

Regional variability among nonlinear chlorophyll–phosphorus relationships in lakes

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Abstract

The relationship between chlorophyll *a* (Chl *a*) and total phosphorus (TP) is a fundamental relationship in lakes that reflects multiple aspects of ecosystem function and is also used in the regulation and management of inland waters. The exact form of this relationship has substantial implications on its meaning and its use. We assembled a spatially extensive data set to examine whether nonlinear models are a better fit for Chl *a*–TP relationships than traditional log-linear models, whether there were regional differences in the form of the relationships, and, if so, which regional factors were related to these differences. We analyzed a data set from 2105 temperate lakes across 35 ecoregions by fitting and comparing two different nonlinear models and one log-linear model. The two nonlinear models fit the data better than the log-linear model. In addition, the parameters for the best-fitting model varied among regions: the maximum and lower Chl *a* asymptotes were positively and negatively related to percent regional pasture land use, respectively, and the rate at which chlorophyll increased with TP was negatively related to percent regional wetland cover. Lakes in regions with more pasture fields had higher maximum chlorophyll concentrations at high TP concentrations but lower minimum chlorophyll concentrations at low TP concentrations. Lakes in regions with less wetland cover showed a steeper Chl *a*–TP relationship than wetland-rich regions. Interpretation of Chl *a*–TP relationships depends on regional differences, and theory and management based on a monolithic relationship may be inaccurate.

Understanding relationships between primary producers and their growth-limiting resources is necessary to evaluate ecosystem functioning and determine ecosystem health (Rapport et al. 1998). Measures of primary producer biomass, including chlorophyll *a* (Chl *a*) concentrations in lakes, are commonly used in studies of ecosystem functioning (Balvanera et al. 2006). Moreover, Chl *a* and TP concentrations have been used throughout the world to understand and classify freshwater ecosystems (Carlson 1977). Early studies of Chl *a*–TP relationships in lakes worldwide showed that Chl *a* concentrations increased as a log-linear function of increasing TP concentrations (Dillon and Rigler 1974; Jones and Bachmann 1976). These relationships suggest that phosphorus limits primary production in most lakes, which has become a long-standing paradigm in limnology (but see Sterner 2008).

Chl *a*–TP relationships have been used worldwide as the empirical basis for managing cultural eutrophication of lakes by reducing TP inputs (Schindler 2012). Predictive models of the Chl *a* response to TP are often used to estimate the target TP concentration that would be required to achieve healthy aquatic ecosystems. For example, the Dillon and Rigler (1974) model, which relates log-transformed average summer Chl *a* concentration to log-transformed average spring TP concentration using data from multiple lakes, is the prototype for this

approach; many analogous models have subsequently followed. Regardless of the details of the specific model, the U.S. Environmental Protection Agency (2010) and other agencies worldwide have endorsed the general strategy of stressor-response modeling to develop nutrient and restoration standards.

There are two important potential sources of error in developing and applying Chl *a*–TP models. For log-linear models, it is assumed that Chl *a* concentrations will respond to TP as a constant power function; however, the log-linear model may be a local approximation that is applicable only over a limited TP concentration range. Several studies have found that sigmoidal models, which have accelerating and decelerating (e.g., asymptotic) phases, best describe Chl *a*–TP relationships (McCauley et al. 1989; Watson et al. 1992). Other factors, such as nitrogen, can account for variation in chlorophyll at higher TP concentrations (Downing and McCauley 1992); consequently, Chl *a* may have asymptotic maximum concentrations relative to TP (McCauley et al. 1989). In these cases, the use of simple log-linear models would overpredict Chl *a* at high TP concentrations. The second source of error in Chl *a*–TP models may occur when data are aggregated at inappropriate spatial extents, such as when data from lakes within and across regions are combined into a single model. Several recent studies have shown that there are differences in Chl *a*–TP relationships across regions (e.g., Soranno et al. 2010). Therefore, accurate application of

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this fundamental limnological relationship may require both model form and spatial specificity.

Numerous factors, including physical processes (Mazumder 1994), zooplankton community composition (Kamarainen et al. 2008), and nitrogen concentrations or nitrogen-to-phosphorus (N:P) ratios (Smith 1982; McCauley et al. 1989), have been hypothesized to influence Chl *a*-TP relationships. Wagner et al. (2011) demonstrated that log-linear Chl *a*-TP relationships differed among regions with regional differences in model parameters being related to regional land use and land cover (LULC). No studies have compared linear vs. nonlinear model formulations across regions explicitly, however, or have examined potential links to regional LULC variables.

In this study, we used a nutrient database from many lakes across diverse regions to investigate regional variability in the shapes of Chl *a*-TP relationships. Our aims were to (1) determine if nonlinear models fit Chl *a*-TP relationships better than linear models, (2) quantify regional variability in the parameters of Chl *a*-TP relationships, and (3) identify LULC characteristics related to any interregional variability.

Methods

Dataset description—The lake nutrient dataset analyzed for this study included Chl *a* and TP concentrations from 2105 lakes across six northeastern and midwestern states in the United States: Iowa, Maine, Michigan, New Hampshire, Ohio, and Wisconsin (Fig. 1A; Cheruvilil et al. 2013a). Data were from surface mixed layer samples collected during summer thermal stratification from unique lakes (i.e., each lake is included only once). Lakes with surface areas of < 0.01 km² or depths of < 2 m were excluded from analyses.

Regional mean Chl *a* and TP concentrations (both in $\mu\text{g L}^{-1}$) were calculated for each of the 35 Ecological Drainage Units (EDUs) contained within the study extent (Table 1; Fig. 1A). We obtained LULC data from the 1992 National Land Cover Dataset (<http://landcover.usgs.gov/natlcover.php>). LULC proportions were determined for each of the 35 regions as described by Wagner et al. (2011). We quantified regional LULC for pastures, urban, and forested wetlands. EDUs were selected as a regionalization framework based on Cheruvilil et al. (2013b), who quantitatively compared seven different frameworks for grouping lakes using water chemistry data from this study area. They found that EDUs were one of three frameworks that most effectively grouped lakes for lake alkalinity and TP. EDUs are watershed-based units that share common physiography, climate, and connectivity (Higgins et al. 2005).

Model-free approximation of relationship form—To visualize regional variability and nonlinearity of Chl *a*-TP relationships, we used locally weighted scatterplot smoothing (LOWESS) on the entire dataset and for each region containing at least 10 lakes ($n = 25$ regions). LOWESS allows underlying trends in datasets to be discerned without model bias (Cleveland and McGill

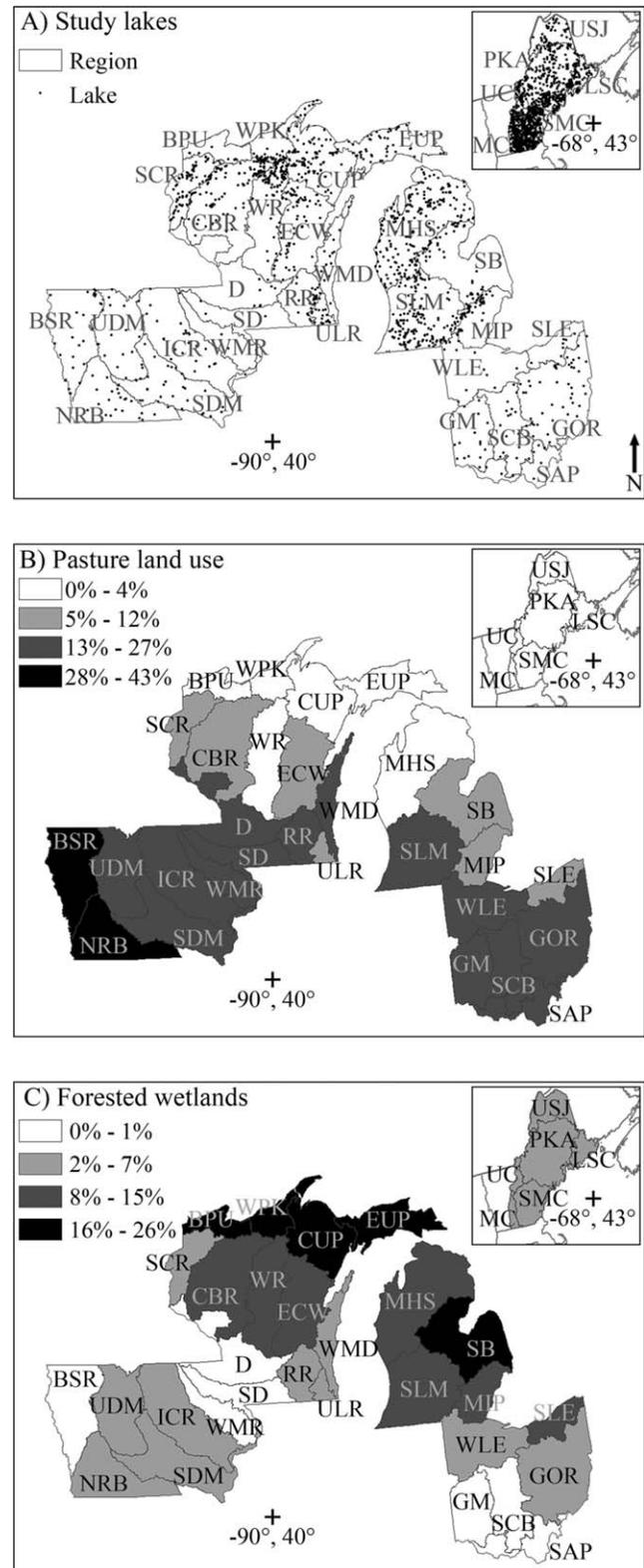


Fig. 1. Map of study area indicating (A) location of lakes (points) and regions (gray boundaries) included in this study, (B) percent pasture land use by region, and (C) percent forested wetlands land cover by region.

Table 1. Region names corresponding to labels in Fig. 1.

Label	Region name
BPU	Bayfield Peninsula and Uplands
BSR	Big Sioux River
CBR	Chippewa–Black River
CUP	Central Upper Peninsula
D	Driftless
ECW	East Central Wisconsin
EUP	East Upper Peninsula
GM	Great Miami–Little Miami
GOR	Glaciated Ohio River Tributaries
ICR	Iowa–Cedar Rivers
LSC	Lower St. Croix–Downeast Maine Coastal
MC	Middle Connecticut
MHS	North Lake Michigan–Lake Huron–Straits of Mackinac
MIP	Southeast Michigan Interlobate and Lake Plain
NRB	Nishnabotna River Basin
PKA	Penobscot–Kennebec–Androscoggin
RR	Rock River
SAP	Southern Alleghany Plateau
SB	Saginaw Bay
SCB	Scioto Basin
SCR	St. Croix River
SD	Southern Driftless
SDM	Skunk–Des Moines–Mississippi
SLE	Southern Lake Erie
SLM	Southeast Lake Michigan
SMC	Saco–Merrimack–Charles
UC	Upper Connecticut
UDM	Upper Des Moines River
ULR	Upper Illinois River
USJ	Upper St. John–Aroostook
WLE	Western Lake Erie
WMD	Western Lake Michigan–Door Peninsula
WMR	Wapsipinicon–Maquoketa Rivers
WPK	Western Upper Peninsula–Keweenaw Peninsula
WR	Wisconsin River

1985). The f -parameter, which is used to determine the degree of smoothing, was allowed to vary ($f = 0.2, 0.5$, or 0.8) depending on the number of lakes considered in each analysis (i.e., regions with many lakes used a smaller f -value). Data were \log_{10} -transformed to decrease heteroscedasticity and to more closely meet the assumption of model error normality. Visual inspection of plots of model residuals vs. predicted values and a histogram of residuals indicated that these assumptions were reasonable. Data visualizations were performed using SigmaPlot 10.0 (SyStat Software Inc. 2006).

Candidate models—We compared two four-parameter (4P) sigmoidal models (the 4P logistic and 4P Gompertz models) to the log-linear model to determine if nonlinear models of \log_{10} -transformed variables better describe Chl a –TP relationships than a log-linear model. We tested these two commonly used sigmoidal models to determine if different formulations of sigmoidal models consistently outperformed the linear model (Zeide 1993), assuming that they would outperform the linear model, and to test several possible shapes for describing Chl a –TP relationships. For example, the inflection point of the logistic model occurs at

the midpoint between the upper and lower asymptotes, whereas the inflection point of the Gompertz model occurs at $\sim 1/3$ of the distance to the upper asymptote (Zeide 1993). Consequently, the Gompertz model outperforms the logistic model when the inflection point occurs earlier in the curve. Sigmoidal model equations were as follows:

4P logistic model:

$$\text{Chl}_{ij} = D_i + \frac{A_i - D_i}{1 + \exp(-C_i(\text{TP}_{ij} - B_i))} + \varepsilon_{ij} \quad (1)$$

4P Gompertz model:

$$\text{Chl}_{ij} = D_i + A_i \left(\exp \left(- \exp \left(- \frac{(\text{TP}_{ij} - B_i)}{C_i} \right) \right) \right) + \varepsilon_{ij} \quad (2)$$

where $\text{Chl}_{ij} = \log_{10}$ Chl a concentration for lake j in region i , $\text{TP}_{ij} = \text{TP}$ concentration for lake j in region i , $A_i =$ upper asymptote of Chl a concentration (i.e., Chl a at infinite TP) in region i , $B_i =$ model inflection point (i.e., where the curve changes from an accelerating increase to a decelerating increase) in region i , $C_i =$ rate of increase (i.e., steepness of curve) in region i , and $D_i =$ lower asymptote of Chl a concentration (i.e., Chl a at $0 \mu\text{g L}^{-1}$ TP) in region i .

Model fitting and selection—All models were estimated using the same lake nutrient dataset with \log_{10} -transformed Chl a ($\mu\text{g L}^{-1}$) as the response variable and grand-mean centered \log_{10} -transformed TP concentrations ($\mu\text{g L}^{-1}$) as the predictor variable. Our Bayesian hierarchical modeling approach used a varying parameter model in which all parameters were allowed to vary across regions. This approach is similar to that used in Wagner et al. (2011) except that we used a nonlinear model with four varying parameters in addition to the linear model with two varying parameters (i.e., slope and intercept). The general form of the nonlinear hierarchical model, using the 4P logistic model (Eq. 1) as an example, was as follows:

$$\varepsilon_{ij} \sim N(0, \sigma^2) \quad (3)$$

$$\begin{pmatrix} A_i \\ B_i \\ C_i \\ D_i \end{pmatrix} \sim MVN(\mu, \Sigma) \quad (4)$$

$$\mu = (\bar{A}, \bar{B}, \bar{C}, \bar{D}) \quad (5)$$

where A_i, B_i, C_i , and D_i are as described above and μ and $\Sigma =$ population mean and population variance-covariance matrix, respectively. Prior probability distributions for σ, μ , and Σ were noninformative (i.e., not based on preexisting information); we used a uniform prior for σ , diffuse normal priors for μ , and modeled Σ using the scaled inverse-Wishart distribution (Gelman and Hill 2007). The program Just Another Gibbs Sampler (JAGS) was used for all analyses (Plummer 2012). Three parallel chains were run with different initial values to generate 670,000 samples

Table 2. Summary of average water chemistry and land use and land cover by region. The regions that had the minimum and maximum values are displayed in parentheses and correspond to the regions displayed in Fig. 1 and Table 1.

Variable	Median	Minimum (region)	Maximum (region)
Water chemistry			
Chlorophyll ($\mu\text{g L}^{-1}$)	11.9	3.5 (LSC)	69.4 (SLE)
Total phosphorus ($\mu\text{g L}^{-1}$)	27.5	7.6 (LSC)	168.1 (WMR)
Land use and land cover			
Pastures (% area)	12.3	0.2 (LSC)	43.2 (NRB)
Forested wetlands (% area)	4.3	0.2 (SAP)	25.5 (EUP)
Urban (% area)	2.8	< 0.1 (BPU)	21.2 (ULR)

from the posterior distributions for each analysis after discarding the first 60,000 samples. We retained every third sample for a total of 70,002 samples. We examined the scale reduction factor (\hat{R}), a convergence statistic, for each parameter, trace plots, and plots of posterior distributions to assess convergence.

We compared a measure of fit from the three candidate models to identify which model best described Chl *a*-TP relationships. We used the deviance information criterion (DIC; Spiegelhalter et al. 2002) to identify the best-fitting (hereafter, best) model. DIC differences (ΔDIC values) were calculated for model *i* as $\Delta\text{DIC}_i = \text{DIC}_i - \text{DIC}_{\min}$, where DIC_{\min} was the smallest DIC value in the model set. Generally, a ΔDIC from 5 to 10 indicates that the model with the smaller DIC is better (Spiegelhalter et al. 2002). DIC calculations require knowledge of the effective number of parameters estimated in a model. We used Monte Carlo simulations to evaluate the performance of DIC to select among the candidate models that were fit in this study. The general approach consisted of (1) simulating 100 datasets that mimicked the structure of the original data (i.e., multiple lakes within 35 regions) using the 4P logistic model as the data-generating model, (2) fitting each of the three candidate models to each dataset, (3) using DIC to select the best model, and (4) calculating DIC-based model weights that provide the relative likelihood of the model given the data (Burnham and Anderson 2002). This analysis allowed us to evaluate how well DIC performed in choosing the best model given that we know the identity of the model (i.e., 4P logistic model) used to generate the test data.

Model parameter covariation with LULC—We subsequently modeled the varying coefficients of the best model as a function of regional (i.e., EDU-level) percentage pasture land use, percentage urban land use, and percentage forested wetlands. Percentage urban land use and forested wetlands were logit transformed prior to analysis because of their skewed distributions, which were characterized by few regions containing high percentages of these LULCs. To limit the number of covariates explaining regional variability in our analyses, we focused on percentage pasture fields and forested wetlands because they were shown to be important in explaining regional variation in slopes and intercepts from a linear model describing Chl *a*-TP relationships using the same data set (Wagner et al. 2011). We also examined percentage urban land use because urban development influences nutrient ratios of runoff; urban runoff and sewage

discharges characteristically have N : P ratios much less than the Redfield ratio (i.e., N : P < 16 by moles; Downing and McCauley 1992). For the 4P-nonlinear models, this approach included modeling each parameter using combinations of percentage pasture land use, percentage urban land use, and percentage forested wetlands. A model with a covariate (*cov*) on each parameter was as follows:

$$\begin{pmatrix} A_i \\ B_i \\ C_i \\ D_i \end{pmatrix} = \begin{pmatrix} \gamma_{0a} + \gamma_{1a} \times \text{cov}_i \\ \gamma_{0b} + \gamma_{1b} \times \text{cov}_i \\ \gamma_{0c} + \gamma_{1c} \times \text{cov}_i \\ \gamma_{0d} + \gamma_{1d} \times \text{cov}_i \end{pmatrix} \quad (6)$$

where A_i , B_i , C_i , and D_i are as described above and γ_{0x} and γ_{1x} are the fixed intercept and slope describing the relationship between parameter *x* and an EDU-level covariate (*cov*). The candidate set consisted of models that contained only a single predictor variable on each of the four parameters, which resulted in four models being fit for each covariate (e.g., four models were fit for percentage pasture land use with one model for each of parameter A_i , B_i , C_i , and D_i). After fitting the single covariate models and based on the DIC and estimated parameters and associated uncertainty estimates, combinations of different LULC covariates were combined to evaluate more complex models. The resulting 15 candidate models were evaluated using DIC and ΔDIC .

Results

Dataset description—Regions in this study differed in both water quality and LULC. Regional mean Chl *a* and TP concentrations varied by greater than one order of magnitude (3.5–69.4 $\mu\text{g L}^{-1}$ and 7.6–168.1 $\mu\text{g L}^{-1}$, respectively; Table 2). Regional pasture land use varied from 0% to 43% (Table 2) and tended to be greatest for regions within the midwestern states of Iowa, Ohio, and Wisconsin (Fig. 1B). Regional forested wetlands land cover varied from 0% to 26% (Table 2) and were most dense in regions within the state of Michigan, especially in the Upper Peninsula (Fig. 1C). Regional urban land use varied from 0% to 21% (Table 2).

Model-free approximation of relationship form—LOW-ESS fits for the entire dataset and by region suggested that Chl *a*-TP relationships were nonlinear across all regions and

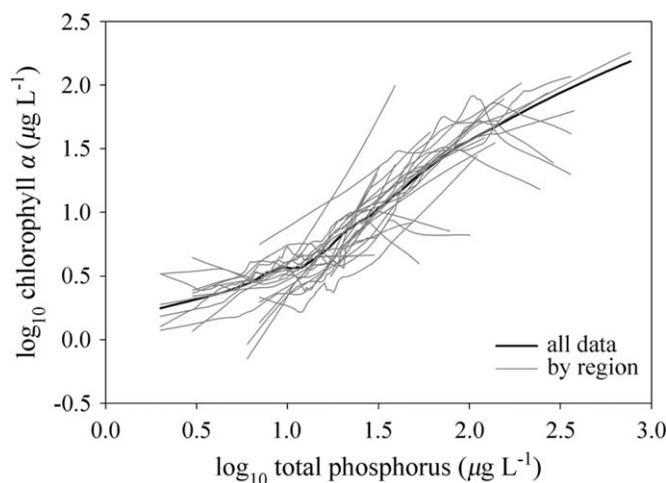


Fig. 2. Fits of Chl *a*–TP relationships for the entire dataset and for individual regions using LOWESS, a locally weighted regression technique. The *f*-parameter, which is used to determine the amount of smoothing, was allowed to vary (*f* = 0.2, 0.5, or 0.8) depending on the number of lakes considered in each analysis.

within individual regions, respectively. Although LOWESS fits indicated that Chl *a*–TP relationships varied widely among regions, these fits were generally nonlinear and more closely resembled sigmoidal models (Fig. 2). Chl *a* concentrations increased minimally with increased TP concentrations below $10 \mu\text{g L}^{-1}$ for LOWESS fits to the entire dataset and within most regions with low TP concentration ranges. Regions with TP concentrations above $10 \mu\text{g L}^{-1}$ typically displayed greater increases in Chl *a* concentrations per unit increase in TP concentration. Numerous regions displayed decelerating or even slightly decreasing Chl *a*–TP relationships near the upper end of their region-specific TP range, although some regions maintained relatively consistent rates of increase even near their upper TP range.

Model fitting and selection—Deviance information criterion (DIC) values supported our hypothesis that hierarchical nonlinear models better describe Chl *a*–TP relationships compared to a log-linear model. Both nonlinear models performed significantly better than the log-linear model. The 4P logistic model had the lowest DIC value (DIC = 808.9; $\Delta\text{DIC} = 0.0$), followed by the 4P-Gompertz model (DIC = 829.3; $\Delta\text{DIC} = 20.4$) and the log-linear model (DIC = 848.4; $\Delta\text{DIC} = 39.5$). The 4P logistic model was selected as the best model to use in subsequent analyses.

DIC performed well in correctly selecting the model used to generate test data when we tested the accuracy of DIC during Monte Carlo simulations (Fig. 3). The 4P logistic model was correctly selected as the best model in 98% of the simulated datasets, with model weights > 0.97 in 96% of simulated datasets. The 4P-Gompertz model was selected as the best model once. The log-linear model was never selected as the best model, and the largest model weight was very small (< 0.0001). Because DIC correctly selected the data-generating model as the best model in almost all simulated datasets, we are confident in the use of DIC to differentiate between nonlinear and log-linear

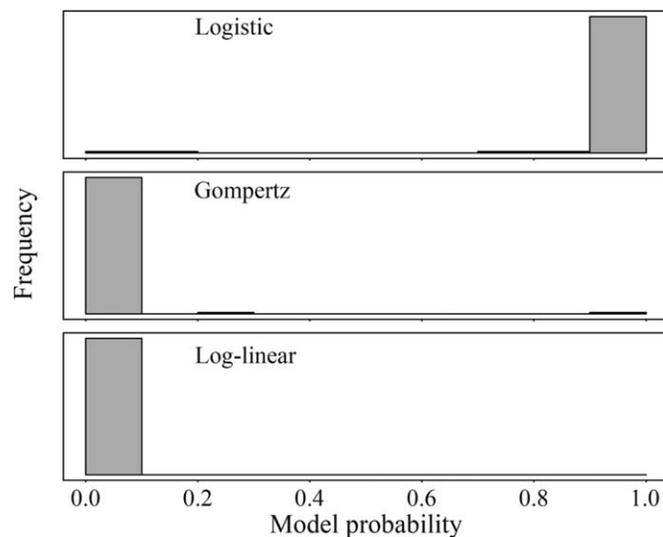


Fig. 3. Histogram of model probabilities from Monte Carlo simulations challenging DIC to select among three candidate models. The 4P logistic model was used to generate the test data. Probabilities near 1 indicate that the model being evaluated is the best fit.

models when selecting for the best model in our observed dataset.

Chl *a*–TP relationships were highly variable among regions, as indicated by differing shapes of the best model for individual regions (Fig. 4). For example, the model for the Saginaw Bay region has a smaller difference in Chl *a* concentrations and flatter shape between the lower and upper asymptotes than the model for the East Central Wisconsin region. Variance in parameter uncertainty by region was likely due, in part, to low numbers of lakes in some regions, while other regions contained lakes with TP concentrations spanning only a portion of the TP range contained in the entire dataset. For example, the East Upper Peninsula region has high uncertainty of Chl *a* concentration predictions at high TP concentrations because the region contained lakes with relatively low TP concentrations.

Regional differences in the shapes of Chl *a*–TP relationships were also reflected in differences in model parameter estimates among regions (Table 3), although each parameter showed relatively unique spatial patterns in parameter estimates and their uncertainty estimates (Fig. 5). Upper asymptote parameter estimates were largest in some of the regions in Iowa, Wisconsin, Ohio, and Maine and were lowest in some of the regions in Michigan (Fig. 5A). The standard deviations of upper asymptote parameter estimates were low in almost all regions in Iowa and some of the regions in Wisconsin and Ohio. The standard deviations were large, however, for regions in Michigan, especially the Upper Peninsula (Fig. 5E), which suggests that these parameter estimates have high uncertainty. Inflection point parameter estimates did not show strong regional patterns in either their values or the standard deviations of these values (Fig. 5B,F). Rate parameter estimates and their standard deviations also did not show strong regional patterns, with both Iowa and

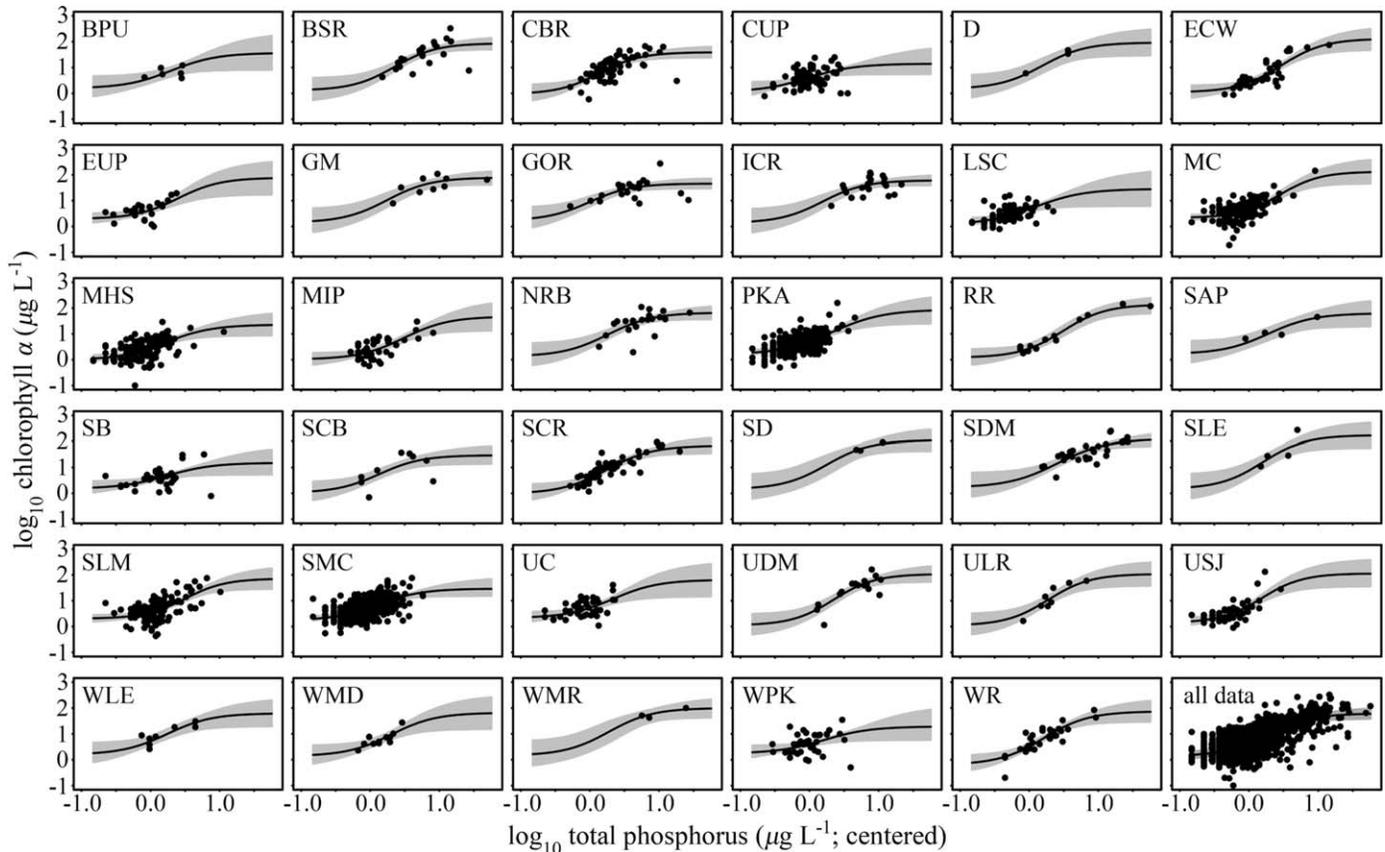


Fig. 4. Regional model fits of a hierarchical logistic model describing Chl *a*-TP relationships. Region names correspond to those presented in Fig. 1 and Table 1. The model fit for all data is shown in lower right panel. Black circles are data points corresponding to individual lakes, solid lines are model fits, and shaded areas are 90% credible regions.

Maine containing regions with both high and low values (Fig. 5C,G). Similarly, lower asymptote parameter estimates generally displayed both high and low values for regions within the same state (Fig. 5D) but were most uncertain in Iowa and Ohio (Fig. 5H). In general, model parameter estimates did not display discernible gradients from east to west across the spatial extent of this study and often displayed both high and low regional mean values within state political boundaries.

Model parameter covariation with LULC—Regional LULC influenced the parameters of sigmoidal Chl *a*-TP relationships across the spatial extent of this study. The best model explaining this regional variability included modeling the lower and upper asymptote parameters as functions of the regional percentage of pasture fields and the rate parameter as a function of the regional percentage of forested wetlands (Table 4). Urban land use was not as important as pastures or wetlands in explaining regional variability in Chl *a*-TP relationships. Similarly, no LULC class was useful in explaining regional variability in the inflection point parameter. There was some support for a model that included only the relationship between regional percentage of forested wetlands and the rate parameter ($\Delta\text{DIC} = 4.4$), indicating some model selection uncertainty (Table 4). Because the effect of wetlands on the rate

parameter in this model was of similar magnitude and direction to the best model, we focus the rest of our results and discussion on the best model.

There was a positive relationship between the regional percentage of pasture land use and the upper Chl *a* asymptote parameter, whereas negative relationships existed between the regional percentage of pasture land use and the lower Chl *a* asymptote parameter and between the regional percentage of forested wetlands and the rate parameter (Fig. 6; Table 5). The positive influence of pastures on the upper asymptote parameter had the largest effect size of any LULC class on model parameters with the highest probability that the direction of this relationship was in the direction of the estimated posterior mean (Table 5). Although the effects of pasture land use on the lower asymptote parameter and forested wetlands on the rate parameter were more uncertain, as indicated by confidence intervals on effect sizes (overlapping zero), there was a 74% and 85% probability that these two LULC classes had negative effects on the lower asymptote and rate parameters, respectively (Table 5).

Discussion

Our findings are consistent with previous studies that Chl *a*-TP relationships are better described by nonlinear

Table 3. Posterior means and 95% credible intervals (CRI; analogous to confidence intervals in frequentist statistics) for estimated parameters from the 4P logistic model (Eq. 1) describing relationships between \log_{10} total phosphorus and \log_{10} Chl *a* by region (Fig. 1 and Table 1) and for the entire dataset. UA = upper asymptote, I = inflection point, R = rate, LA = lower asymptote.

Region name	UA	I	R	LA
	Mean (95% CRI)	Mean (95% CRI)	Mean (95% CRI)	Mean (95% CRI)
BPU	1.56 (0.84, 2.57)	0.30 (−0.40, 0.94)	3.00 (1.30, 4.71)	0.19 (−0.50, 0.72)
BSR	1.94 (1.67, 2.30)	0.35 (0.07, 0.64)	3.26 (2.03, 4.68)	0.11 (−0.50, 0.67)
CBR	1.59 (1.36, 1.90)	0.14 (−0.09, 0.36)	3.35 (2.16, 4.68)	−0.03 (−0.57, 0.38)
CUP	1.15 (0.71, 2.19)	−0.02 (−0.60, 0.79)	2.91 (1.06, 4.79)	0.05 (−0.59, 0.46)
D	1.97 (1.39, 2.72)	0.19 (−0.27, 0.64)	3.17 (1.79, 4.69)	0.17 (−0.49, 0.77)
ECW	2.12 (1.61, 2.73)	0.47 (0.21, 0.70)	3.19 (2.00, 4.57)	0.04 (−0.41, 0.33)
EUP	1.89 (1.15, 2.75)	0.40 (−0.01, 0.77)	3.24 (1.78, 4.81)	0.29 (−0.07, 0.53)
GM	1.90 (1.59, 2.31)	0.25 (−0.17, 0.63)	3.14 (1.76, 4.58)	0.15 (−0.51, 0.77)
GOR	1.66 (1.45, 1.96)	−0.01 (−0.40, 0.38)	3.25 (1.92, 4.72)	0.23 (−0.43, 0.82)
ICR	1.79 (1.58, 2.11)	0.19 (−0.20, 0.52)	3.23 (1.87, 4.70)	0.14 (−0.52, 0.75)
LSC	1.46 (0.74, 2.47)	0.09 (−0.53, 0.65)	2.79 (1.26, 4.46)	0.07 (−0.45, 0.34)
MC	2.12 (1.60, 2.79)	0.45 (0.25, 0.69)	3.45 (2.30, 4.83)	0.34 (0.16, 0.47)
MHS	1.36 (0.89, 2.10)	0.22 (−0.10, 0.60)	2.96 (1.48, 4.50)	−0.01 (−0.38, 0.18)
MIP	1.67 (1.06, 2.54)	0.49 (0.09, 0.88)	3.07 (1.73, 4.49)	0.01 (−0.48, 0.29)
NRB	1.82 (1.54, 2.29)	0.26 (−0.09, 0.65)	3.05 (1.70, 4.45)	0.13 (−0.53, 0.70)
PKA	1.94 (1.33, 2.76)	0.33 (0.00, 0.65)	2.67 (1.48, 3.91)	0.20 (−0.18, 0.38)
RR	2.14 (1.75, 2.58)	0.49 (0.21, 0.76)	3.21 (1.99, 4.61)	0.08 (−0.43, 0.45)
SAP	1.80 (1.22, 2.56)	0.29 (−0.26, 0.85)	3.03 (1.51, 4.60)	0.22 (−0.45, 0.79)
SB	1.18 (0.68, 2.08)	0.24 (−0.45, 0.94)	2.98 (1.03, 4.78)	0.18 (−0.44, 0.51)
SCB	1.48 (1.09, 2.04)	0.13 (−0.23, 0.54)	3.23 (1.72, 4.8)	0.02 (−0.57, 0.50)
SCR	1.84 (1.51, 2.33)	0.24 (−0.02, 0.53)	3.02 (1.88, 4.28)	−0.02 (−0.58, 0.38)
SD	2.04 (1.58, 2.69)	0.25 (−0.27, 0.71)	3.17 (1.80, 4.68)	0.16 (−0.52, 0.82)
SDM	2.09 (1.79, 2.61)	0.41 (0.05, 0.85)	2.81 (1.49, 4.20)	0.23 (−0.48, 0.89)
SLE	2.23 (1.68, 2.93)	0.20 (−0.20, 0.58)	3.24 (1.90, 4.73)	0.17 (−0.53, 0.83)
SLM	1.86 (1.41, 2.49)	0.50 (0.28, 0.76)	3.41 (2.21, 4.89)	0.31 (0.08, 0.46)
SMC	1.47 (1.15, 2.06)	0.11 (−0.09, 0.40)	3.10 (1.74, 4.60)	0.23 (−0.04, 0.39)
UC	1.81 (1.08, 2.72)	0.34 (−0.20, 0.76)	3.04 (1.53, 4.61)	0.33 (−0.15, 0.59)
UDM	2.03 (1.70, 2.54)	0.35 (0.09, 0.63)	3.31 (2.07, 4.81)	0.05 (−0.55, 0.55)
ULR	2.04 (1.51, 2.68)	0.28 (−0.03, 0.60)	3.27 (2.02, 4.69)	0.04 (−0.58, 0.56)
USJ	2.06 (1.48, 2.76)	0.19 (−0.04, 0.43)	3.40 (2.14, 4.92)	0.14 (−0.17, 0.36)
WLE	1.80 (1.23, 2.57)	0.24 (−0.22, 0.74)	3.07 (1.66, 4.57)	0.20 (−0.46, 0.71)
WMD	1.82 (1.10, 2.68)	0.31 (−0.18, 0.75)	3.10 (1.67, 4.59)	0.14 (−0.47, 0.60)
WMR	2.00 (1.58, 2.55)	0.27 (−0.25, 0.75)	3.13 (1.74, 4.61)	0.16 (−0.53, 0.81)
WPK	1.29 (0.72, 2.33)	0.21 (−0.54, 0.99)	2.96 (1.01, 4.82)	0.24 (−0.45, 0.57)
WR	1.87 (1.41, 2.51)	0.21 (−0.06, 0.51)	3.06 (1.95, 4.33)	−0.20 (−0.73, 0.20)
All data	1.79 (1.55, 2.08)	0.27 (0.11, 0.42)	3.12 (2.30, 4.00)	0.13 (−0.10, 0.33)

and sigmoidal models than log-linear models (McCauley et al. 1989; Watson et al. 1992). The sigmoidal shape suggests that there are three phases to fertilization response in lakes: an initial lag phase, an acceleration phase, and a deceleration phase (Fig. 4). During the initial lag phase, Chl *a* concentrations increase only slightly in response to increasing TP concentrations, suggesting a minimum TP concentration threshold that must be crossed before a noticeable increase in phytoplankton biomass is observed. Although initial increases in TP were not related to phytoplankton biomass increases in the pelagic zone, TP may have initially stimulated growth of benthic algae, which typically respond to environmental stressors more rapidly than pelagic phytoplankton (Lambert et al. 2008). Above this critical TP concentration, Chl *a* concentrations increase more rapidly with increasing TP concentrations. During the deceleration phase, Chl *a* concentrations increase more slowly with increasing TP concentrations and approach upper maximum Chl *a* concentrations. This limit to maximum phytoplankton biomass in regions

suggests that other factors became limiting at high TP concentrations (e.g., light and nitrogen), supporting the findings of McCauley et al. (1989).

Assuming that the empirical correlation between Chl *a* and TP is a causal relationship, this sigmoidal relationship suggests that management decisions based on log-linear models may be inaccurate because the degree of Chl *a* response to TP depends on TP concentration. Our analysis suggests that the development of management strategies to accurately produce achievable restoration targets may be more useful if lake managers consider the phase of Chl *a*–TP relationships. For example, large TP reductions will be required to achieve noticeable decreases in Chl *a* concentrations if TP concentrations in the lake are at the high end of the deceleration phase. Contrastingly, TP reductions are predicted to produce relatively large decreases in Chl *a* concentrations if the lake is in the acceleration phase. Smith and Shapiro (1981) concluded that the failure of measured TP reductions to produce decreases in Chl *a* concentrations in a previous study may have resulted from the curvilinearity

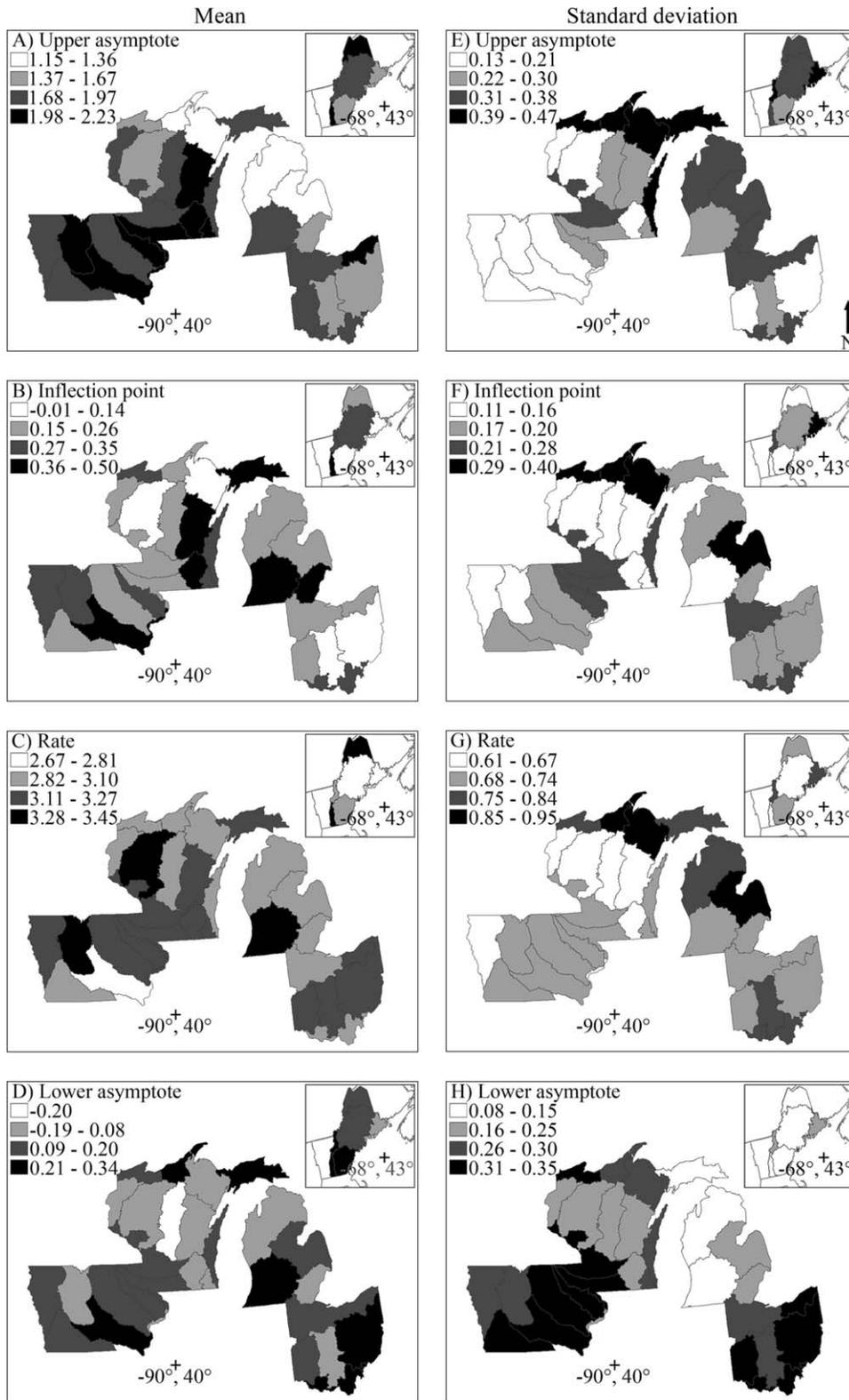


Fig. 5. (A–D) Map of the mean and (E–H) standard deviation of the posterior distribution of model parameters by region for the best 4P hierarchical logistic model describing Chl *a*–TP relationships. Region names correspond to those presented in Fig. 1 and Table 1.

Table 4. Candidate models for modeling variation in region-specific parameters from a 4P hierarchical logistic model describing the relationship between \log_{10} total phosphorus and \log_{10} Chl *a* among regions. DIC = deviance information criterion. Models are listed from lowest-to-highest DIC. Covariates (land use and land cover measured as percentages) included in the model are shown with the model parameter being modeled in parentheses (UA = upper asymptote, LA = lower asymptote, R = rate, and I = inflection point). Δ DIC = DIC differences and were calculated for model *i* as Δ DIC_{*i*} = DIC_{*i*} – DIC_{min}, where DIC_{min} was the smallest DIC value in the model set. nc = model did not converge.

Model no.	Candidate model	DIC	Δ DIC
1	Pastures (UA), pastures (LA), wetlands (R)	797.7	0
2	Wetlands (R)	802.1	4.4
3	Pastures (UA), urban (LA), wetlands (R)	803.5	5.8
4	Pastures (UA)	803.6	5.9
5	Pastures (R)	804.1	6.4
6	Urban (LA)	806.4	8.7
7	Urban (UA)	808.2	10.5
8	Pastures (LA)	808.5	10.8
9	Pastures (I)	810.4	12.7
10	Wetlands (LA)	810.6	12.9
11	Wetlands (UA)	811.0	13.3
12	Wetlands (I)	818.2	20.5
13	Pastures (UA), wetlands (R)	nc	nc
14	Urban (R)	nc	nc
15	Urban (I)	nc	nc

of Chl *a*–TP predictive models. Our findings support this conclusion and argue for applying the best available predictive model to develop effective management strategies.

Although nonlinear models best described regional Chl *a*–TP relationships, the shapes of these relationships varied considerably among regions, as reflected in regional variability in model parameter estimates across the study extent (Figs. 4, 5). These findings support the conclusions of Wagner et al. (2011), who used a similar hierarchical modeling approach to characterize regional variability in slope and intercept parameters for log-linear models of Chl *a*–TP relationships. Because Chl *a*–TP relationships vary among regions, accurate management strategies may require models developed at the appropriate regional scale rather than at the whole-state or large-jurisdiction scale. For example, regions with greater upper asymptote parameter estimates (cf. Rock River region vs. Saginaw Bay region; Fig. 4) are likely to contain lakes with higher maximum phytoplankton biomass concentrations than lakes in other regions. Lakes in regions with greater rate parameter values (cf. Upper Des Moines River region vs. West Upper Peninsula–Keweenaw Peninsula; Fig. 4) are likely to have greater proportional increases of phytoplankton biomass relative to increasing TP than other regions. These sensitive regions will likely display noticeable increases in phytoplankton biomass for small increases in TP. As a result, region-specific management strategies and restoration targets may be more effective for managing lakes compared to those at larger scales. The “one-size-fits-all” approach to lake management at the state or national

level would be ineffective, especially in states or countries with highly variable regions, as has been recognized for some states in setting nutrient standards (Heiskary and Wilson 2008; Soranno et al. 2008).

The Bayesian hierarchical modeling approach enabled us to estimate region-specific parameters for the best model, although data for individual regions may not fully describe a sigmoid shape. This capability, referred to as “partial pooling,” uses a common prior distribution on model parameter estimates to effectively provide a loose constraint that allows regions to share information without forcing parameter estimates to be identical (Gelman and Hill 2007). In contrast, “full pooling,” which has been commonly used in previous approaches (Dillon and Rigler 1974), would estimate regional model parameters under the assumption that lakes in all regions behave identically (i.e., model parameter estimates would be identical for all regions). It would have been difficult to estimate region-specific model parameters if we had used data from individual regions separately (i.e., “no pooling”) because wide ranges of Chl *a* and TP concentrations are required to reveal the shapes of sigmoidal relationships. Partial pooling is a reasonable compromise that enabled us to estimate model parameters for individual regions under the assumption that regions exhibit common but not identical behaviors. Although imposing an assumption of sigmoidal relationships in regions with limited data carries some risk, model uncertainties partly compensate for this by being relatively high where they are outside of the data range for that region (e.g., region the East Upper Peninsula region in Fig. 4).

Regional LULC was related to the region-specific model parameter estimates describing Chl *a*–TP relationships. During the deceleration phase, regions with greater pasture land use had greater maximum phytoplankton biomass concentrations at high TP concentrations (i.e., greater upper asymptote values; Fig. 6A). In agricultural regions, pasture runoff may supply phosphorus in a more bioavailable form to lakes than is supplied by other LULCs. Sharpley et al. (2004) found that 49–80% of soil TP was inorganic in manure-treated soils vs. 26–57% in untreated soils. Similarly, He et al. (2004) demonstrated that water-extractable P, which is immediately bioavailable, accounted for the largest fraction of TP in dairy manure with inorganic and organic P accounting for 12–44% and 2–23% of manure TP, respectively. Water-extractable P has been shown to be a good indicator of potential P loss during runoff events (Kleinman et al. 2002). As a result, TP can be more effectively assimilated into phytoplankton biomass in regions with more pasturelands, resulting in greater Chl *a* concentrations for similar TP concentrations. In regions with less pasturelands, TP may consist of greater percentages of biologically unavailable fractions (e.g., phosphate bound to clay particles) or fractions that require additional processing before assimilation (e.g., recalcitrant organic phosphorus fractions).

Interestingly, pasture land use had a negative effect on the initial lag phase (i.e., lower asymptote) of Chl *a*–TP relationships in contrast to the positive relationship with the deceleration phase (Fig. 6B). This finding suggests that

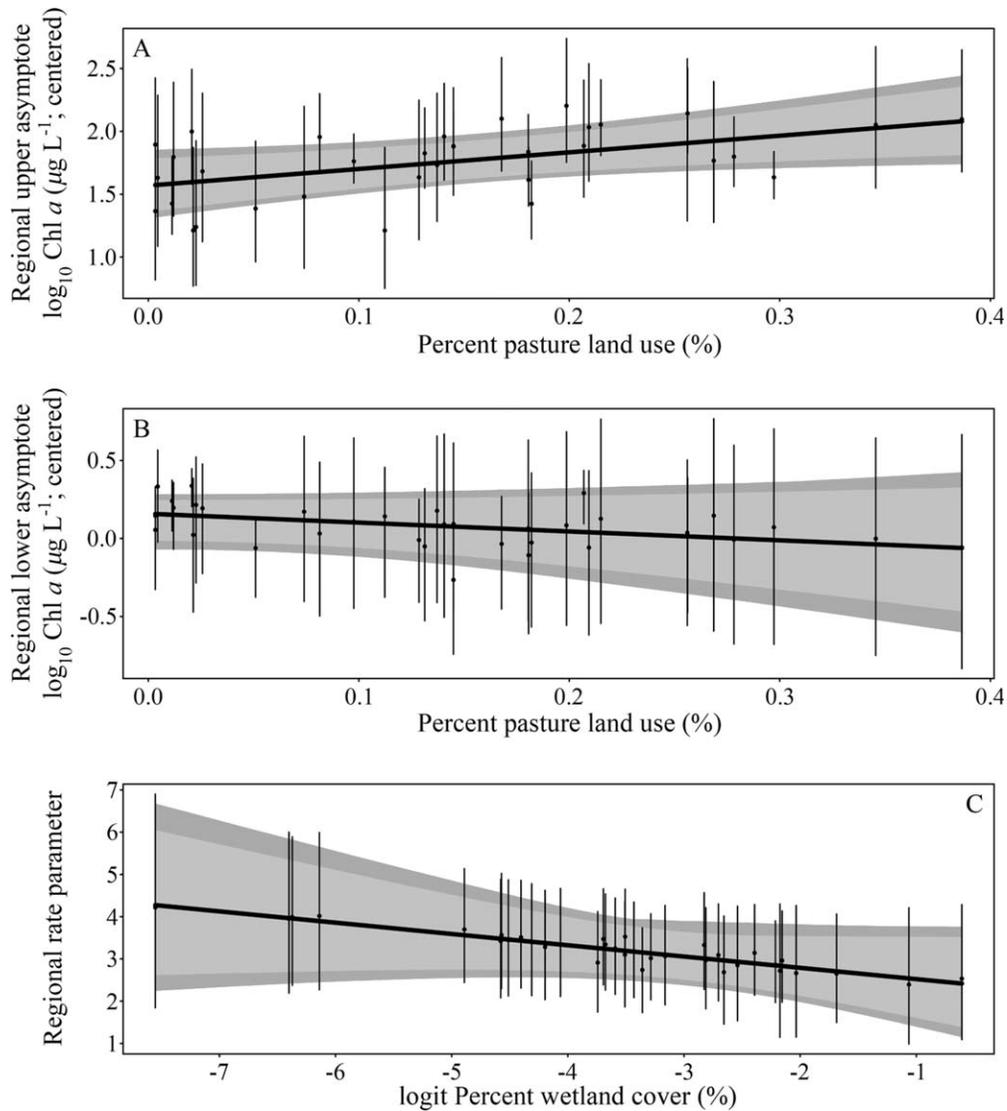


Fig. 6. Relationships between regional parameters from a 4P hierarchical logistic model describing Chl *a*–TP relationships and land use and land cover for (A) the upper asymptote of \log_{10} Chl *a* vs. region percentage pasture land use, (B) the lower asymptote of \log_{10} Chl *a* vs. region percentage pasture land use, and (C) the rate parameter vs. region percentage forested wetlands (logit transformed). Points are estimated posterior means, and vertical lines are 90% credible intervals (analogous to confidence intervals in frequentist statistics). Solid line is estimated hierarchical regression line, and light and dark shaded areas are 80% and 90% credible regions, respectively.

Table 5. Summary of the effects of regional covariates on region-specific parameters from the best model (4P logistic model) describing the relationship between \log_{10} total phosphorus and \log_{10} Chl *a* among regions. Covariates (land use and land cover measured as percentages) included in the model are shown with the model parameter being modeled in parentheses (UA = upper asymptote, LA = lower asymptote, R = rate), posterior means, 90% credible intervals (CRI; analogous to confidence intervals in frequentist statistics), and the probability that the effect is the direction of the estimated posterior mean (positive or negative; Pr[direction of posterior mean]).

Regional predictor	Posterior mean (effect size)	90% CRI (lower, upper)	Pr (direction of posterior mean)
Pastures (UA)	1.32	0.0894, 2.539	0.96
Pastures (LA)	−0.538	−1.99, 0.861	0.74
Wetlands (R)	−0.282	−0.736, 0.148	0.85

mechanisms by which pastures affect Chl *a*–TP relationships may differ depending on the amount of TP in the region. Pasturelands can have complex effects on phytoplankton by creating light deficiency through increased turbidity while concurrently contributing large loads of bioavailable P (North et al. 2013). At low TP concentrations, pastures may have a larger effect on underwater light climate (i.e., increased erosion of soils and particulate organic matter leading to increased turbidity), which masks additional TP concentrations contributed by surface runoff. Agricultural regions, including those with substantial pasturelands, may contribute greater sediment loads to streams both during low-flow conditions and during storm events (Allan et al. 1997), suggesting that the potential for light limitation increases in these regions (Julian et al. 2008). However, our findings showed that regional pasture land use

had a stronger statistical effect on the upper asymptote parameter than the lower asymptote parameter (Table 4).

Alternatively, correlations between pasture land use and model parameter estimates may be indicative of different underlying stressor-response mechanisms in different regions. These relationships may be not directly attributed to changes in the percentage of pasturelands among regions but, rather, indirectly to how changes in percentage of pasturelands affect other LULCs in diverse regions. For example, in the state of Iowa, where 90% of the total land area is under some form of agricultural land use (Arbuckle and Downing 2001), regions with more pasturelands may be expected to have better water quality than surrounding regions with less pasturelands that are subjected to increased row-crop agriculture and chemical P fertilizer applications. In the states of Maine and New Hampshire, which contain the six most heavily forested regions in this study, regions with more pasturelands may be expected to have poorer water quality than surrounding regions with greater percentages of nonagricultural LULCs. Therefore, pasturelands may be expected to have different effects on water quality depending on the dominant LULCs in the region.

Regional wetland land cover had an overall negative relationship with the rate parameter characterizing the acceleration phase (Fig. 6C), suggesting that wetlands mediate the influence of nutrients on phytoplankton growth and thus may play a role in improving regional water quality. Wetlands can influence the proportional increase in Chl *a* relative to TP concentrations through a variety of potential mechanisms. Previous studies have demonstrated the phosphorus removal capabilities of wetlands (Kynkääniemi et al. 2013). The P-removal capacity of wetlands is finite, however, resulting in substantial export of TP when the sediments become P saturated (Richardson 1985). Wetlands also play major roles in nutrient transformations (i.e., mineralization and assimilation) among different forms of P. The composition of the organic P fraction is important in determining the bioavailability of P in wetlands and depends on soil type, allochthonous organic matter sources, and deposition of detritus (Reddy et al. 1999). If wetlands were exporting large percentages of recalcitrant P, such as humic acids that can make up large fractions of wetlands soils (Bridgman et al. 1998), then a smaller percentage of TP would be available for assimilation into phytoplankton biomass once it reached the lake basin. Phytic acids, which have low bioavailability to terrestrial plants because plants have limited abilities to produce phytase (Unno and Shinano 2013), may also contribute large fractions of organic phosphorus in these regions. Phytic acids are also likely of low bioavailability to phytoplankton.

Alternatively, wetlands may influence the acceleration phase of Chl *a*–TP relationships by modifying the underwater light climate of lakes. At both the lake (Gergel et al. 1999) and regional (Fergus et al. 2011) scales, lake colored dissolved organic carbon (CDOC) is positively related to neighboring wetlands. Wetland-derived CDOD, in turn, affects Chl *a*–TP relationships in lakes by increasing the chlorophyll to TP ratio (Webster et al. 2008), although chlorophyll:TP ratios can be negatively affected by color in mixed lakes (Havens and Nurnberg

2004). Humic color limits light availability throughout the water column, resulting in photosynthesis being restricted to near the lake surface (Christensen et al. 1995). Phytoplankton can physiologically adapt to low-light climates by increasing cellular Chl *a* content (Foy 1987). If regions with greater wetland cover contain large numbers of humic lakes, lakes with low TP concentrations may support higher-than-expected Chl *a* concentrations and therefore result in reduced rates of increase with TP from these elevated baseline concentrations. Experimental manipulation of microcosms suggests that organic matter loading rates may induce large changes in within-lake dynamics, including regime shifts (Sirota et al. 2013).

Although urban land use composed a maximum of 21% of regional LULC (Table 2), it did not explain regional variability in model parameter estimates for the best model (Table 3). Ninety percent credible intervals, which are analogous to confidence intervals in statistics based on the normal distribution, for the effect of urban land use on model parameters for rate, inflection point, and lower and upper asymptotes contained zero (posterior mean and 90% credible interval = 0.39 [−0.16, 0.99], 0.01 [−0.07, 0.09], −0.01 [−0.11, 0.09], and 0.08 [−0.45, 0.22], respectively). Urban land uses are typically characterized by runoff or discharges with very low N:P ratios (< 22 molar ratio), and N limitation occurs more frequently in lakes with low N:P ratios (Smith 1982; Downing and McCauley 1992). Although N limitation would be predicted to decouple Chl *a*–TP relationships, McCauley et al. (1989) showed that TN influenced Chl *a*–TP relationships in lakes, especially in lakes with high TP concentrations. These authors suggested that variation in the TN:TP ratios would determine characteristics of the deceleration phase of Chl *a*–TP relationships. Because urban land uses did not explain regional variability in the upper asymptote parameter in our best model in the current study, this finding suggests that either maximum TP concentrations were not great enough for lakes to develop N limitation or pasture land use had stronger effects on covarying TN and TP concentrations in our study area. Pasturelands typically have very low TN:TP ratios, whereas row-crop agricultural lands have high TN:TP ratios (Arbuckle and Downing 2001), which may help explain why pasture land use better explained regional variability in model parameter estimates than total agricultural land use or row-crop agricultural land use (Wagner et al. 2011).

In conclusion, our findings suggest that Chl *a*–TP relationships are nonlinear in most regions despite diverse landscape characteristics and that these relationships can differ substantially in shape among regions. Both the TP concentration of the ecosystem and the LULC of the region interact to produce complex responses of concentrations of phytoplankton biomass to TP that ultimately affect overall ecosystem functioning in lakes. Our results suggest that management models are most appropriately developed at both the local and the regional scale. Because of regional influences on parameters describing Chl *a*–TP relationships, management activities developed for larger jurisdiction areas, such as states, provinces, or countries, may be flawed unless political units are homogeneous in LULCs.

Coordinating management strategies across regions that cross jurisdictional boundaries may lead to more effective management by government agencies. Although best management practices are implemented at the local scale, information from regional Chl *a*-TP relationships can be used to target LULCs that will provide the maximum return for desired management outcomes.

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