

Nutrient, chlorophyll, and water clarity relationships in Florida's nearshore coastal waters with comparisons to freshwater lakes

Mark V. Hoyer, Thomas K. Frazer, Sky K. Notestein, and Daniel E. Canfield, Jr.

Abstract: Models relating chlorophyll to nutrients and Secchi depth to chlorophyll using data from nearshore coastal waters of Florida were successfully developed. The models suggest that phosphorus is the primary limiting factor for phytoplankton in the nearshore coastal waters of Florida and that total phosphorus concentration accounts for 81% of the variance in chlorophyll concentration. The models also show that chlorophyll is the dominant factor determining Secchi depth in nearshore coastal waters of Florida and that chlorophyll concentrations account for 68% of the variance in Secchi depth. Thus, these models are robust and should be useful for eutrophication management of Florida's coastal marine systems. The models developed with data from nearshore coastal waters of Florida are similar to models developed for freshwater lakes in Florida, but the amount of chlorophyll per unit of phosphorus and Secchi depth per unit of chlorophyll are both significantly less for marine samples. This suggests that the chlorophyll to biovolume ratios in the nearshore coastal waters of Florida are less than in freshwater systems of Florida. Therefore, nutrient to chlorophyll and chlorophyll to Secchi depth models developed for freshwater systems are probably ill suited for use in Florida's marine systems.

Résumé : Nous avons élaboré des modèles efficaces qui relient la chlorophylle aux nutriments et la profondeur de Secchi à la chlorophylle à l'aide de données récoltées dans les eaux côtières près du littoral de la Floride. Les modèles indiquent que le phosphore est le principal facteur limitant du phytoplancton dans ces eaux et que la concentration de phosphore total explique 81 % de la variance de la concentration de chlorophylle. De plus, la chlorophylle est le facteur principal qui détermine la profondeur de Secchi et les concentrations de chlorophylle expliquent 68 % de la variance de la profondeur de Secchi. Ces modèles s'avèrent donc robustes et devraient être utiles pour gérer l'eutrophisation des systèmes marins côtiers de la Floride. Les modèles élaborés à partir de données provenant des eaux côtières près du littoral de la Floride sont semblables à ceux qui ont été créés pour les lacs d'eau douce de la Floride, mais la quantité de chlorophylle par unité de phosphore et la profondeur de Secchi par unité de chlorophylle sont significativement moins grandes en milieu marin. Il semble donc que les rapports entre la chlorophylle et le biovolume sont plus petits dans les eaux marines côtières de la Floride que dans les milieux d'eau douce du même état. En conséquence, les modèles élaborés en eau douce, qui mettent en relation les nutriments et la chlorophylle ainsi que la chlorophylle et la profondeur de Secchi, s'appliqueront assez mal aux systèmes marins de la Floride.

[Traduit par la Rédaction]

Introduction

Strong relationships between phosphorus, chlorophyll, and water clarity have been observed and reported for freshwater systems around the world (e.g., Sakamoto 1966; Brown et al. 2000). Moreover, there has been a suite of both small- and large-scale experiments implicating phosphorus as the primary nutrient limiting primary production in many, if not most, freshwater systems (see e.g., Schindler 1975). The generality of the relational data coupled with the experimental findings has led to the development of empirical

loading models to predict in-lake phosphorus concentrations as a function of annual phosphorus load, adjusting for differences in lake morphometry and hydraulic residence time (e.g., Vollenweider 1976; Canfield and Bachmann 1981). These models have been the principle tools of lake managers concerned with eutrophication issues over the last 30 years.

With regard to lakes, phosphorus concentrations are typically calculated with phosphorus loading models, and the calculated phosphorus concentrations are, in turn, used in regression models to estimate chlorophyll concentrations. As chlorophyll concentrations are, in many cases, strongly related to water clarity as measured by Secchi depth, the chain of relations allows for a determination of how much nutrient needs to be controlled to achieve a specified reduction in chlorophyll and concomitant increase in water clarity. This general approach has been successful in eutrophication management for many lakes in both Europe and North America (e.g., OECD 1982; Cooke et al. 1993), although it has not been widely applied to the management of coastal marine systems.

Eutrophication of estuaries and coastal waters is, relative

Received 23 October 2001. Accepted 23 May 2002.
Published on the NRC Research Press Web site at
<http://cjfas.nrc.ca> on 25 July 2002.
J16584

M.V. Hoyer,¹ T.K. Frazer, S.K. Notestein, and
D.E. Canfield, Jr. Department of Fisheries and Aquatic
Sciences, University of Florida, Gainesville, FL 32653, U.S.A.

¹Corresponding author (e-mail: mvhoyer@ufl.edu).

to lakes, a recent problem (Smith et al. 1999; Cloern 2001), though global in scope (Nixon 1995). The possibility of applying an empirically based modeling approach to marine systems to facilitate nutrient-related management strategies was first considered by Vollenweider (1992), and the development of such a modeling framework was a major recommendation of a recent U.S. national nutrient assessment workshop (U.S. EPA 1996). Meeuwig et al. (2000) subsequently used a total phosphorus mass balance model and a total phosphorus and chlorophyll model to accurately predict chlorophyll concentrations in 19 Finnish estuaries. Similar success was had using data from 15 estuaries in Prince Edward Island (Meeuwig 1999). These studies clearly suggest a potential for the use of empirically based models that predict the consequences of increased nutrient loading to estuaries and coastal marine waters. Unfortunately, there are a limited number of such models in existence.

A major objective of this work was to develop nutrient–chlorophyll and chlorophyll – water clarity models using broad-scale survey data collected from nearshore coastal waters around Florida. Because research on the eutrophication of freshwater systems is well advanced compared with that of marine systems, we also compared the models that we developed with existing freshwater models to determine if freshwater models could be applied to coastal systems.

Methods

Between October 2000 and July 2001, surface water (0.5 m) samples were collected on three separate dates (for most sites) from 300 sites located around the entire coast of Florida (Fig. 1). All sampling sites were located within 10 km of shore and some were within the intercoastal waterways of Florida. On each date and at each sampling station, dissolved oxygen concentration ($\text{mg}\cdot\text{L}^{-1}$), temperature ($^{\circ}\text{C}$), and salinity (‰) were measured in situ with a hand-held meter (model 85; Yellow Springs Instrument Company Inc., Yellow Springs, Ohio). Water clarity was also measured on each visit with a Secchi disk (m), and the actual water depth was recorded.

Surface water samples were collected in acid-cleaned bottles and transported on ice to the laboratory where they were analyzed for total phosphorus ($\mu\text{g}\cdot\text{L}^{-1}$), total nitrogen ($\mu\text{g}\cdot\text{L}^{-1}$), chlorophyll ($\mu\text{g}\cdot\text{L}^{-1}$), and color (Pt-Co units). Following persulfate digestion (Menzel and Corwin 1965), total phosphorus concentrations were determined using the procedures of Murphy and Riley (1962). Total nitrogen concentrations were determined from whole water samples by oxidizing water samples with persulfate and determining nitrate-nitrogen concentrations with a Bran-Luebbe (Houston, Tex.) autoanalyzer with a cadmium column reduction method (APHA 1989). Surface water chlorophyll concentrations were measured by filtering water through a 47-mm type A/E glass-fiber filter (Pall Corporation, Ann Arbor, Mich.) in the field. Subsequently, filters were stored over silica gel desiccant and then frozen before analysis. Chlorophyll was extracted with a hot ethanol method described by Sartory and Grobbelarr (1984), and chlorophyll concentrations were determined spectrophotometrically (Method 10200 H; APHA 1989). Color was determined spectrophotometrically on filtered water samples (APHA 1989).

Of the total 300 sites, 259 were sampled on three different dates, 35 were sampled on only two dates, and six sites were sampled on four dates. All data were averaged by site and the means were used for model development. All data were \log_{10} -transformed before statistical analyses to accommodate heterogeneity of variance (Snedecor and Cochran 1967). Computations were performed with the aid of a statistical software package (SAS Institute 2000), and statements of statistical significance imply $p < 0.05$ unless otherwise stated.

Results and discussion

The 300 sites sampled for this project covered almost all of the nearshore coastal waters around Florida (Fig. 1). All of the sites were within about 10 km of land with an average depth of 4.6 m (Table 1). The average salinity at the sites was 32‰, and average salinity was less than 10‰ at only 5 of the 300 sites. Samples were collected during both winter (2000) and summer (2001) periods, and as expected, there was a wide range in average temperatures among the sites (14.6–27.5°C). Mean oxygen concentrations were always greater than 4.4 $\text{mg}\cdot\text{L}^{-1}$. Color was generally low, averaging only 8 Pt-Co units, especially when compared with an average color of 44 Pt-Co units reported by Brown et al. (2000) for 360 Florida lakes. Secchi depth readings averaged 2.1 m and also exceeded the average of 1.9 m reported by Brown et al. (2000) for 354 Florida lakes. Total phosphorus and total nitrogen concentrations averaged 25 $\mu\text{g}\cdot\text{L}^{-1}$ and 309 $\mu\text{g}\cdot\text{L}^{-1}$, respectively (Table 1), which is less than the averages of 37 $\mu\text{g}\cdot\text{L}^{-1}$ and 690 $\mu\text{g}\cdot\text{L}^{-1}$ reported for Florida lakes (Brown et al. 2000). Chlorophyll concentrations averaged 3.7 $\mu\text{g}\cdot\text{L}^{-1}$, which was also less than the average of 23 $\mu\text{g}\cdot\text{L}^{-1}$ reported for Florida lakes (Brown et al. 2000).

Total phosphorus alone accounted for 81% of the variance in chlorophyll concentrations of nearshore coastal Florida waters, whereas nitrogen alone accounted for only 44% of the variance in chlorophyll concentrations (Table 2). These percentages are similar to those reported for Florida lakes (Table 2), where total phosphorus alone accounted for 76% of the variance in chlorophyll concentrations and total nitrogen accounted for only 46% of the variance in chlorophyll concentrations. Thus, the phosphorus–chlorophyll models presented for Florida's nearshore coastal waters (Table 2) are as robust as those developed for lakes and suggest that phosphorus accounts for more variance in chlorophyll than in nitrogen in both systems. Although nitrogen has been shown to limit algal populations in both freshwater and coastal systems (Elser et al. 1990; Downing 1997), the data presented here suggest that phosphorus is the primary nutrient limiting algal populations among the 300 nearshore coastal locations sampled in this study. We recognize, however, that some of these 300 stations may at some times be limited by nitrogen. Nevertheless, phosphorus explains most of the variance in chlorophyll concentrations among all 300 sites.

Chlorophyll accounted for 68% of the variance in Secchi depth for Florida's nearshore coastal waters, whereas color accounted for only 45% of the variance in Secchi depth (Table 2). Color has the potential to impact water clarity more in Florida lakes than in coastal waters because color values are generally higher in the lakes, as we indicated earlier. Therefore, to compare chlorophyll–Secchi and color–Secchi

Fig. 1. Location of 300 Florida nearshore coastal sites sampled three times between October 2000 and July 2001. The approximate center of Florida, U.S.A., is located at longitude 81°46'W and latitude 28°59'N.



Table 1. Mean, standard error, and minimum and maximum values for nine physical and chemical parameters estimated for 300 nearshore sites in the coastal waters around Florida.

Parameter	No. samples	Mean	Standard error	Minimum	Maximum
Depth (m)	300	4.6	0.2	0.5	17.7
Salinity (‰)	300	32.8	0.3	0.5	40.9
Temperature (°C)	300	21.4	0.2	14.6	27.5
Oxygen (mg·L ⁻¹)	300	6.9	0.1	4.4	22.7
Total phosphorus (µg·L ⁻¹)	300	25	1	3	122
Total nitrogen (µg·L ⁻¹)	300	309	10	93	1337
Chlorophyll (µg·L ⁻¹)	300	3.7	0.2	0.2	28.2
Secchi (m)	253	2.1	0.1	0.6	7.3
Color (Pt-Co units)	300	8	1	0	92

relationships for the nearshore coastal waters of Florida and Florida lakes, we selected a set of Florida lakes ($n = 297$) that averaged color values less than 32 Pt-Co units. We selected a maximum of 32 Pt-Co units for the lake data because 97.5% of the nearshore coastal sites had color values less than 32 Pt-Co units. As in the nearshore coastal sites, chlorophyll accounted for 72% and color accounted for 49% of the variance in Secchi depth among the 297 Florida lakes with color values less than 32 Pt-Co units. Thus, chlorophyll – water clarity models (Table 2) for nearshore coastal waters are as robust as those developed for lakes, and chlorophyll accounts for more variance in Secchi depth than does color.

The similarity in the relationships above for coastal marine and freshwater lakes (see Table 2) is intriguing. The data indicate clearly that phosphorus in both nearshore coastal waters and lakes of Florida accounts for most of the

variance in chlorophyll concentrations and suggest that phosphorus is likely the primary nutrient limiting phytoplankton production in both. Canfield (1983) and Brown et al. (2000) have previously stated that phosphorus is the primary limiting nutrient in Florida lakes, and as the total nitrogen to total phosphorus ratio moves below 10, nitrogen may become limiting. It is generally assumed, however, that nitrogen is the primary limiting nutrient for phytoplankton production in most coastal waters (Downing 1997). There are few empirical data or direct experimental results to corroborate this for Florida's coastal environment, and the data reported here suggest otherwise.

Although the nature of the relationship between total phosphorus and chlorophyll is similar for both freshwater lakes and coastal marine waters in Florida (slopes and r^2 values are about the same), we observed that the intercept in

Table 2. Empirical models and summary statistics describing the association of annual average nutrient and chlorophyll concentrations, Secchi depth and chlorophyll, and color (Pt-Co) and total phosphorus values using data from the nearshore coastal waters of Florida and Florida freshwater lakes (Brown et al. (2000) and M.V. Hoyer, unpublished data).

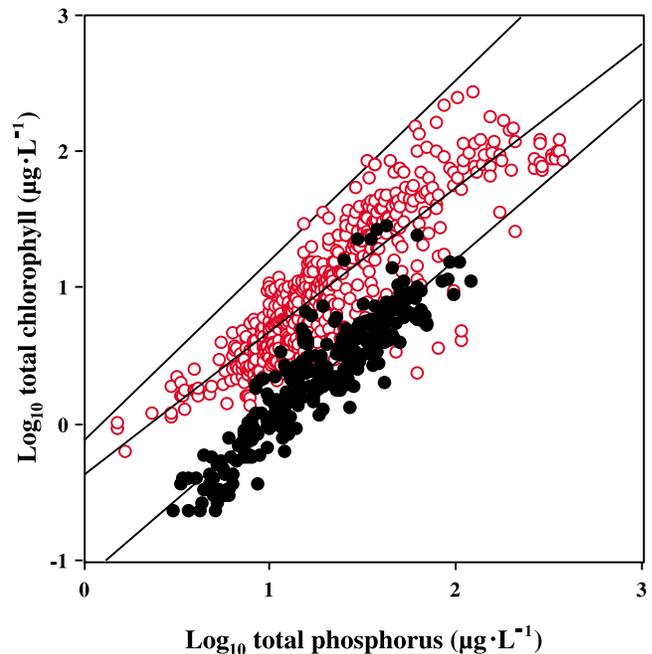
Model	<i>N</i>	<i>F</i>	<i>p</i> > <i>F</i>	<i>r</i> ²
Florida nearshore coastal waters				
log ₁₀ CHL = -1.13 + 1.17log ₁₀ TP	300	1297	<0.01	0.81
log ₁₀ CHL = -2.99 + 1.38log ₁₀ TN	300	209	<0.01	0.41
log ₁₀ Secchi = 0.48 - 0.48log ₁₀ CHL	253	544	<0.01	0.68
log ₁₀ Secchi = 0.55 - 0.41log ₁₀ Color	253	212	<0.01	0.45
log ₁₀ Secchi = 1.04 - 0.59log ₁₀ TP	253	393	<0.01	0.61
Brown et al. (2000) for Florida lakes				
log ₁₀ CHL = -0.37 + 1.05log ₁₀ TP	533	1712	<0.01	0.76
log ₁₀ CHL = -2.42 + 1.21log ₁₀ TN	533	444	<0.01	0.46
Florida freshwater lakes with average color <32 Pt-Co units				
log ₁₀ Secchi = 0.65 - 0.43log ₁₀ CHL	297	789	<0.01	0.72
log ₁₀ Secchi = 0.76 - 0.43log ₁₀ Color	297	106	<0.01	0.26
log ₁₀ Secchi = 0.88 - 0.48log ₁₀ TP	296	270	<0.01	0.47

Note: CHL, chlorophyll (µg·L⁻¹); TP, total phosphorus (µg·L⁻¹); TN, total nitrogen (µg·L⁻¹); Secchi, Secchi depth (m).

the resultant regression equations appeared different for the two system types. Analysis of covariance shows that indeed both the slopes and the intercept for these relations are different. Importantly, the intercept for nearshore coastal waters was much less than the respective intercept in the lake model. To examine this difference further, we plotted the maximum and the mean chlorophyll response equations published by Brown et al. (2000) on the total phosphorus and chlorophyll data collected for both studies (Fig. 2). All of the nearshore coastal data fall well below the maximum response equation, and all but five sites fall well below the mean response equation. Thus, although the amount of variance in chlorophyll concentrations accounted for by total phosphorus is similar, it appears that the amount of chlorophyll per unit of phosphorus is much less in the nearshore coastal water than in the freshwater lakes of Florida.

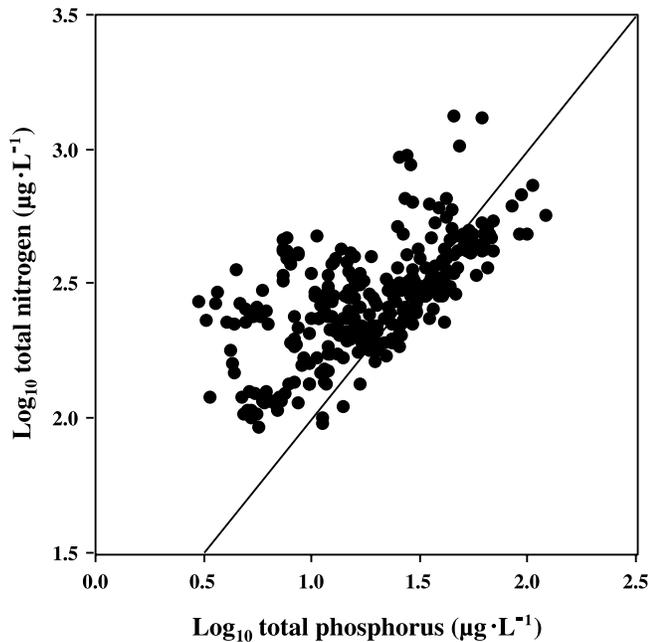
In freshwater lakes, when the chlorophyll response per unit of phosphorus is below published averages, researchers often suggest that nitrogen may be the nutrient most limiting chlorophyll concentrations and note that this usually occurs when the total nitrogen to total phosphorus ratio (by weight) falls below 10 (e.g., Sakamoto 1966; Smith 1982). As marine scientists and oceanographers typically prefer to examine molar ratios of nitrogen to phosphorus, we note that atomic N to P ratios less than 16 (equivalent to 7 by weight) are generally considered nitrogen limited in marine systems (e.g., Heckey and Kilham 1988; Downing 1997). To further examine the relationship between and nitrogen and phosphorus for the nearshore coastal waters of Florida, we plotted total phosphorus (µg·L⁻¹) against total nitrogen (µg·L⁻¹) and placed a line on the graph representing a total nitrogen to total phosphorus ratio of 10 by weight (Fig. 3). The vast majority of the sites have annual average total nitrogen to total phosphorus ratios greater than 10 and almost all would exceed a ratio of 7, suggesting as do the models (Table 2), that phosphorus may be the primary limiting nutrient for phytoplankton at most sites. The high N to P ratios do not explain, however, why the chlorophyll yield per unit of phosphorus is so low (Fig. 2).

Fig. 2. Relations between total phosphorus and chlorophyll for 300 nearshore Florida coastal sites (solid circles) and 533 Florida lakes (open circles, Brown et al. 2000). The uppermost regression line is the maximum chlorophyll response to phosphorus reported for Florida lakes (Brown et al. 2000). The other two lines represent the linear regressions for each data set. Analysis of covariance indicates that both the slopes and the intercepts of these regressions are significantly different (*p* = 0.05).



High concentrations of inorganic suspended solids and color can cause light limitation and have been shown to suppress chlorophyll concentrations per unit of phosphorus in freshwater lakes (Hoyer and Jones 1983; Brown et al. 2000). The impacts of the inorganic suspended solids and color, however, generally occur at higher chlorophyll concentrations, resulting in extremely low Secchi depths. This was not

Fig. 3. Relation between total phosphorus and total nitrogen for the nearshore coastal waters of Florida. The line represents the ratio of total nitrogen to total phosphorus (by weight).



observed in the nearshore coastal data reported here. The average Secchi depth for all 300 sites was 2.1 m (Table 1), and color values for all 300 sites averaged only 8 Pt-Co units. Thus, it is highly unlikely that inorganic suspended solids or color could be suppressing the amount of chlorophyll per unit of phosphorus in the nearshore coastal waters of Florida.

A high flushing rate of freshwater aquatic systems impacts chlorophyll concentrations by washout or removal of phytoplankton before algal standing crop reaches levels determined by concentrations of limiting nutrients (Swanson and Bachmann 1976; Soballe and Kimmel 1987). High flushing has also been shown to suppress algal biomass in the York River estuary (Sin et al. 1999) and the Hudson River estuary (Howarth et al. 2000). A mechanism explaining this suggests that water from springs or rainfall with few or no algal cells needs time for the algal cells to grow and exploit available nutrients in the water. Thus, as the water ages, algal cells eventually reach a level where some nutrient or other factor limits further growth. Bioassays from 20 Florida rivers suggest that it takes from 3 to 7 days to reach this level (Canfield and Hoyer 1988). All of the sites for this study are considerably distant from the headwaters of any river or spring run (Fig. 1). The sites also have an average salinity of 32‰, suggesting that freshwater has mixed with marine water and that the water we sampled probably had 3–7 days for algal populations to reach some level determined by nutrients or some other limiting factor. Therefore, it is unlikely that flushing rates are suppressing the chlorophyll per unit of phosphorus in the nearshore coastal waters of Florida.

Zooplankton and shellfish have both been shown to decrease chlorophyll concentrations in lakes and estuaries (Quiros 1990; Meeuwig et al. 1998). Thus, differential levels of top-down control on algal populations are another possible explanation for the low chlorophyll concentrations per

Fig. 4. Relations between chlorophyll and Secchi depth for 300 nearshore Florida coastal sites (solid circles) and 297 Florida lakes with color values less than 32 Pt-Co units (open circles; M.V. Hoyer, unpublished data). The two lines represent the linear regressions for each data set. Analysis of covariance indicates that both the slopes and the intercepts of these regressions are significantly different ($p = 0.05$).

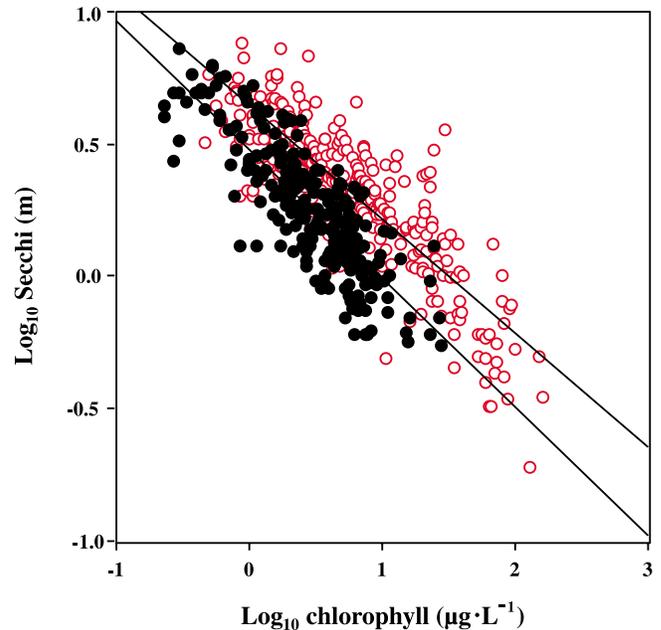


Fig. 5. Relations between total phosphorus and Secchi depth for 300 nearshore Florida coastal sites (solid circles) and 297 Florida lakes with color values less than 32 Pt-Co units (open circles; M.V. Hoyer, unpublished data). The two lines represent the linear regressions for each data set. Analysis of covariance shows that both the slopes and the intercepts of these regressions are not significantly different ($p = 0.05$).

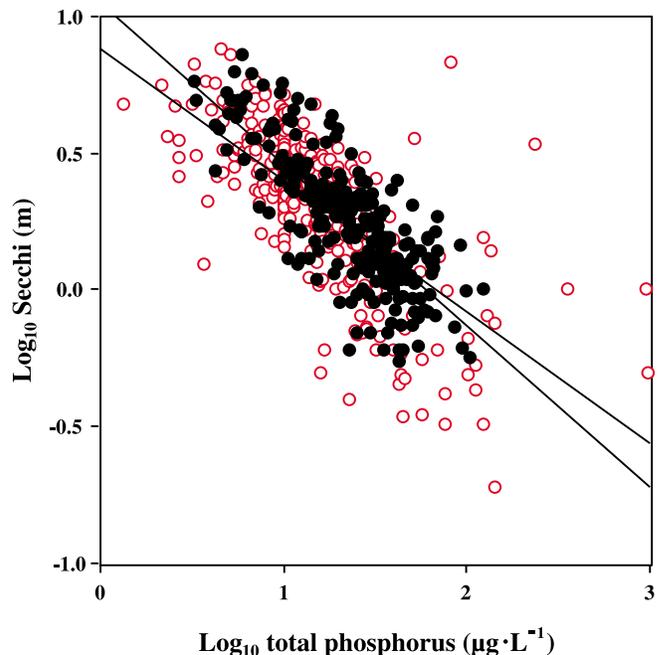


Table 3. Frequency distributions for the ratio of chlorophyll ($\mu\text{g}\cdot\text{L}^{-1}$) to volatile suspended solids ($\text{mg}\cdot\text{L}^{-1}$) for three different Florida gulf coast saltwater habitats (T.K. Frazer, unpublished data), three different freshwater habitat types (Kings Bay/Crystal River, Florida (Hoyer et al. 2001), and Lake Istokpoga and Lake Hatchineha, Florida (Lamb 2000)), and 53 Missouri reservoirs (Hoyer and Jones 1983).

System	No. samples	Percentiles				
		10%	25%	50%	75%	90%
Saltwater						
Marsh	14	0.1	0.2	0.3	0.5	0.9
Estuary	40	0.1	0.1	0.4	0.7	1.5
Gulf	26	0.1	0.2	0.3	0.4	0.9
Freshwater						
Kings Bay	217	2.3	3.4	5.3	7.7	10.7
Lake Istokpoga	288	1.8	2.7	3.5	5.0	6.7
Lake Hatchineha	334	3.5	4.4	5.8	8.1	11.1
Missouri reservoirs	53	2.1	3.8	4.8	5.8	7.5

unit of phosphorus observed in nearshore coastal waters. The whole body of nearshore coastal chlorophyll data, however, is suppressed below that of Florida lakes (Fig. 2) per unit of phosphorus, suggesting that if top-down control is occurring than it is occurring around the whole state of Florida. This would be inconsistent with areas that are devoid of shellfish or areas in the nearshore coastal waters that have large populations of planktivores (Florida Marine Research Institute 2001) that would minimize any impacts of zooplankton grazing. These areas should then have higher chlorophyll per unit of phosphorus, which is not observed in any of the 300 nearshore coastal sites.

As nitrogen, suspended solids, color, flushing rate, or top-down control are not likely factors responsible for the suppression of chlorophyll per unit of phosphorus in the nearshore coastal waters of Florida, other alternatives must be explored. One possible hypothesis to explain the relatively low chlorophyll yield per unit phosphorus is that the chlorophyll per unit biomass of algal cells is less in nearshore coastal waters than in lakes of Florida. The use of chlorophyll as an indicator of algal biomass can be problematic, however, because the ratio of chlorophyll to biomass or biovolume varies among species, systems, and environmental conditions (Heyman and Lundgren 1988; White et al. 1988; Kalchev et al. 1996). Nevertheless, if the chlorophyll to biomass ratio in nearshore coastal waters of Florida is significantly less than the chlorophyll to biomass ratio in freshwater lakes, this may explain the low yields of chlorophyll per unit of phosphorus in nearshore coastal waters (Fig. 2), and we can still assert that phosphorus is likely the primary limiting factor for phytoplankton in the nearshore coastal waters. On the other hand, if the chlorophyll to biomass ratios in nearshore coastal waters is the same as those in lakes, then some other factor is needed to explain the suppression of chlorophyll per unit phosphorus.

To examine this possibility further, we compared the models relating Secchi depth to chlorophyll for nearshore coastal waters and freshwater lakes (Table 2). An analysis of covariance shows that both the slope and intercept are significantly different. Looking at the plotted data for both systems (Fig. 4), it is easy to see that the Secchi depth per unit of

chlorophyll in the nearshore coastal waters is less than that in Florida lakes. If the chlorophyll to biomass ratio was the same for both systems, then the Secchi depths per unit of chlorophyll should overlap considerably because the algal populations are the dominant factors determining water clarity in both systems (Table 2).

Following similar logic, we compared the models relating Secchi depth to total phosphorus for nearshore coastal waters and freshwater lakes (Table 2). An analysis of covariance shows that both the slope and intercept are not significantly different. Looking at the plotted data for both systems (Fig. 5), it is easy to see that the Secchi depth per unit of phosphorus in the nearshore coastal and Florida lakes overlap almost completely. Assuming algal cells are the dominate factor determining Secchi depth in both systems and that phosphorus is the primary limiting factor, which we discussed earlier, then Secchi depth per unit of phosphorus should exhibit considerable overlap. If some other factor (other than phytoplankton) was suppressing Secchi depth in nearshore coastal waters, then the Secchi depths per unit of phosphorus in the coastal waters should be suppressed similar to the Secchi – chlorophyll models (Fig. 4). These data strongly suggest that the chlorophyll to biomass ratio of algal cells in nearshore coastal waters is less than that in freshwater lakes.

Additional data provide further support that chlorophyll to biomass ratios in nearshore coastal waters are less than in Florida lakes. Suspended solids and chlorophyll data, both from marine and freshwater systems, are provided in Table 3. The median values for the ratio of chlorophyll to volatile suspended solids in saltwater marsh, estuary, and gulf coast habitats were 0.3, 0.4, and 0.3, respectively (T.K. Frazer, unpublished data). The median values for the same ratio in four freshwater systems (Kings Bay, Florida (Hoyer et al. 2001), Lake Istokpoga, and Lake Hatchineha, Florida (Lamb 2000)) and 53 Missouri reservoirs (Hoyer and Jones 1983) are much higher at 5.3, 3.5, 5.8, and 4.8, respectively. The difference is large enough that the upper 90th percentile for the marine data does not overlap with the lower 10th percentile of the freshwater data (Table 3).

Many factors could impact the ratio between chlorophyll and volatile suspended solids, especially the presence of organic matter other than algal cells. However, chlorophyll and color account for a large percent of Secchi depth variance in both nearshore coastal waters and lakes (Table 2), and the presence of other organic substances would probably weaken those relations. In addition, Kings Bay, Lake Istokpoga, and Lake Hatchineha are shallow systems with abundant aquatic macrophytes, suggesting that the water column could have additional organics other than algal cells, which would only tend to lower the chlorophyll to volatile solids ratio for these freshwater systems. For the Missouri reservoirs, Jones and Hoyer (1982) showed a strong relation between volatile suspended solids and chlorophyll. These findings, and those above, all support the hypothesis that the chlorophyll to algal biomass ratio in the nearshore coastal waters is much less than that in Florida lakes.

Finally, we observed that average chlorophyll to biovolume ratios appear to be less in marine systems than in Florida lakes. Phlips et al. (1999) reported the seasonal average chlorophyll to biovolume ratios for four sites in Florida

Bay, sampled in four different seasons for 5 years. The average for these data was 0.0036 mg chlorophyll-mm⁻³ with a range of 0.0014 to 0.0076 mg chlorophyll-mm⁻³. Similar to these values, Tolstoy (1979) reported the chlorophyll to biovolume ratios for four marine systems from the literature that averaged 0.0034 mg chlorophyll-mm⁻³ with a range of 0.0019 to 0.0063 mg chlorophyll-mm⁻³. These average values are both less (by over 25%) than the average chlorophyll to biovolume ratio of 0.0049 mg chlorophyll-mm⁻³ reported for data from 165 Florida lakes (Canfield et al. 1985) and lend further support to the hypothesis above.

In conclusion, it appears that the general principles applied successfully to the control of eutrophication in freshwaters can be applied to coastal marine systems in Florida. In this study, we successfully developed models relating chlorophyll to nutrients and Secchi depth to chlorophyll using data from nearshore coastal waters of Florida. The models suggest that phosphorus is often the primary limiting factor for phytoplankton production in the nearshore coastal waters of Florida and that phosphorus can account for 81% of the variance in chlorophyll concentrations. The models also show that chlorophyll is the dominant factor determining Secchi depth in nearshore coastal waters of Florida and that chlorophyll can account for 68% of the variance in Secchi depth. Thus, these models are robust and should be useful for eutrophication management of marine systems.

The eutrophication models that we developed using data from nearshore coastal waters of Florida are similar to models developed for freshwater lakes in Florida, but the amount of chlorophyll per unit of phosphorus and Secchi depth per unit of chlorophyll are both significantly less. This suggests that the chlorophyll to biovolume ratios in the nearshore coastal waters of Florida are less than those in freshwater systems of Florida. Therefore, chlorophyll to phosphorus and Secchi depth to chlorophyll models developed for freshwater systems are probably ill suited for use in marine systems. Freshwater models used for prediction in nearshore coastal systems would overestimate chlorophyll based on phosphorus concentrations and overestimate Secchi depth based on chlorophyll concentrations.

Acknowledgments

This article is Journal Series No. R-08677 of the Florida Agricultural Experiment Station. We thank David Girardin (St. John's River Water Management District) and Fred Vose (Florida Marine Research Institute) for supplying boats and assistance in collecting some samples. We thank Rebecca Varner, David Gietbrock (Florida LAKEWATCH), and others for collecting samples around the coast of Florida. We thank Mary Stonecipher and others for laboratory analyses. We thank Roger Bachmann for comments on an early draft of this manuscript. Dr. Jessica Meeuwig and an anonymous reviewer added significantly to the strength of the final manuscript. This project was funded, in part, by the Southwest Florida Water Management District via the Surface Water Improvement and Management Program and the Coastal River Basin Board and the State of Florida Water Quality Assurance Trust Fund.

References

- American Public Health Association (APHA). 1989. Standard methods for the examination of water and wastewater. 17th ed. American Public Health Association, Washington, D.C.
- Brown, C.D., Hoyer, M.V., Bachmann, R.W., and Canfield, D.E., Jr. 2000. Nutrient–chlorophyll relationships: an evaluation of empirical nutrient–chlorophyll models using Florida and northern temperate lake data. *Can. J. Fish. Aquat. Sci.* **57**: 1574–1583.
- Canfield, D.E., Jr. 1983. Prediction of chlorophyll *a* concentrations in Florida lakes: the importance of phosphorus and nitrogen. *Water Res. Bull.* **19**(2): 255–262.
- Canfield, D.E., Jr., and Bachmann, R.W. 1981. Prediction of total phosphorus concentrations, chlorophyll *a*, and Secchi depths in natural and artificial lakes. *Can. J. Fish. Aquat. Sci.* **38**: 414–423.
- Canfield, D.E., Jr., and Hoyer, M.V. 1988. Nutrient assimilation capacity of the Little Wekiva River. Final Report. City of Altamonte Springs, Altamonte Springs, Florida.
- Canfield, D.E., Jr., Linda, S.B., and Hodgson, L.M. 1985. Chlorophyll–biomass–nutrient relationships for natural assemblages of Florida phytoplankton. *Water Resour. Bull.* **21**: 381–391.
- Cloern, J.E. 2001. Our evolving conceptual model of the coastal eutrophication problem. *Mar. Ecol. Prog. Ser.* **210**: 223–253.
- Cooke, G.D., Welch, E.B., Peterson, S.A., and Newroth, P.R. 1993. Restoration and management of lakes and reservoirs. 2nd ed. CRC Press, Inc., Boca Raton, Fla.
- Downing, J.A. 1997. Marine nitrogen: phosphorus stoichiometry and the global N:P cycle. *Biogeochemistry*, **37**: 237–252.
- Elser, J.J., Marzolf, E.R., and Goldman, C.R. 1990. Phosphorus and nitrogen limitation of phytoplankton growth in the freshwaters of North America: a review and critique of experimental enrichments. *Can. J. Fish. Aquat. Sci.* **47**: 1448–1477.
- Florida Marine Research Institute. 2001. Status and trends 2001 report—Florida's inshore and nearshore species. Florida Fish and Wildlife Conservation Commission, Florida Marine Research Institute, Education and Information Program, St Petersburg, Fla.
- Hecky, R.E., and Kilham, P. 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effects of enrichment. *Limnol. Oceanogr.* **33**: 796–822.
- Heyman, U., and Lundergren, A. 1988. Phytoplankton biomass and production in relation to phosphorus—some conclusions from field studies. *Hydrobiologia*, **170**: 211–227.
- Howarth, R.W., Swaney, D.P., Butler, T.J., and Marino, R. 2000. Climate control on eutrophication of the Hudson River estuary. *Ecosystems*, **3**: 210–215.
- Hoyer, M.V., and Jones, J.R. 1983. Factors affecting the relation between phosphorus and chlorophyll *a* in midwestern reservoirs. *Can. J. Fish. Aquat. Sci.* **40**: 192–199.
- Hoyer, M.V., Frazer, T.K., Canfield, D.E., Jr., and Lamb, J.M. 2001. Vegetation evaluation in Kings Bay/Crystal River. Final Report. Southwest Florida Water Management District, Surface Water Improvement and Management Department, Tampa, Fla.
- Jones, J.R., and Hoyer, M.V. 1982. Sportfish harvest predicted by summer chlorophyll *a* concentration in midwestern lakes and reservoirs. *Trans. Am. Fish. Soc.* **111**: 176–179.
- Kalchev, R.K., Beshkova, M.B., Boumbarova, C.S., Tsvetkova, R.L., and Sais, D. 1996. Some allometric and non-allometric relationships between chlorophyll-*a* and abundance variables of phytoplankton. *Hydrobiologia*, **341**: 235–245.
- Lamb, J.M. 2000. Wind-induced sediment resuspension in relation to varying submerged macrophyte coverage in two shallow Florida lakes (Lake Istokpoga and Lake Hatchineha). M.S. thesis, University of Florida, Gainesville, Fla.

- Meeuwig, J.J. 1999. Predicting coastal eutrophication from land-use: an empirical approach to small non-stratified estuaries. *Mar. Ecol. Prog. Ser.* **176**: 231–241.
- Meeuwig, J.J., Rasmussen, J.B., and Peters, R.H. 1998. Turbid waters and clarifying mussels: their moderation of empirical chl:nutrient relations in estuaries in Prince Edward Island, Canada. *Mar. Ecol. Prog. Ser.* **171**: 139–150.
- Meeuwig, J.J., Kauppila, P., and Pitkanen, H. 2000. Predicting coastal eutrophication in the Baltic: a limnological approach. *Can. J. Fish. Aquat. Sci.* **57**: 844–855.
- Menzel, D.W., and Corwin, N. 1965. The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulfate oxidation. *Limnol. Oceanogr.* **10**: 280–282.
- Murphy, J., and Riley, J.P. 1962. A modified single solution method for the determination of phosphate in natural waters. *Anal. Chim. Acta*, **27**: 31–36.
- Nixon, S.W. 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. *Ophelia*, **41**: 199–219.
- Organisation for Economic Cooperation and Development (OECD). 1982. Eutrophication of waters: monitoring, assessment and control. Organisation for Economic Cooperation and Development, Paris.
- Phlips, E.J., Badylak, S., and Lynch, T.C. 1999. Blooms of the picoplanktonic cyanobacterium *Synechococcus* in Florida Bay, a subtropical inner-shelf lagoon. *Limnol. Oceanogr.* **44**: 166–175.
- Quiros, R. 1990. Factors related to variance of residuals in chlorophyll – total phosphorus regressions in lakes and reservoirs of Argentina. *Hydrobiologia*, **200/201**: 343–355.
- Sakamoto, M. 1966. Primary production by phytoplankton community in some Japanese lakes and its dependence on lake depth. *Arch. Hydrobiol.* **62**: 1–28.
- Sartory, D.P., and Grobbelarr, J.U. 1984. Extraction of chlorophyll *a* from freshwater phytoplankton for spectrophotometric analysis. *Hydrobiologia*, **114**: 117–187.
- SAS Institute. 2000. JMP Statistics and Graphics Guide. SAS Institute, Inc., Cary, N.C.
- Schindler, D.W. 1975. Whole-lake eutrophication experiments with phosphorus, nitrogen and carbon. *Ver. Int. Ver. Theor. Angew. Limnol.* **19**: 3221–3231.
- Sin, Y.S., Wetzel, R.L., and Anderson, I.C. 1999. Spatial and temporal characteristics of nutrient and phytoplankton dynamics in the York River estuary, Virginia: analyses of long-term data. *Estuaries*, **22**: 260–275.
- Smith, V.H. 1982. The nitrogen and phosphorus dependence of algal biomass in lakes: an empirical and theoretical analysis. *Limnol. Oceanogr.* **27**(6): 1101–1112.
- Smith, V.H., Tillmen, G.D., and Nekola, J.C. 1999. Eutrophication: impacts of excess nutrient inputs on freshwater, marine and terrestrial ecosystems. *Environ. Pollut.* **100**: 179–196.
- Snedecor, G.W., and Cochran, W.G. 1967. Statistical methods. 6th ed. Iowa State University Press, Ames, Iowa.
- Soballe, D.M., and Kimmel, B.L. 1987. A large-scale comparison of factors influencing phytoplankton abundance in rivers, lakes and impoundments. *Ecology*, **68**: 1943–1954.
- Swanson, C.D., and Bachmann, R.W. 1976. A model of algal exports in some Iowa Streams. *Ecology*, **57**: 1076–1080.
- Tolstoy, A. 1979. Chlorophyll *a* in relation to phytoplankton volume in some Swedish lakes. *Archiv. Hydrobiol.* **85**: 133–151.
- United States Environmental Protection Agency (U.S. EPA). 1996. National nutrient assessment workshop. Proceedings, December 4–6, 1995, USEPA 822-R-96-004. Office of Water, U.S. Government Printing Office, Washington, D.C.
- Vollenweider, R.A. 1976. Advances in defining critical loading levels of phosphorus in lake eutrophication. *Mem. Ist. Ital. Idrobiol.* **33**: 53–83.
- Vollenweider, R.A. 1992. Coastal marine eutrophication: principles and control. *In* Marine coastal eutrophication. The response of marine transitional systems to human impacts: problems and perspectives for restoration. *Edited by* R.A. Vollenweider, R. Marchetti, and R. Viviani. Science of the Total Environment 1992, Elsevier Science, Amsterdam, The Netherlands.
- White, E.G., Payne, G., and Pickmore, S. 1988. A limitation to the usefulness of chlorophyll *a* as a biomass indicator in eutrophication studies. *Verh. Internat. Verein. Limnol.* **23**: 598–601.