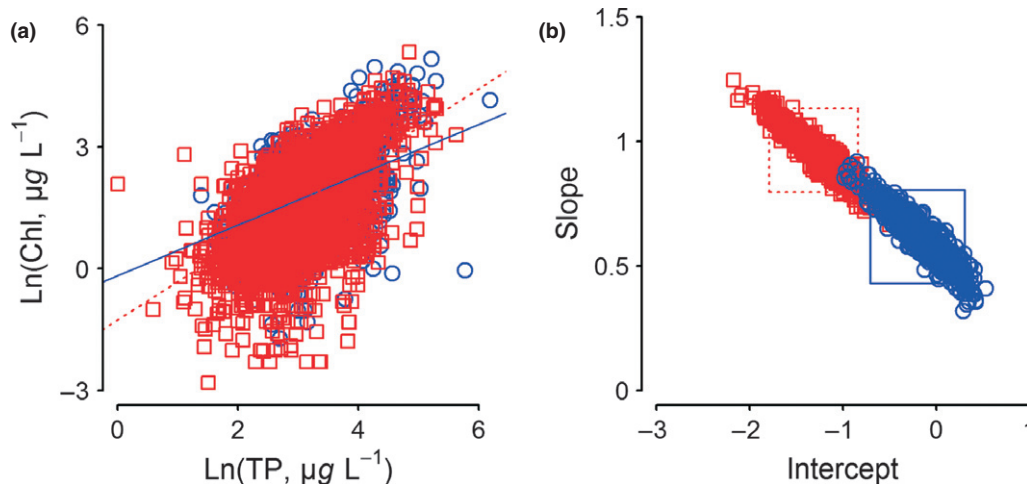
**Fig. 3** Relationships between lake morphology (for panels (a) and (b), mean depth, m, and for (c) and (d), surface area, km<sup>2</sup>) and mixing status on decreasing Chl,  $\mu\text{g L}^{-1}$  [(a) and (c)] and TP,  $\mu\text{g L}^{-1}$  [(b) and (d)] concentrations. Solid green dots represent stratified lakes; open violet dots represent mixed lakes. In panels (a) and (b), regression lines are shown for stratified lakes (solid green). In panels (c) and (d), horizontal lines denote  $\text{Pr-X} = 0.5$ .

by classical statistical standards, the consistency of the pattern is intriguing, inviting further exploration. Adding a lake-level predictor to a model structure at the higher level (eqn 6) allowed us to examine the relationships between the individual lake intercept and slope parameters and lake mean depth. Incorporating the additional structure uses the entire posterior distribution of each intercept and slope to estimate the relationship with lake mean depth, instead of using just a point estimate such as the mean for each intercept and slope. Thus, the resultant regression lines (Fig. 6) were differentially weighted based on the precision of each intercept and slope in a manner analogous to a weighted regression. The results showed that the slopes were negatively related to lake mean depth (Fig. 6), indicating that Chl tends to respond more rapidly to changes in TP in shallow than in deep lakes. In the pre-invasion period, the slope parameters can be grouped into two categories: high slopes for mixed lakes and low slopes for stratified lakes (Fig. 6a). After the mussel invasion, although most slopes increased, the difference between the mixed and stratified lakes became smaller and the

relationship with mean depth became less pronounced (Fig. 6b). Concurrently, because the slopes and intercepts are highly correlated, a pre-invasion, positive relationship between the intercepts and mean depth (Fig. 6c) diminished following the invasion, with the difference between mixed and stratified lakes becoming indiscernible.

## Discussion

Changes in dissolved and particulate nutrient concentrations and water column transparency noted in US lake ecosystems during the last two decades have been attributed to dreissenid filtration activities that remove suspended particles from the water column and redirect them to the lake bottom (Macisaac, 1996; Hecky *et al.*, 2004). Consistent with previous findings, most of the lakes in our study exhibited decreases in Chl and TP concentrations. However, changes in mean Chl and TP concentrations were relatively small and changes in overall Chl and TP distributions were statistically discernible in fewer than half of the lakes.



**Fig. 4** Comparison of Chl-TP concentration relationships for pre- and post-invasion periods across 25 US lakes. (a) Blue open dots represent pre-invasion observations, and red open triangles represent post-invasion observations across lakes. Blue solid line indicates Bayesian hierarchical regression lines derived from pre-invasion overall mean parameters ( $\mu_{\alpha,pre}$  and  $\mu_{\beta,pre}$ ), and red dashed line indicates the regression line derived from pre-invasion overall mean parameters ( $\mu_{\alpha,post}$  and  $\mu_{\beta,post}$ ). (b) Posterior joint distributions of overall mean intercept and slope during pre-invasion (blue circles) and post-invasion (red triangles). Blue rectangles for pre-invasion and red rectangles for post-invasion each indicate the 95% credible interval of the corresponding joint distribution.

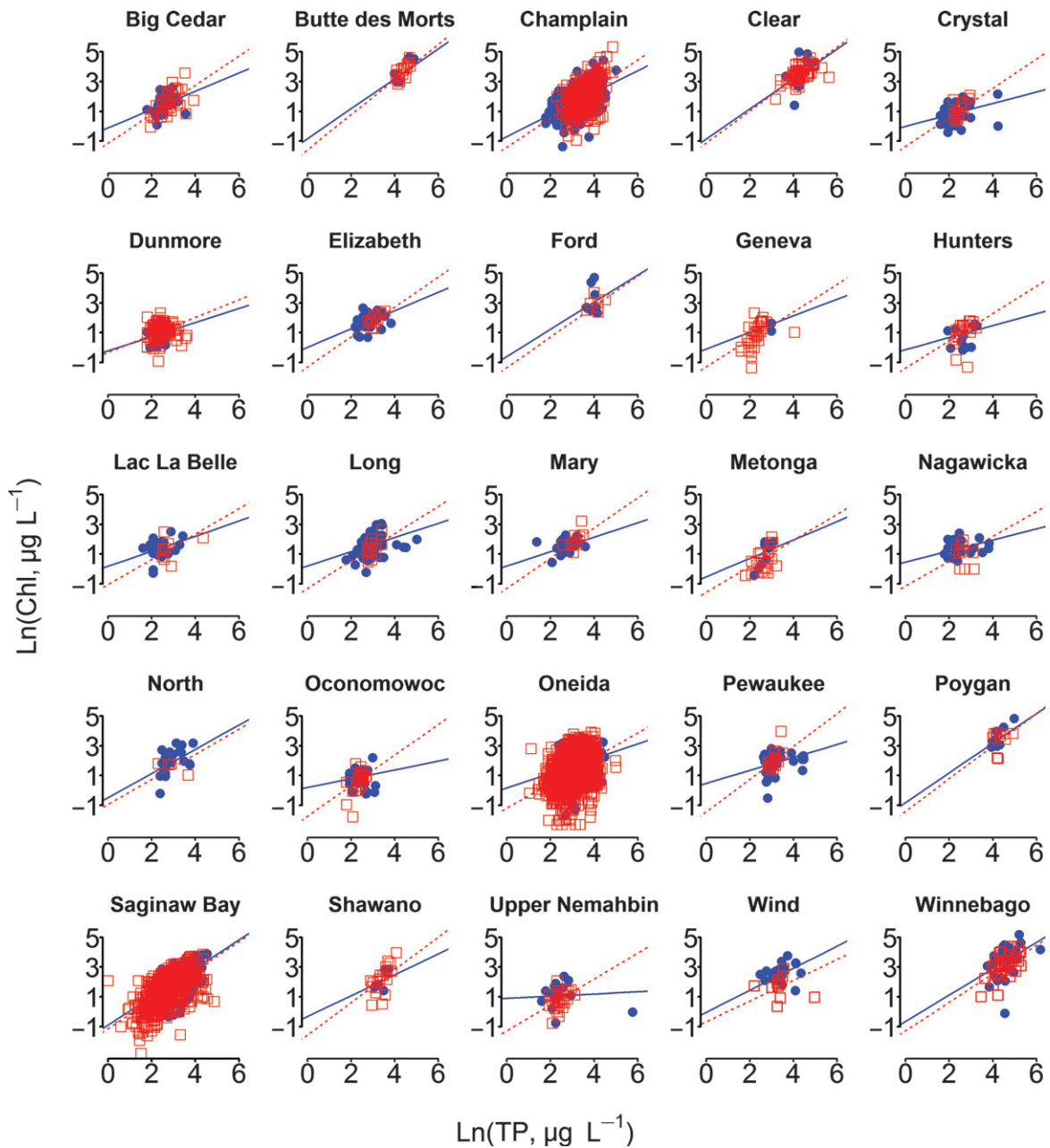
Our results also indicate that dreissenid impacts on Chl and TP have been influenced by lake thermal structure. Chl and TP decreases have been fairly consistent in mixed lakes where benthic–pelagic coupling is tight. Even in mixed lakes, however, sporadic stratification may limit mussel impacts by reducing vertical transport of particulates to mussels on the lake bottom (Macisaac *et al.*, 1999; Ackerman, Loewen & Hamblin, 2001; Boegman *et al.*, 2008). Periodic restrictions on mussel access to the water column may explain why, even in many mixed lakes, Chl and TP decreases were moderate.

Impacts were less predictable in stratified lakes, where mussel colonisation may be more spatially heterogenous and their effect may be buffered because the mussels are effectively removed from a portion of the water column for part of the year. Thus, stratified lakes are less likely to show a decrease than mixed lakes of comparable depth. Notably, however, Pr-Chl and Pr-TP increased with increasing mean depth in stratified lakes, indicating that Chl and TP reductions were more clearly discernible in deeper, stratified lakes. Water residence time may be important in determining the magnitude of dreissenid filtration impacts in stratified lakes. Generally associated with increased mean depth, longer water residence time increases the chance of mussels having contact with phosphorus-bearing particles or phytoplankton in the water column. Mussels may increase the sediment loss coefficient (Klerks, Fraleigh & Lawniczak, 1996; Goedkoop, Naddafi & Grandin, 2011) in the general mass balance equation:

$$P_{in} = P_w / (1 + k \cdot \tau_w)$$

where  $P_{in}$  = in-lake phosphorus concentration (mass/volume),  $P_w$  = phosphorus loading (mass/time),  $k$  = sediment loss coefficient and  $\tau_w$  = water residence time (Reckhow & Chapra, 1983). The equation reveals that mussels should be more effective in reducing  $P_{in}$  in lakes with long residence time. The recent expansion of quagga mussels into colder, deeper waters, which were inaccessible to zebra mussels, may also be a factor. Measurable increases in water clarity, decreases in TP and Chl and changes in phytoplankton abundance have been documented in the offshore regions of the lower Great Lakes since quagga mussel colonisation of the deep, offshore waters (Fahnenstiel *et al.*, 2010; Evans *et al.*, 2011; Vanderploeg *et al.*, 2012).

Predictions using Bayesian hierarchical regression modelling illustrate that at oligo-mesotrophic status ( $TP < 15 \mu\text{g L}^{-1}$ ), lower Chl concentrations are expected for a given TP concentration in the post-mussel period (Fig. 7), due to an increased slope and decreased intercept, both across and within lakes. Lower Chl : TP ratios have been used as evidence of a ‘decoupling’ of the Chl-TP relationship, indicative of a shift from bottom-up to top-down control of primary production (Mellina *et al.* 1995). However, a comparison of pre- and post-invasion  $R^2$  values indicates a generally tighter correlation between Chl and TP after the mussel invasion (Fig. 8), suggesting the ongoing importance of bottom-up nutrient limitation. Although not widely appreciated, estimates of regression

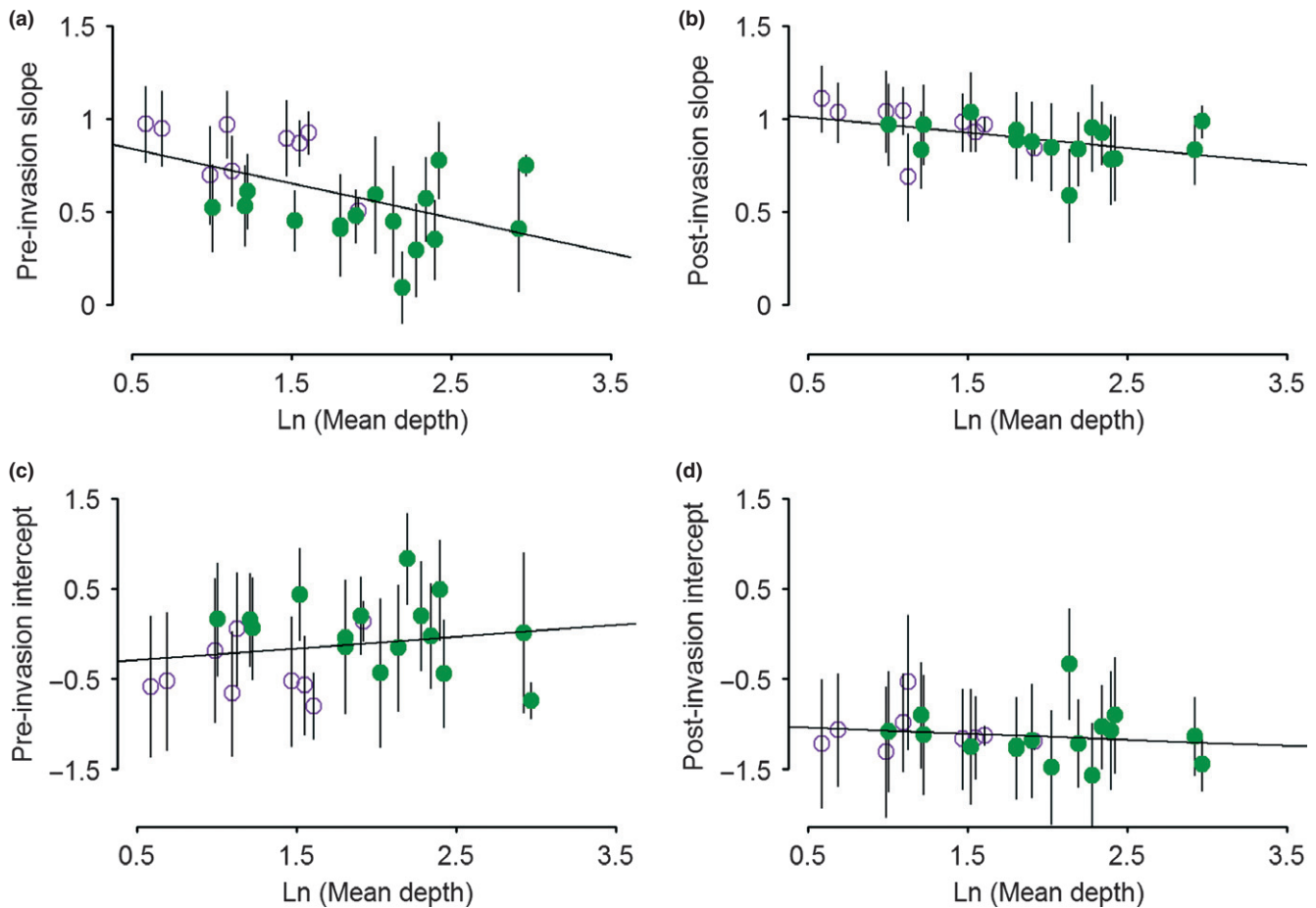


**Fig. 5** Comparison of Chl–TP concentration relationship for pre- and post-invasion periods in individual lakes. Blue solid dots represent pre-invasion observations, and red open squares represent post-invasion observations in each lake. Lines indicate Bayesian hierarchical regression for pre-invasion (blue solid line) and post-invasion (red dashed line).

intercepts and slopes are generally negatively correlated (Gould, 1966) and considering them independently can be misleading. When intercepts and slopes are negatively correlated, an increase or a decrease in the Chl yield per unit TP depends on the range of TP used for the prediction.

The Bayesian hierarchical regression results also show a relationship between the slope of Chl–TP relationship and mean depth; in both pre- and post-invasion periods, the estimated slopes increase as lake depth decreases. Previ-

ous studies have also shown lower slopes in deeper lakes, suggesting that the role of self-shading in limiting phytoplankton production in deep lakes is important (Stauffer, 1991; Phillips *et al.*, 2008). In the post-mussel period, the slope and intercept differences between mixed and stratified lakes decreased, possibly because mussel filtration results in more consistent water transparency and a relaxation of light limitation in deeper, stratified lakes.



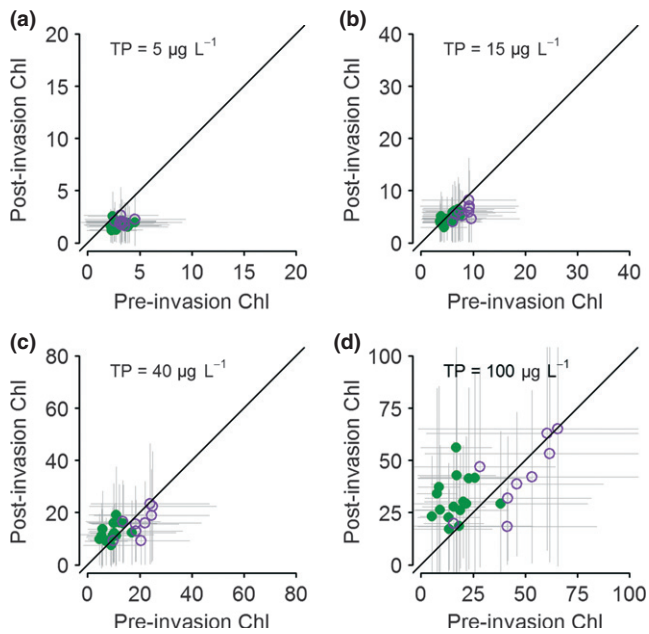
**Fig. 6** Bayesian hierarchical regression parameters modelled as a function of mean depth at the lake level. (a) Slope for pre-invasion, (b) slope for post-invasion, (c) intercept for pre-invasion and (d) intercept for post-invasion. Solid lines represent regression line, and error bars indicate  $\pm$  one standard deviation. Solid green dots represent stratified lake, and open violet dots represent mixed lake.

Our results indicate that dreissenid invasions are most often associated with subsequent TP and Chl declines, although these changes are usually small and in some instances increases in either TP or Chl are noted. These results are generally consistent with those of Higgins *et al.* (2011), who reported significant TP decreases for stratified but not mixed lakes and significant Chl decreases in both stratified and mixed lakes. However, our results suggest that post-invasion decreases in both TP and Chl were more likely in mixed lakes, while the changes in stratified lakes exhibited large variability. Also, Higgins *et al.* (2011) reported that in stratified lakes, the 'magnitude' of the post-invasion decrease in Chl 'declined' with increasing lake epilimnetic volume, while an epilimnetic volume relationship was not found in mixed lakes. In contrast, we found that the probability of a Chl decrease following mussel invasion in stratified lakes was positively related to lake mean depth and thus probably with increasing epilimnetic volume. These results are not necessarily

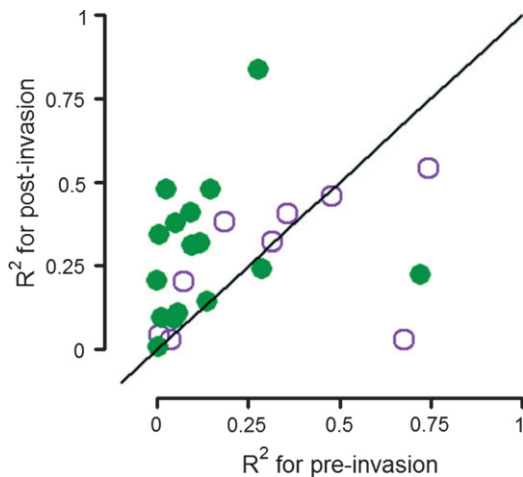
inconsistent, as we examined probabilities, while Higgins *et al.* (2011) used size as a metric. Further investigations, as more data become available, may reconcile any apparent discrepancy.

We also report a joint intercept increase and slope decrease in the Chl-TP relationship, which differs from the results reported by Higgins *et al.* (2011), who showed slope decreases in 24 of 27 lakes. Differences in data treatment may be responsible for these disparate outcomes. Higgins *et al.* (2011) used sample averages, while we used individual observations to analyse the Chl-TP relationship. Using sample averages as point-estimate surrogates for true, but unknown mean values discards information regarding uncertainty and does not account for differing sample sizes or variances among samples. In particular, using imprecise measures of independent variables in a regression analysis is known to induce a systematic bias in regression slope estimators (Madansky, 1959). Higgins *et al.* (2011) also log-transformed sample





**Fig. 7** Comparison of post-invasion Chl predictions and pre-invasion Chl predictions at four levels of TP concentration: (a) 5, (b) 15, (c) 40 and (d) 100  $\mu\text{g L}^{-1}$ . Dots denote the mean of predictive distribution; lines denotes  $\pm$  one standard deviation of predictive distributions for pre-invasion (grey horizontal line) and post-invasion (grey vertical line) periods. Solid green symbols represent stratified lake, and open violet symbols represent mixed lake. Black diagonal lines represent one-to-one line.



**Fig. 8** Comparison of  $R^2$ , estimated from the linear regression of Chl using TP (both concentrations on logarithmic scales) within individual lakes between pre- and post-invasion periods. Solid green dots represent stratified lakes, and open violet dots represent mixed lakes. Black diagonal lines represent one-to-one line.

averages, but sample averages are not invariant to log transformations; this procedure can also introduce a slight bias (Stow, Reckhow & Qian, 2006). These practices are extremely common, but are generally inconsistent with

the assumptions supporting regression model estimation. Higgins *et al.* (2011) expressed concern that their result, that slope decreases, could be used to justify a relaxation of phosphorus standards. Our results indicate that such an action would be unwarranted.

It should be noted that there are potential limitations on the interpretation of our results arising from several sources of uncertainty. One source of uncertainty is the time of dreissenid invasion; by the time mussels are discovered, the population may have been established for a few years. Also, the population density information required to quantify the impacts of mussel filtration activities is rarely available and the patterns of the population growth, which are expected to reveal a high level of variability over time and space within a lake, are typically unknown. Thus, even though a time-lag between the introduction of mussels and lake responses on Chl or TP levels would be significant, it can hardly be estimated. However, previous studies reported that the dreissenid impacts on lake Chl or TP changes were immediate and drastic. Nicholls & Hopkins (1993) found significant decreases in phytoplankton densities, which showed a high correlation with Chl, between the 2-year period of pre-invasion (1986–1987) and the 2-year period of post-invasion (1989–1990) in western Lake Erie. In inner Saginaw Bay, Lake Huron, apparent reductions in Chl and TP concentrations were observed in autumn 1991 continuing through 1992 and 1993, with the zebra mussel colonisation initiating in summer/autumn 1991 (Fahnenstiel *et al.*, 1995a,b).

### Acknowledgments

This research was sponsored by a grant from the National Oceanic and Atmospheric Administration Center for Sponsored Coastal Ocean Research. GLERL contribution number 1637. We would like to thank Amy Benson at US Geological Survey for providing the information on mussel invasion and Michaela Margida for assistance in collecting the data and Ibrahim Alameddine, Tara Stow and anonymous reviewers for their insightful comments.

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(Manuscript accepted 6 October 2012)