Nutrient–chlorophyll relationships: an evaluation of empirical nutrient–chlorophyll models using Florida and north-temperate lake data[1]

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Abstract: Nutrient–chlorophyll (CHL) relationships were developed using a large data set collected in Florida over the last 10 years consisting of monthly total phosphorus (TP), total nitrogen (TN), and CHL concentrations from 360 lakes. The precision of these and five additional published relationships was examined. The 95% confidence interval for the best available TP–CHL model is 30–325% of the calculated CHL value. Analysis of associated Florida monthly nutrient and CHL data indicate that the TP–CHL relationship is sigmoid, although a linear response is found for TP concentrations in the range of 3–160 $\mu g \cdot L^{-1}$. The maximum CHL responses for a sigmoid curve and straight line are similar for TP concentrations of 3–100 $\mu g \cdot L^{-1}$. Both relationships describe P limitation when the CHL response falls on or near the line and provide a benchmark to evaluate other limiting or colimiting factors that are indicated when the CHL response falls below the line. Florida and global data are similar, exhibiting a lessening of slope above a TP concentration of 100 $\mu g \cdot L^{-1}$. A global median line is derived from a large population of lake data for use in general lake management.

Résumé : Nous avons examiné les relations entre les nutriants et la chlorophylle à partir d'une grande base de données recueillies en Floride depuis 10 ans, représentant les concentrations moyennes de phosphore total (PT), d'azote total (NT) et de chlorophylle (CHL) dans 360 lacs. Nous avons examiné la précision de ces relations et de cinq autres études publiées sur le sujet. L'intervalle de confiance de 95% pour le meilleur modèle PT–CHL correspond à 30% à 325% de la valeur calculée de CHL. L'analyse des données mensuelles associées (pour la Floride) sur les nutriants et la CHL indique que la relation PT–CHL est sigmoïde, tandis qu'on observe une réponse linéaire pour les concentrations de PT dans la fourchette de 3 à 160 $\mu g \cdot L^{-1}$. La réponse maximum de CHL pour la courbe sigmoïde et la ligne droite sont similaires dans la plage de concentration de PT de 3–100 $\mu g \cdot L^{-1}$. Les deux relations révèlent une limitation par le phosphore quand la réponse de CHL tombe sur la ligne ou à proximité, et fournissent un jalon permettant d'évaluer d'autres facteurs limitants ou colimitants qui sont signalés par le fait que la réponse de CHL tombe au-dessous de la ligne. Les données obtenues en Floride et ailleurs dans le monde sont similaires, et montrent un abaissement de la courbe au-dessus d'une concentration de PT de 100 $\mu g \cdot L^{-1}$. Nous avons calculé une ligne médiane globale à partir d'un vaste corpus de données sur les lacs, ce qui peut servir à la gestion d'ensemble des lacs.

[Traduit par la Rédaction]

Introduction

During the last 60 years, several researchers have demonstrated a strong correlation between chlorophyll (CHL), total phosphorus (TP), and total nitrogen (TN) concentrations in north-temperate lake waters from around the world (Sakamoto 1966; Ahlgren 1980; Aizaki et al. 1981) and in Florida lakes (Huber et al. 1982; Canfield 1983). Large- and small-scale experiments further suggested that P was the primary limiting nutrient in northern lakes (Schindler 1975). Consequently, simple empirical TP–CHL regression models (Dillon and Rigler 1974; Jones and Bachmann 1976) have been used to predict changes in CHL concentrations (algal biomass) as a result of changes in TP concentrations.

In Florida, lake surveys using limited sampling (i.e., three times per year) have indicated a significant amount of variance in the yield of CHL per unit of TP (Huber et al. 1982; Canfield 1983). Several empirical nutrient–CHL models derived from this data yielded lower estimates of CHL than temperate models (Baker et al. 1981). Canfield (1983) further demonstrated that even the best empirical nutrient–CHL models had 95% confidence intervals of 29–319% of the calculated CHL concentration. He further suggested that this level of variance needs to be considered when using empirical models with TP and TN to predict CHL. Although TN seems to be an important factor influencing the yield of CHL per unit of TP (Smith 1982; Canfield 1983), studies of lakes suggest that other environmental factors such as sus-

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pended solids (Hoyer and Jones 1983), aquatic plants (Canfield et al. 1984), lake flushing rates and light availability (Soballe and Kimmel 1987), and grazing effects (Shapiro 1979; Pace 1984) need to be considered. A number of these factors have led to reductions in the variance of predicted CHL concentrations when they were included in simple empirical models.

Some of the variability associated with published TP–CHL models has been attributed to the curvilinear nature of the general TP–CHL relationship with an asymptote around 100 μg TP·L^{-1} (Canfield 1983; Prairie et al. 1989). Straskraba (1980) suggested that the TP–CHL relationship is sigmoid and concluded that the slope coefficient of the TP–CHL relationship varies over a continuum of TP concentrations. McCauley et al. (1989) observed a sigmoid nature in the TP–CHL relationship for north-temperate lakes suggesting that a second nutrient such as TN had a significant impact on CHL values when TP concentrations were high. Mazumder and Havens (1998) described the TP–CHL relationship for both north-temperate lakes and Florida subtropical lakes as sigmoid. The apparent nonlinear character of the TP–CHL relationship based on mean CHL and TP concentrations has led researchers to revisit the assumption of limitation on which the relationship is based.

A recent paper (Kaiser et al. 1994) strongly emphasized the importance of the "law of the minimum" as a foundation of empirical nutrient–CHL models. Kaiser et al. (1994) also suggested that the description of maximum responses across levels of the potentially limiting factor (TP) should be the focus of statistical models derived from the law of the minimum and that all measured CHL concentrations below this line would indicate that environmental factors other than TP were limiting. A similar observation was advanced by Hosper (1980), who suggested that it would be more appropriate to interpret the effects of nutrients as posing an upper limit to summer CHL concentrations.

Over the last 10 years, a unique data set consisting of a large number of paired monthly nutrient and CHL estimates has been established by Florida LAKEWATCH, a citizen-based volunteer lake monitoring program (Florida LAKEWATCH 1998). The database represents paired sampling of monthly TP, TN, and CHL concentrations from 1986 to 1997, yielding over 12 450 monthly estimates from 360 lakes. All samples were collected following the same field procedures and analyzed in the same laboratory. This database permits a detailed examination of nutrient–CHL relationships.

In this paper, we use the Florida LAKEWATCH database to specifically examine TP–CHL relationships for Florida lakes using 1068 lake–year averages from 360 lakes. We further compare TP–CHL relationships in Florida with those of more northern lakes and evaluate the potential effects of TN on CHL yields because TN has been shown to be a limiting nutrient in some lakes (Smith 1982; Canfield 1983). We also evaluate the uncertainty associated with newly developed and previously published empirical nutrient–CHL models and establish a line expressing the maximum CHL response per unit of TP. Finally, we describe an empirical median line that describes the median CHL response per unit of TP for lakes having TP concentrations ranging from <1.0 to 100 μg·L^{-1}.

Materials and methods

Sampling program

Monthly TP, TN, and CHL data collected by citizen volunteers in the Florida LAKEWATCH program were used to establish a database to examine nutrient–CHL relationships. Canfield (1991) reported that water samples collected by citizen volunteers provided equivalent estimates of TP, TN, and CHL concentrations as data collected by professional biologists for 125 individual lakes.

In the field, citizen volunteers collected surface (0.5 m) water samples for TP and TN analyses from one to six evenly distributed locations. Water samples were collected using acid-washed, triple-rinsed 250-mL Nalgene bottles. Volunteers collected additional surface water samples at each location in tap water rinsed 4-L plastic bottles for CHL analyses. Upon returning to shore, a measured volume of lake water from the 4-L bottles was filtered through a Gelman type A-E glass fiber filter. All samples (water and filters) were frozen and sent to the Department of Fisheries and Aquatic Sciences' water quality laboratory where samples were analyzed for TP, TN, and CHL concentrations.

TP concentrations (micrograms per litre) were determined by the procedures of Murphy and Riley (1962) with a persulfate digestion (Menzel and Corwin 1965). TN concentrations (micrograms per litre) were determined by oxidizing water samples with persulfate and determining nitrate-N with second-derivative spectroscopy (Bachmann and Canfield 1996). CHL concentrations (micrograms per litre) were determined spectrophotometrically following pigment extraction with 90% ethanol (Sartory and Grobbelaar 1984).

Statistical procedures

A database consisting of paired annual mean nutrient and CHL data was established from the Florida LAKEWATCH database. Data from 360 lakes were collected on 11–13 dates over an annual cycle (January–December) for a minimum of 1 year. All stations within a lake (one to six) were averaged by month to obtain monthly means. For these 360 lakes, the data for each given year were designated as a lake–year average. This resulted in 1068 lake–year averages.

All analyses used in this paper were also conducted on data rearranged to avoid overweighting individual lakes by taking lake averages and by randomly selecting a single year for each lake with multiple years of data. The results were no different from the 1068 lake–year averages, so the results of the larger data set were reported.

Our 1068 lake–year averages data set was randomly sorted into two equal-sized data subsets to evaluate nutrient–CHL relationships for Florida lakes. A model development subset consisting of 533 lake–year averages from 274 lakes was used to develop three new empirical nutrient–CHL regression models using TP, TN, and TP + TN as variables in the models. A model confirmation subset consisting of 533 lake–year averages from 282 lakes was used to evaluate the predictive abilities of the three newly developed models and 10 published nutrient–CHL models. Models selected from the literature for comparison represent well-known work based on data covering a wide range of geographical areas and limnological conditions.

Four measures of precision (correlation coefficients, confidence limits, average errors, and percentage errors) were calculated for each new and published model following the procedures of Canfield (1983). Calculated CHL concentrations were obtained from developed and published nutrient–CHL models by using the measured TP and TN concentrations in the model confirmation subset. Pearson's correlation coefficients were determined for the relationship between measured and calculated CHL concentrations. An empirical 95% confidence limit (CL) was determined for the calculated CHL concentrations of each model by calculating the standard deviation of the mean difference between the logarithms of the measured and calculated CHL concentrations. Standard deviations rather than standard errors were used because we were interested in the precision of estimating individual values rather than means. The standard deviation was multiplied by 1.96, the z value corresponding to a 95% CL given $n > 100$ (Dixon and Massey 1969). This value (standard deviation × 1.96) was both subtracted and added to the mean difference. Antilogs of the mean difference ± (standard deviation × 1.96) were multiplied by 100 to express values as a percentage. The average error was calculated as the mean of the absolute values of the differences between untransformed measured and calculated monthly CHL values. The percentage error was the mean of the same differences divided by the measured values and multiplied by 100.

A model development subset consisting of 533 seasonal means (average of July–August) from 274 lakes was used to develop a summer TP–CHL regression model for Florida. A model confirmation subset consisting of 533 seasonal averages from 282 lakes was used to evaluate the predictive abilities of the newly developed model and the Jones and Bachmann (1976) empirical model developed from 189 north-temperate lakes. The four measures of precision (correlation coefficients, confidence limits, average errors, and percentage errors) were then calculated for both models. In addition, $\log_{10}$-transformed seasonal measured TP concentrations from our database were used in the Jones and Bachmann (1976) equation to obtain predicted seasonal (calculated) $\log_{10}$ CHL concentrations. The antilog of the predicted CHL was subtracted from observed CHL and plotted versus TP concentrations to determine if the Jones and Bachmann (1976) equation predicted significantly different CHL concentrations for Florida lakes.

A maximum CHL line was determined using associated monthly TP and CHL data (n = 12 463 from Florida LAKEWATCH 1998). The monthly values for $\log_{10}$ TP and $\log_{10}$ CHL were sorted into 28 groups according to the values for $\log_{10}$ TP. The first group ranged from 0 to 0.1, the next from 0.1 to 0.2, and the last group from 2.7 to 2.8. We calculated the mean values for $\log_{10}$ TP and $\log_{10}$ CHL for each group and plotted them. We fitted a third-degree polynomial equation to the resulting sigmoid curve. This equation represents a mean P–CHL relationship that is equally weighted across the range of TP concentrations in our sample and was used to calculate an expected CHL concentration for each TP concentration. The differences between the actual and the calculated CHL concentration were found. The next step involved ranking all of the monthly values according to TP concentration and then taking the first 623 pairs and placing them in the first group, the next 623 pairs in the next group, and so on to form 20 groups. Within each group, the six CHL values that had the largest positive deviation above the line were plotted against their respective TP concentrations and then the next six highest points were plotted on the same graph. A smooth line was drawn roughly between these two sets of points to represent the most probable maximum P–CHL relationship. A polynomial regression was fitted through a set of points on that line.

A composite of 928 associated CHL and TP data from 818 lakes taken from the literature (e.g., Jones and Bachmann 1976; Aizaki et al. 1981; Prepas and Trew 1983) was used to create a representative global data set. Literature data were examined to avoid repeating data that were included in more than one study. The global data set and 1068 lake–year averages from 360 Florida lakes (Florida LAKEWATCH 1998) were used to evaluate differences between linear and sigmoid regression lines.

A linear regression line fitted to the 1068 lake–year averages was compared with a sigmoid curve developed from Florida monthly data. The same sigmoid curve was then compared with a linear regression line fitted to the global data set. Lakes in the global data set with TP concentrations less than 100 $\mu g \cdot L^{-1}$ were then used to develop a world median line to describe the TP–CHL relationship.

All data were transformed to their logarithms (base 10) before any statistical analyses to accommodate heterogeneity of variance. Computations were performed using various procedures in JMP (SAS Institute Inc. 1994). Statements of statistical significance are at $p \leq 0.05$ unless otherwise stated.

Results and discussion

The 360 Florida lakes used in this study represent a wide range of limnological conditions (Table 1). Mean TP concentrations ranged from 2.6 to 362 $\mu g \cdot L^{-1}$ and mean TN concentrations ranged from 56 to 4120 $\mu g \cdot L^{-1}$. Mean CHL concentrations ranged from <1.0 to 260 $\mu g \cdot L^{-1}$. The following additional summary statistics, although not available for all lakes, provide background information as to the types of lakes used to evaluate models. Surface areas ranged from 0.8 to 11 207 ha and average mean depths ranged from 0.4 to 7.7 m. Mean pH ranged from 4.1 to 9.8 and mean total alkalinity ranged from 0 to 137 $mg \cdot L^{-1}$ as calcium carbonate. Mean specific conductance ranged from 16 to 3050 $\mu S \cdot cm^{-1}$ and color averaged from <1.0 to 690 platinum–cobalt units. Mean water transparency ranged from 0.2 to 7.7 m. These ranges are similar to those previously reported by Canfield and Hoyer (1988) for a large data set of 165 Florida lakes. However, there are relationships despite the wide range of limnological conditions between CHL and nutrients (TP or TN) whether monthly or annual data are examined (Fig. 1).

Variance component analysis (SAS 1994) was used to determine those factors that contribute most to observed variability in measurements of TP, TN, and CHL. Variance component analysis indicated that 87, 86, and 66%, respectively, of the observed variance was attributable to differences among lakes. Less than 1% of the TP variance, 3% of the TN variance, and 15% of the CHL variance was associated with the year of sampling. Similar to Canfield (1983), the greatest amount of variance in measurements of TP, TN, and CHL in our data set is attributed to lake differences.

TP–CHL relationships

A plot of associated monthly mean CHL as a function of monthly mean TP suggested a sigmoid pattern for the TP–CHL relationship in Florida lakes. A third-order polynomial regression for mean CHL response was developed to evaluate the sigmoid pattern in terms of best fit for the data cluster. The curve fitted to the data is described by the following equation:

$$\log(\mathrm{CHL}) = 0.078 - 0.42\log(\mathrm{TP}) + 1.27\log(\mathrm{TP})^2 - 0.32\log(\mathrm{TP})^3 \tag{1}$$

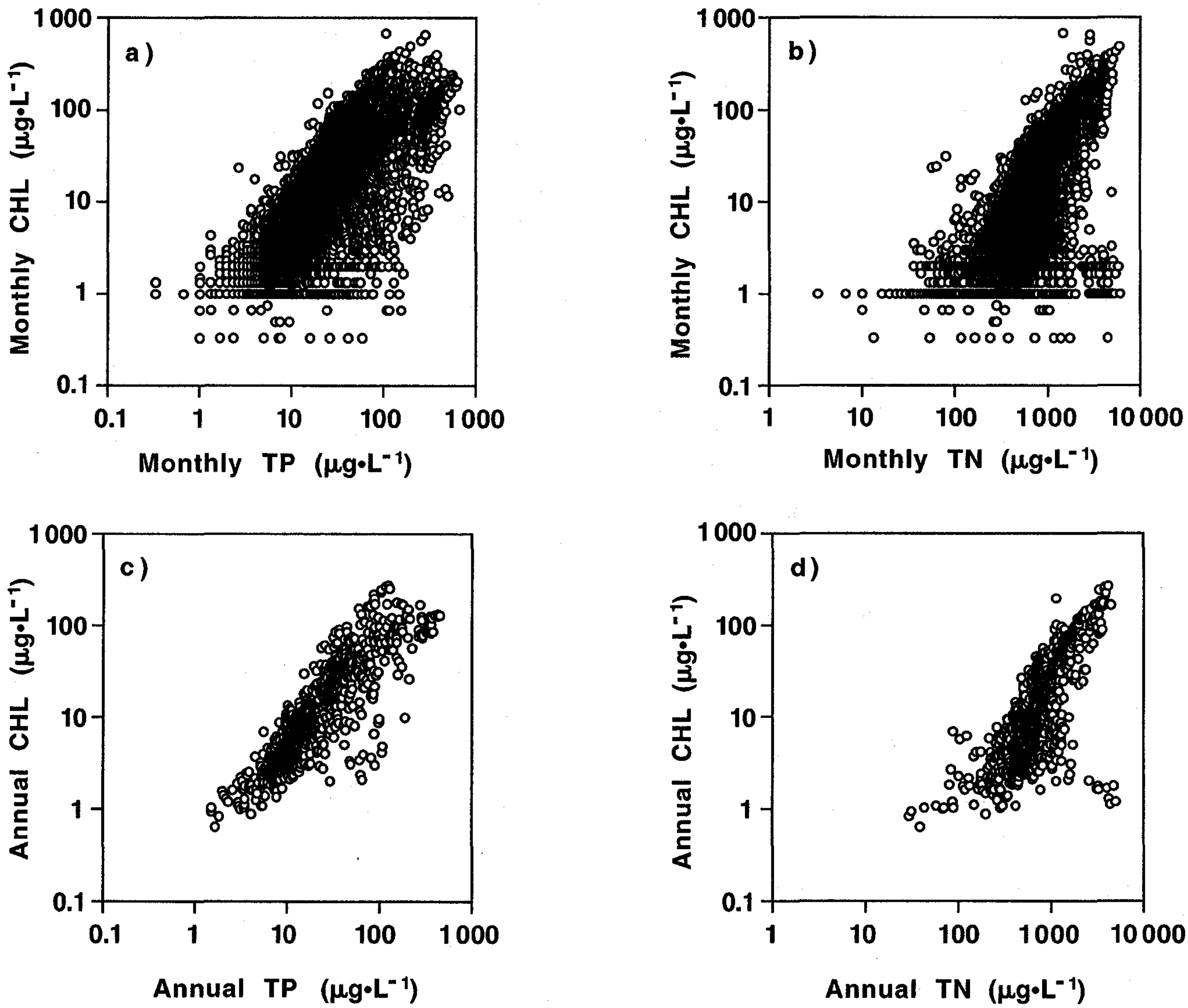
where CHL and TP are the average of one to six stations sampled once monthly. The p value for each coefficient in the polynomial equation was statistically significant. The predicted CHL responses of the polynomial equation (R^2 = 0.69) and a simple least squares regression line (R^2 = 0.67) fitted to the same data, however, were highly correlated (r = 0.99). Although the polynomial curve explains more variance of CHL estimates than the linear regression equation, the strong correlation for predicted CHL estimates suggests that both models would not predict very different mean CHL

Table 1. Summary statistics of available average limnological data from 360 Florida lakes located in 29 counties.

	n	Minimum	Median	Mean	Maximum
Surface area (ha)	262	0.8	50	360	11 207
Mean depth (m)	199	0.4	2.7	3.1	7.7
pH	231	4.1	7.0	6.9	9.8
Total alkalinity ($mg \cdot L^{-1}$ as $CaCO_3$)	231	0	13	24	137
Specific conductance ($\mu S \cdot cm^{-1}$ at 25°C)	231	16	141	167	3 050
Color (Pt–Co units)	231	<1.0	20	44	690
TP ($\mu g \cdot L^{-1}$)	360	2.6	18	37	362
TN ($\mu g \cdot L^{-1}$)	360	56	690	860	4 120
TN/TP ratio	360	5	35	42	1 157
CHL ($\mu g \cdot L^{-1}$)	359	<1.0	8.9	23	260
Secchi (m)	354	0.2	1.7	1.9	7.7

Note: Lakes were sampled monthly by Florida LAKEWATCH citizen volunteers from 1986 through 1997 for estimates of TP, TN, and CHL concentrations.

Fig. 1. TP–CHL and TN–CHL relationships for the association of 12 463 months and 1068 annual Florida lake averages.



responses. The same results were observed for a third-order polynomial ($R^2 = 0.78$) and a linear equation ($R^2 = 0.76$) fitted to 1068 Florida lake–year averages of TP and CHL. The similarity of the slopes for both equations over a wide range of TP from log 0.5 (3 $\mu g \cdot L^{-1}$) to log 2.2 (160 $\mu g \cdot L^{-1}$) indicates that simple models provide similar mean CHL estimates, particularly for TP concentrations, which would be considered most limiting. More than 93% of mean TP values from Florida and most published data sets fall in this range (≤160 $\mu g \cdot L^{-1}$).

It has been shown that three or four samples collected over a year can be used to estimate mean annual CHL concentrations in Florida lakes with a 25–35% coefficient of variation (Brown 1997). Earlier models describing the TP–CHL relationship in Florida were developed using lake survey data with this level of variance associated with sampling design. Using monthly data to obtain annual estimates of CHL concentrations results in a 15% coefficient of variation (Brown 1997); however, there remains considerable variation in the amount of CHL yielded per unit of TP (0.03–2.6) or per unit of TN (<0.001–0.17) using annual data based on monthly sampling (Fig. 1).

New empirical Florida nutrient–CHL models based on annual CHL and nutrient averages

Empirical nutrient–CHL models were developed from the model development subset using the annual means based on monthly data for Florida lakes (n = 533 lake–year averages from 274 lakes) (Table 2). TP alone accounted for a significant amount of the variance (R^2 = 0.76) of observed CHL measurements (Table 2). TN alone accounted for less variance of observed CHL measurements (R^2 = 0.46), but a multivariate model using both TP and TN also accounted for a significant amount of the observed variance (R^2 = 0.78). The coefficient of determination values for TP–CHL and the multivariate nutrient–CHL model, however, were similar (R^2 = 0.76 versus 0.78) (Table 2), suggesting that CHL concentrations can be predicted reasonably well using TP alone.

Precision of empirical TP–CHL models

The model confirmation subset consisting of 533 lake–year averages from 282 lakes was used to test the abilities of the newly developed empirical models and 11 published nutrient–CHL models to predict CHL values (Tables 3, 4, and 5). The new TP–CHL model developed from annual Florida lake data (Table 3) had the smallest 95% CL (30–325% of the calculated CHL value) and average error (13%). Even assuming an 80% CL, CHL estimates ranged from 46 to 216% of the calculated CHL value.

Of the published Florida models, the Canfield (1983) model had the second lowest average error (15%) and smallest percentage error (49%) and the Huber et al. (1982) model had the highest average error (30%) and percentage error (84%). Even though all of the TP–CHL models had similar correlation coefficients (r = 0.87) for measured versus calculated CHL values, there remains a large degree of uncertainty in CHL predictions using TP alone (Table 3).

July–August TP–CHL relationships: Florida lakes versus northern lakes

The mean TP and CHL concentrations in Florida lakes during July–August ranged considerably as did July–August concentrations for northern lakes, as reported by Jones and Bachmann (1976). Average TP ranged from 1.0 to 390 $\mu g \cdot L^{-1}$ for Florida lakes and TP ranged from 2.7 to 350 $\mu g \cdot L^{-1}$ for northern lakes. Mean CHL ranged from <1.0 to 315 $\mu g \cdot L^{-1}$ for Florida lakes and CHL ranged from <1.0 to 400 $\mu g \cdot L^{-1}$ for northern lakes. The range of observed CHL per unit of TP (0.02–3.4) for Florida lakes was greater than the range (0.1–2.1) observed for northern lakes, suggesting that some Florida lakes during July and August may have more CHL per unit of TP than northern lakes.

A Florida TP–CHL model developed from 533 mean measured TP and CHL values collected in July and August from 273 lakes was somewhat different from the Jones and Bachmann (1976) north-temperate TP–CHL model (Table 4). The slope for the Florida model (m = 1.03) was not significantly different from 1.0. The north-temperate model's slope (m = 1.46) was significantly greater than 1.0, and the model's intercept (b = –1.09) was less than the Florida model's intercept (b = –0.299), indicating that the two lines would intersect at a TP concentration of around 63 $\mu g \cdot L^{-1}$. The northern equation would therefore tend to predict higher CHL concentrations at high TP concentrations and lower CHL concentrations at low TP concentrations. The coefficient of determination for the relationship between TP and CHL for both equations was positive and significant. The coefficient of determination of the Florida data set (R^2 = 0.72) was lower compared with that of the Jones and Bachmann (1976) data set (R^2 = 0.90).

Both the Florida and northern seasonal models were tested for their ability to predict CHL values in a July–August model confirmation subset (Table 4). The Florida model had lower average error (14%) and percentage error (65%) and smaller 95% CL (27–365% of the calculated CHL value) compared with the Jones and Bachmann (1976) model. Both TP–CHL equations had similar correlation coefficients (r = 0.86) for measured and calculated CHL values. The Jones and Bachmann (1976) TP–CHL model was less precise when used to predict seasonal (July–August mean) CHL concentrations for Florida.

Jones and Bachmann (1976) used July–August averages of TP because P was considered limiting during this time of year, with most of the TP in the water column involved in the algal population. In north-temperate regions, distinct seasonal cycles of algal biomass are correlated with temperature and solar radiation patterns that are considered to limit algal biomass at other times of the year. In Florida, there is evidence that the maximum CHL per unit of TP is not limited to July–August and could occur at other times of the year (Brown et al. 1998). The Jones and Bachmann (1976) model underestimates CHL concentrations in Florida lakes at extremely low TP concentrations and overestimates CHL concentrations at extremely high TP concentrations (Fig. 2). Reasonable estimates of CHL, however, were obtained for the majority of Florida lakes. Models derived from the basic TP–CHL relationships for July–August Florida and north-temperate lake data sets also share a large number of common data points, with the majority of these data points falling in a large cluster within certain confidence limits. Slope differences between the two models tend to mask similarities in the fundamental TP–CHL relationships (Fig. 2; Table 4).

TN–CHL relationships

A plot of associated monthly mean CHL as a function of monthly mean TN also suggested a sigmoid pattern for the TN–CHL relationship in Florida lakes. A third-order polynomial regression for mean CHL response was developed to

Table 2. Three new empirical models and associated statistics.

Models	n	F	$p > F$	R^2
log(CHL) = −0.369 + 1.053log(TP)	533	1712	<0.01	0.76
log(CHL) = −2.42 + 1.206log(TN)	533	444	<0.01	0.46
log(CHL) = −1.10 + 0.91log(TP) + 0.321log(TN)	533	949	<0.01	0.78

Note: The models describe the association of annual average nutrient and CHL concentrations collected monthly at the same time and location for 273 Florida lakes (Florida LAKEWATCH 1998).

Table 3. Correlation (r) between measured and calculated CHL concentrations for TP–CHL models evaluated using the model confirmation subset.

		Error estimates		
Model	r	AE	PE	CL
Florida models				
Florida LAKEWATCH (1998), annual				
log(CHL) = −0.369 + 1.053log(TP)	0.87	13	58	30–325
Baker et al. (1981)				
log(CHL) = −0.41 + 0.79log(TP)	0.87	18	57	66–900
Huber et al. (1982)				
log(CHL) = −1.08 + 1.52log(TP)	0.87	30	84	27–553
Canfield (1983)				
log(CHL) = −0.15 + 0.744log(TP)	0.87	15	49	40–593
Northern models				
Dillon and Rigler (1974)				
log(CHL) = −1.14 + 1.449log(TP)	0.87	21	70	41–725
Jones and Bachmann (1976)				
log(CHL) = −1.09 + 1.46log(TP)	0.87	23	72	35–633
Midwestern model				
Hoyer (1981)				
log(CHL) = −0.77 + 1.24log(TP)	0.87	16	56	40–488

Note: Error estimates include average error (AE), percentage error (PE), and 95% CL as percentages of the calculated CHL values.

Table 4. Correlation (r) between measured and calculated CHL concentrations for TP–CHL models evaluated using the model confirmation subset.

		Error estimates		
Model	r	AE	PE	CL
Florida LAKEWATCH (1998), July–August				
log(CHL) = −0.299 + 1.03log(TP)	0.86	14	65	27–365
Jones and Bachmann (1976)				
log(CHL) = −1.09 + 1.46log(TP)	0.86	25	77	36–771

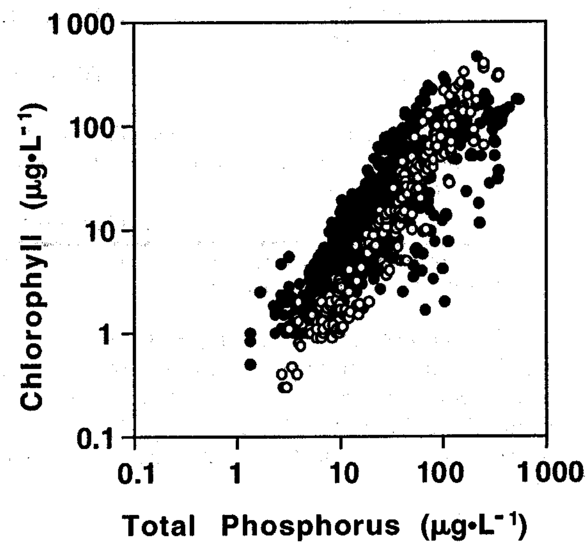
Note: Error estimates include average error (AE), percentage error (PE), and 95% CL as percentages of the calculated CHL values. Seasonal confirmation tests of the Florida LAKEWATCH (1998) and Jones and Bachmann (1976) equations used average July–August data from the model confirmation subset (n = 282 lakes).

evaluate the sigmoid pattern in terms of best fit for the data cluster. The curve fitted to the data is described by the following equation:

$$(2) \quad \log(\mathrm{CHL}) = 5.35 - 7.14\log(\mathrm{TN}) + 2.87\log(\mathrm{TN})^2 - 0.32\log(\mathrm{TN})^3$$

where CHL and TN are the average of one to six stations sampled once monthly. The p value for each coefficient in the polynomial equation was statistically significant. The

Fig. 2. Comparison of average July–August data used to derive Jones and Bachmann (1976) north-temperate model (n = 189) and a new Florida model (n = 533) derived from annual averages based on monthly sampling. The Jones and Bachmann (1976) data are represented as open circles and the Florida data as solid circles.



predicted CHL responses of the polynomial equation (R^2 = 0.50) and a simple least squares regression line (R^2 = 0.48) fitted to the same data, however, were highly correlated (r = 0.97) for the entire range of TN concentrations. Similar results were noted for a polynomial (R^2 = 0.57) and linear equation (R^2 = 0.54) fitted to 1068 Florida lake–year averages of associated TN and CHL concentrations. The slopes for both equations were similar for a wide range of TN from log 2.1 (126 $\mu g \cdot L^{-1}$) to log 3.8 (6300 $\mu g \cdot L^{-1}$), suggesting that they provide comparable mean CHL estimates.

Precision of empirical TN–CHL and (TP + TN)–CHL models

Examining TN–CHL models shows that the new TN–CHL model developed from annual Florida lake data collected monthly had the smallest 95% CLs (23–486% of the calculated CHL value) of all TN–CHL models evaluated (Table 5). The average error of 14% was also the smallest of all TN–CHL models examined. Comparison of percentage error estimates calculated for each TP–CHL model with percentage error estimates for each TN–CHL model showed that TP models had greater precision in estimating CHL concentrations in Florida lakes (Tables 3 and 5).

Comparing simple TP–CHL relationships with multivariate (TP + TN) models indicates that percentage errors were similar (Table 5). Increases in precision were observed, how-

Table 5. Correlation (*r*) between measured and calculated CHL concentrations for TN–CHL and multivariate nutrient–CHL models.

		Error estimates		
Model	*r*	AE	PE	CL
Florida TN–CHL models				
Florida LAKEWATCH (1998)				
log(CHL) = –2.42+ 1.206log(TN)	0.79	14	76	23–486
Canfield (1983)				
log(CHL) = –2.99 + 1.38log(TN)	0.79	14	66	29–562
Midwestern TN–CHL model				
Hoyer (1981)				
log(CHL) = –1.23 + 0.798log(TN)	0.79	16	90	18–552
Florida multivariate nutrient–CHL models				
Florida LAKEWATCH (1998), all data				
log(CHL) = –1.10 + 0.91log(TP) + 0.321log(TN)	0.88	12	55	33–311
Smith (1982)				
log(CHL) = –2.488 + 0.374log(TP) + 0.935log(TN)	0.87	17	57	68–796
Canfield (1983)				
log(CHL) = –2.49 + 0.269log(TP) + 1.06log(TN)	0.85	14	54	39–518
Midwestern multivariate nutrient–CHL model				
Hoyer (1981)				
log(CHL) = –1.136 + 1.19log(TP) + 0.155log(TN)	0.88	16	56	40–473

Note: All models were evaluated using the model confirmation subset. Error estimates include average error (AE), percentage error (PE), and 95% CL as percentages of the calculated CHL values. See text for methods of determination.

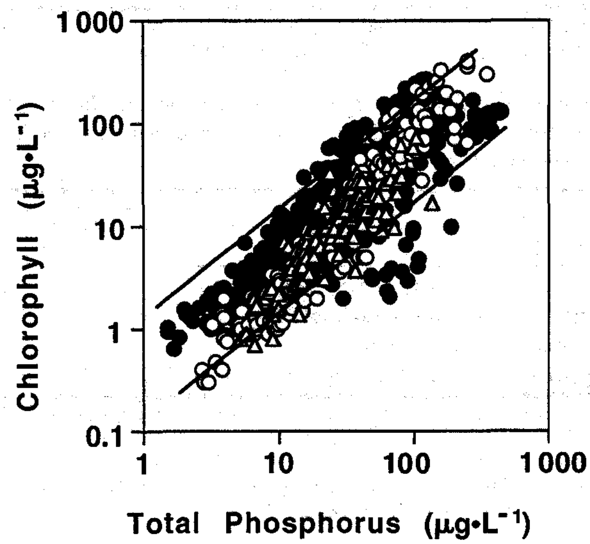
ever, with the addition of TN to simple TP–CHL models (Table 5). While the addition of TN to published TP–CHL models led to reductions in variance for Florida and northern lakes (Smith 1982; Canfield 1983), the 95% CLs for all of the empirical models examined remained large (33–311% to 68–796%).

Commonality of data associations

Researchers have noted a bending in simple TP–CHL models at high concentrations of TP (Forsberg and Ryding 1980; Canfield and Bachmann 1981). Canfield (1983) observed the tendency of published empirical TP–CHL models to overestimate CHL values in lakes with high TP concentrations (>100 µg·L^{-1}). Some earlier Florida empirical nutrient–CHL models predict lower estimates of CHL per unit of TP than temperate models (Baker et al. 1981). Inspection of Florida July–August averages indicated that Florida lakes with seasonal CHL concentrations < 100 µg TP·L^{-1} do not necessarily have lower algal CHL per measured TP concentration when compared with north-temperate lakes (Fig. 2).

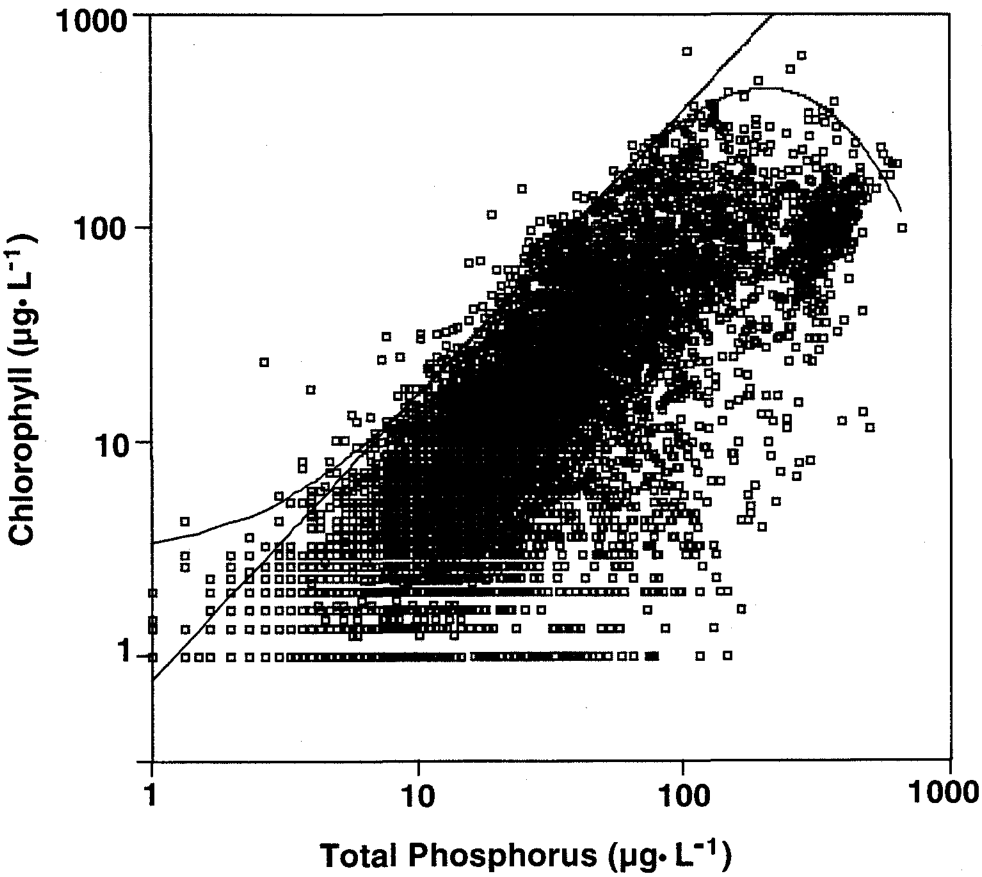
Once again, we reiterate that all data sets examined here have a large number of common data points. Enumeration of the plotted data points that fall above or below the confidence limits associated with some published models (Jones and Bachmann 1976; Hoyer and Jones 1983) indicated that 5–18% of the Florida, northern, or midwestern data points fell outside any other model's 95% predictive CLs. This suggests, as noted by Kaiser et al. (1994), that TP–CHL models describe the same basic TP–CHL relationship (Fig. 3). The large number of common data points shared among different data sets also confirms the Kaiser et al. (1994) supposition of an upper CHL response per unit of TP. Consequently, a maximum line of CHL response per unit of TP could be used as a benchmark to evaluate other limiting factors.

Fig. 3. Linear regression lines from several published models fall within the 95% CLs of the 1998 Florida LAKEWATCH database (n = 12 463) monthly TP and CHL associations. Temperate lake data of Jones and Bachmann (1976) are represented by open circles and of Hoyer (1981) by triangles, and Florida lake data are represented by solid circles.



Monthly data provide the greatest amount of information concerning the annual range of possible CHL values along a continuum of TP values (Brown 1997). In an attempt to address the maximum CHL response in terms of the nonlinear nature of the TP–CHL relationship, a sigmoid maximum CHL response curve was generated from 12 463 months of paired TP and CHL values from Florida lakes (Fig. 4). The maximum CHL response curve is described by the following equation:

Fig. 4. Comparison of a calculated sigmoid and linear maximum CHL response curves generated from 12 463 months of associated TP and CHL concentrations from 360 Florida lakes in 29 counties from 1986 to 1997.



(3) $\log(\text{maximum CHL}) = 0.528 + 0.18\log(\text{TP}) + 0.33\log(\text{TP})^2 + 0.29\log(\text{TP})^3 - 0.128\log(\text{TP})^4$

where maximum CHL and TP are the average of one to six stations sampled once monthly. We interpret the maximum CHL response curve as describing P limitation (nutrient limitation) when the CHL response falls on or near the line and indicating other limiting environmental factors when the CHL response falls below the line. For example, Florida lakes that fall below the line with low TP are generally dark-color lakes. Other lakes that fall below the line with high TP generally have low TN/TP ratios, suggesting that TN may be limiting rather than TP (Fig. 4). The maximum CHL response curve is essentially linear over a range of TP concentrations from 8 to 76 $\mu g \cdot L^{-1}$ and can also be estimated by the following equation:

(4) $\log(\text{maximum CHL}) = -0.12 + 1.33\log(\text{TP})$

where maximum CHL and TP are the average of one to six stations sampled once monthly. A multiple analysis of variance of the predictive abilities of both the curvilinear and linear maximum CHL response models over this range is identical. When we expand the range to include TP concentrations from 3 to 100 $\mu g \cdot L^{-1}$, the predicted CHL responses are still highly correlated ($r = 0.99$). Only when we begin to include CHL responses for TP concentrations >100 $\mu g \cdot L^{-1}$ does the characteristic bending of the sigmoid relationship significantly reduce expected maximum CHL responses.

As stated above, lakes with high TP tend to have low TN/TP ratios and are considered N limited (Forsberg and Ryding 1980; Canfield 1983). There is evidence that CHL levels associated with TP concentrations above 100 $\mu g \cdot L^{-1}$ are influenced more by TN (Fig. 4). In the Florida LAKEWATCH database, 32 lakes with 90 lake–year averages of data have high TP concentrations (>100 $\mu g \cdot L^{-1}$). Simple univariate models derived from this data range indicate that TN is more strongly correlated ($R^2 = 0.55$) than TP ($R^2 = 0.05$) with CHL. Also, the TP coefficient is no longer significant in a multivariate nutrient–CHL model developed from the same data. The median TN/TP ratio for this data is 10 compared with 38 for lakes with lower TP concentrations ($\leq$100 $\mu g \cdot L^{-1}$). Canfield (1983) observed a bending in the Florida TP–CHL relationship similar to that for lakes in other areas (Forsberg and Ryding 1980; Canfield and Bachmann 1981) where it appears that lakes with TP concentrations above 100 $\mu g \cdot L^{-1}$ are not limited by TP. These observations support the contention that TP is no longer limiting above 100 $\mu g \cdot L^{-1}$ and that N takes on a more important role.

Cursory observation of monthly Florida lake data suggested that factors other than TP may also limit CHL responses in a large number of lakes at concentrations below 100 $\mu g \cdot L^{-1}$ (Fig. 3). Environmental factors such as suspended solids (Canfield and Bachmann 1981; Hoyer and Jones 1983), color, and low TN/TP ratios have been shown to influence CHL responses in other areas and would also tend to cause CHL responses in Florida to fall below the maximum line. Suspended solids and color can lead to light attenuation that would potentially reduce CHL responses at any TP concentration.

A straight line fitted to the global data set and plotted with the sigmoid curve of means based on Florida monthly data indicated that Florida mean CHL responses fall above the straight-line regression of TP–CHL for the global data set over a wide range of TP from log 1.0 (10 $\mu g \cdot L^{-1}$) to log 2.4 (250 $\mu g \cdot L^{-1}$). When a polynomial equation was fitted to the global data set, the lower end of the sigmoid tail was no longer evident and the curve fell entirely below the sigmoid curve of Florida means. Overall, Florida lakes do not have less CHL than lakes in the global data set.

Management alternative: the global median

There are a number of empirical models that are reported to be different from each other. These differences are most likely the result of the range of data incorporated in the databases. Florida annual data from 1068 lake–years were combined with the global data set to expand the range of possible CHL responses. Other empirical models used to predict CHL response per unit of TP often incorporate other known factors when available to explain more of the variance associated with CHL estimations. In some instances, other factors remain unknown, so a general model based on median mean CHL response could provide reasonable estimates of CHL responses: 50% of responses would be greater and 50% would be less than the observed concentration. Such a model can be used for ballpark CHL estimates in an individual lake as well as in a population of lakes without the drawback of trying to find a specific model to apply to individual lake cases or develop models for each individual lake.

To assure the generality of a median model for universal application requires it to be derived from a large population of lakes from around the globe. We calculated a global median line using paired mean TP and CHL data from lakes in Europe, Japan, and the United States with TP concentrations <100 $\mu g \cdot L^{-1}$. The global median line is described by the following equation:

$$\text{(5)} \quad \log(\text{median CHL}) = -0.44 + 1.10\log(\text{TP})$$

where median CHL and TP are the average of one to six stations sampled once monthly. This line predicts the median expected mean CHL concentration. Lakes with TP concentrations >100 $\mu g \cdot L^{-1}$ were excluded when determining the median line in an attempt to reduce the possible influence of N-limited lakes. As associated TN data were not available for the complete global data series, it was impossible to sort on the basis of the TN/TP ratio.

The global median line can be a useful tool to predict CHL yields, as it maintains the generality of the TP–CHL relationship and was derived from data collected from a broad range of lakes. The global median is adequate for general application, but there are published models that may be more appropriate if certain colimiting factors are known to affect CHL yields in lakes within a region. For example, in Missouri reservoirs where suspended solids may bind nutrients or reduce light, Hoyer and Jones (1983) found that incorporating suspended solids into their TP–CHL model explained more CHL variance.

Summary and conclusion

In this study, Florida models were reconstructed and tested on annual means derived from monthly data. However, there is still a limit to the precision of the simple nutrient–CHL models. The 95% CL for the best available TP–CHL model is 30–325% of the calculated CHL value. Even assuming an 80% CL, CHL estimates ranged from 46 to 216% of the calculated CHL value. The best available multivariate model (TP + TN) has a 95% CL of 33–311% of the calculated CHL value. These large confidence intervals are not suprising, as similarly large intervals have previously been reported for nutrient loading models that predict P (31–288%; Canfield and Bachmann 1981) and N (41–255%; Bachmann 1980) concentrations.

Analyses of associated nutrient and CHL data indicate that the TP–CHL relationship is sigmoid in character but that the majority of CHL responses for TP concentrations (3–160 $\mu g \cdot L^{-1}$) are not much different from estimates from linear relationships for all practical purposes.

A large number of common data points shared among different data sets suggested that there is an upper response per unit of TP often representing algal bloom conditions. A maximum CHL response curve derived from over 12 400 months of paired TP and CHL data from Florida lakes is sigmoid. The maximum CHL response for both the curve and straight line is similar for a wide range of TP concentrations (3–100 $\mu g \cdot L^{-1}$). The maximum CHL response curve and straight line both define the upper limit of expected CHL concentrations based on the TP–CHL relationship and provide a benchmark to evaluate other limiting factors. The maximum curve describes P limitation when the CHL response falls on or near the line but indicates other limiting or colimiting factors when the CHL response falls below the line.

Florida lakes do not yield less CHL than north-temperate lakes. Both Florida and global data sets are similar, exhibiting a lessening of slope above a TP concentration of 100 $\mu g \cdot L^{-1}$. Almost all of the global data points fall below the maximum CHL response curve, as they are means and would in effect vary less than the monthly data used to develop the maximum CHL response.

The large confidence intervals associated with CHL predictions reflect the real-world variability of algal biomass in lakes as well as the limitation of simple mathematical descriptions of complex biological systems. Different responses of individual lakes to changes in TP account for a large amount of the total variance in TP–CHL regression models. Each lake's individual response confounds the general assumption that individual lakes will respond in a similar fashion to a given change in TP concentration. Efforts to describe the TP–CHL relationship using models more representative of the law of the minimum (Kaiser et al. 1994) are often complex, but the underlying concept remains important for applied lake management. Other factors beyond nutrients need to be considered, particularly when applying population models to individual lakes.

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