



RAPID COMMUNICATION / COMMUNICATION RAPIDE

Predicting Cyanobacteria dominance in lakes

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Abstract: A controversial precept of aquatic ecology asserts that low ratios of nitrogen to phosphorus (N:P) lead to noxious and sometimes toxic blooms of Cyanobacteria. Cyanobacteria dominance is a major risk to human and ecosystem health. The stoichiometric control of Cyanobacteria therefore has become central to freshwater resource management. This controversial concept is based on observed Cyanobacteria dominance in lakes with low N:P and the results of lab and field experiments. Here we analyze data from 99 of the temperate zone's most studied lakes and show that this model is flawed. We show that the risk of water quality degradation by Cyanobacteria blooms is more strongly correlated with variation in total P, total N, or standing algae biomass than the ratio of N:P. Risks associated with Cyanobacteria are therefore less associated with N:P ratios than a simple increase in nutrient concentrations and algal biomass.

Résumé : Un précepte controversé de l'écologie aquatique veut que des faibles rapports azote:phosphore (N:P) entraînent la formation de fleurs d'eau à cyanobactéries, nocives et parfois toxiques. Une dominance des cyanobactéries constitue, en effet, un risque important pour la santé humaine et celle des écosystèmes. Le contrôle stoichiométrique des cyanobactéries est ainsi devenu une des préoccupations principales de la gestion des ressources d'eau douce. Ce concept controversé se base sur l'observation de la dominance des cyanobactéries dans les lacs à faible rapport N:P et sur les résultats d'expériences en laboratoire et en nature. Nous analysons ici des données provenant de 99 des lacs tempérés les mieux étudiés et démontrons que le modèle est incorrect. Le risque d'une dégradation des eaux par les fleurs d'eau à cyanobactéries est en corrélation plus forte avec les variations du P total, du N total ou de la biomasse des algues qu'avec le rapport N:P. Les risques reliés aux cyanobactéries sont donc moins associés aux rapports N:P qu'à la simple augmentation des concentrations d'éléments nutritifs et de la biomasse des algues.

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Cyanobacteria dominance in anthropogenically eutrophic lakes is an increasing problem that impacts recreation, ecosystem integrity, and human and animal health. Blooms of Cyanobacteria deposit unsightly, bad-smelling, mucilaginous clumps of dead and senescing cells on the shore and surface of lakes, impeding recreational uses. Blooms of some Cyanobacteria produce toxins during growth or decay that kill aquatic animals, and have semiochemical properties (antibiotic or allelopathic). Cyanobacterial poisoning of livestock, pets, and humans has been widely documented (Sivonen 1996). Cyanotoxins, including hepatotoxins, neurotoxins, cyto-

toxins, and dermatotoxins (Sivonen 1996), have been linked to carcinoma and other diseases (Falconer and Humpage 1996). Cyanobacterial metabolites produce taste and odor problems that elude conventional drinking water treatment.

Remediation of these problems requires understanding the mechanisms favouring Cyanobacteria dominance in lakes. A recent review (Hyenstrand et al. 1998) lists nine mechanisms hypothesized to promote Cyanobacterial dominance in freshwaters, including resource ratio (N:P) competition, differential light requirements, CO₂ competition, buoyancy, high temperature tolerance, avoidance by herbivores, superior cellular nutrient storage, ammonium-N exploitation, and trace element competition. However, knowledge that blooms of these taxa are frequently found in nutrient rich lakes and the existence of technology to limit nutrient enrichment have made the control of Cyanobacteria by nutrients the most prominent and attractive paradigm (e.g., Reynolds 1999; Smith and Bennett 1999).

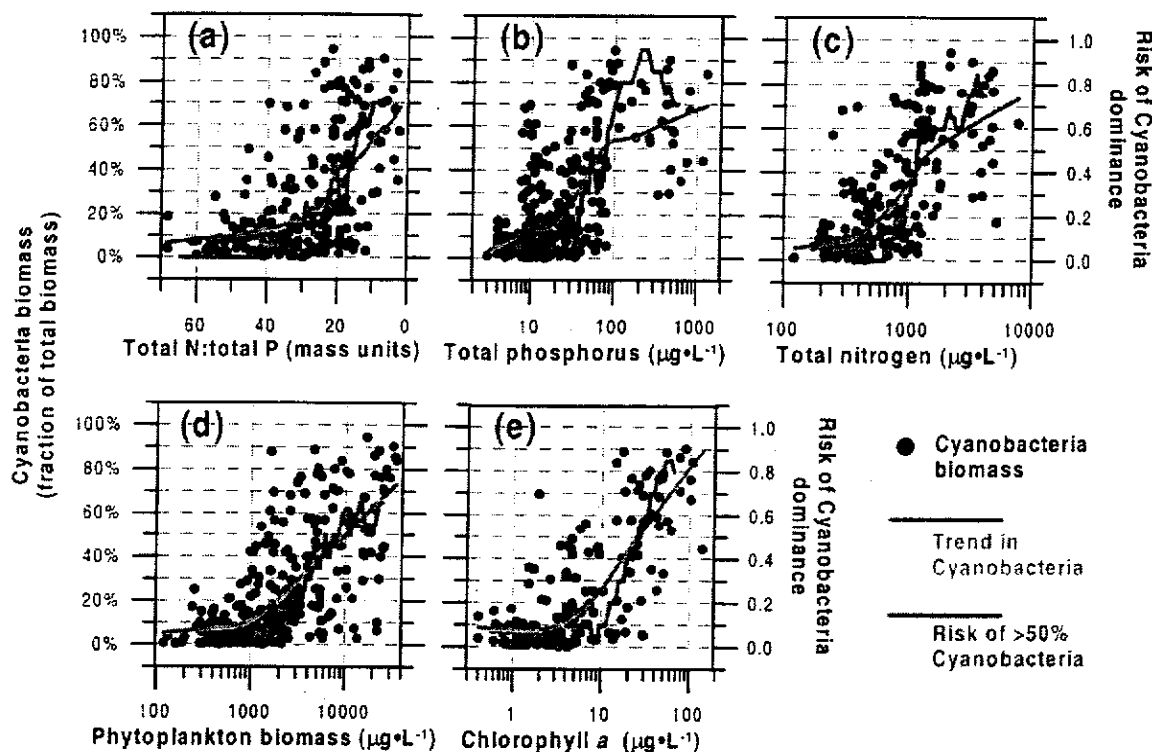
Controversy surrounds current models of Cyanobacteria dominance in surface waters. Many bloom-forming Cyanobacteria can fix atmospheric N₂ so it has been reasoned that Cyanobacteria should dominate at low N:P. This hypothesis was supported by an analysis of average seasonal data from 20 mostly northern European lakes, which concluded that ambient N:P influenced the dominance of Cyanobacteria in the phytoplankton (Smith 1983). This widely cited analysis has been debated (Trimbee and Prepas 1987) because it used

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Fig. 1. The relative abundance of Cyanobacteria in the plankton of north temperate zone lakes. Dots represent the observations collected using the sources and methods indicated in the legend of Table 1. Solid lines are average LOWESS trend lines ($f = 0.3$, number of steps = 2) in the fraction of Cyanobacteria in the plankton (green) and the risk of plankton dominated (>50%) by Cyanobacteria (red). The risk values (see text) thus represent the fraction of world lakes with similar values of total N:total P, total P, total N, chlorophyll, or biomass that have phytoplankton composed of >50% Cyanobacteria biomass.



a small sample size, included several years' data from lakes undergoing significant changes in nutrient regime, treated data from multiple points within a lake as independent samples, and mixed data from enclosure experiments with whole-lake observations. A subsequent re-analysis (Trimbee and Prepas 1987) eliminated most of these analytical problems and suggested that nutrient concentrations (e.g., total P, total N) were better predictors of average Cyanobacteria dominance than N:P in the original dataset and another small set of lakes in Alberta, Canada. A detailed analysis of Florida lakes (Canfield et al. 1989) found only weak correlations between nutrients (concentrations or ratios) and Cyanobacteria dominance but stronger relationships of Cyanobacteria dominance with standing algal biomass. Our research seeks to discriminate between the competing hypotheses of control of Cyanobacterial dominance by nutrient stoichiometry (N:P) versus nutrient concentration (P or N) or algal biomass by using a much larger set of published data that are more representative of economically important temperate zone lakes.

We analyzed published data by synthesizing studies and reports, collecting estimates of mean ($n \geq 5$ samples) summer euphotic zone relative biomass of Cyanobacteria (as a fraction of the total phytoplankton biomass), summer mean phytoplankton biomasses measured as cell volume, and chlorophyll *a* and nutrient concentrations (total N, total P, N:P) (see most lake and data descriptions in Watson et al. (1992, 1997)). We excluded reservoirs, recently manipulated (e.g., fertilized, dredged, acidified, fish-stocked, etc.) lakes, and dystrophic brown-water lakes. Our analysis consisted of

269 observations, collected from 99 lakes around the world. Data from multiple years or sites within a given lake were included if we judged that different years or sites represented differing equilibrium conditions. No single lake dominated the data collection; the maximum representation came from 18 divergent sites and dates for Lake Ontario. None of the data included picoplankton but these small algae are generally insignificant in noxious bloom formation. Trends in the fraction of the phytoplankton community composed of Cyanobacteria were characterized using LOWESS sequential smoothing. Trends in estimates of risk of Cyanobacteria dominance were empirically calculated as the running average percent frequency of the plankton where there was an average of >50% Cyanobacteria by biomass, sequentially considering the 20 neighbouring lakes with the most similar values of the abscissa in Figure 1, i.e., total N:total P (Fig. 1a), total P (Fig. 1b), total N (Fig. 1c), chlorophyll *a* (Fig. 1d), or biomass (Fig. 1e). These points were plotted against the average value of the abscissa for each set of 20 lakes. The strength of correlations between these independent variables and the degree of Cyanobacteria dominance was analyzed using the "BG index" (sensu Trimbee and Prepas 1987). The BG index used as a dependent variable was calculated as $\ln(\%BG/(100 - \%BG))$, where %BG is the Cyanobacteria biomass expressed as a percentage of total phytoplankton biomass, to avoid the statistical limitations of proportional and percentage data (Trimbee and Prepas 1987).

In contrast to prevailing theory, our regression analysis of temperate zone lake data (Table 1) showed that ambient N:P

Table 1. Efficacy of major variables for predicting Cyanobacterial abundance in temperate zone lake plankton.

Variable	Regression equation	n	RMS	r ²
Phytoplankton biomass	BG index = -8.44 + 2.07log ₁₀ biomass	268	1.77	0.43
Chlorophyll <i>a</i> (chloro)	BG index = -3.10 + 1.94log ₁₀ chloro	157	1.84	0.43
Total nitrogen (TN)	BG index = -10.0 + 3.03log ₁₀ TN	204	1.85	0.42
Total phosphorus (TP)	BG index = -4.16 + 1.88log ₁₀ TP	268	2.06	0.34
TN/TP	BG index = 3.15 - 3.29log ₁₀ TN/TP	204	2.34	0.26

Note: Analyses were by regression. Variables and models tested were those suggested by the recent literature as most valuable for these predictions (Smith 1983; Trimbee and Prepas 1987). The data were collated from recent published studies (Watson et al. 1992, 1997) and additional data sources that are available from Dr. S.B. Watson. The BG index used as a dependent variable was calculated as $\ln(\%BG/(100 - \%BG))$, where %BG is the Cyanobacteria biomass expressed as a percentage of total phytoplankton biomass, to avoid the statistical limitations of proportional and percentage data (Trimbee and Prepas 1987). All regression analyses are statistically significant at <0.001 . Although sample sizes differ among analyses, bootstrapping by randomly sampling equal numbers of observations (with replacement) showed rankings of regressions, coefficients of determination, and RMS (residual mean square error) values that are identical to those shown here. N:P impacts on Cyanobacteria do not appear to improve with consideration of light climate (see Smith and Bennett 1999) because log₁₀ TP, lake depth, or water clarity (Secchi disk measurements) do not enter significantly ($\alpha < 0.05$) into a multiple regression analysis of BG index with log₁₀ TN. All ambient concentrations are expressed in units of $\mu\text{g}\cdot\text{L}^{-1}$.

was the poorest predictor of Cyanobacterial dominance, compared with the trends in Cyanobacteria relative biomass with separate nutrient concentrations and total phytoplankton biomass estimates. Total P concentration alone yielded a coefficient of determination (r^2) nearly 30% larger than that of N:P. Residual mean square error estimates (RMS) show that total P yielded a prediction of Cyanobacteria relative abundance that is 12% more precise than N:P. Despite the prevalence of P limitation in north-temperate freshwater ecosystems, total N is more strongly correlated with Cyanobacteria dominance than total P. This is due to a more pronounced asymptote in Cyanobacteria dominance at high phosphorus than at high nitrogen concentrations (cf., Figs. 1b, 1c). Phytoplankton biomass is the best linear correlate of Cyanobacteria dominance, followed by concentrations of single limiting nutrients (N and P) and lastly by the ratio N:P (Table 1).

Past analyses may have perceived correlations between N:P and Cyanobacteria abundance because of a strong negative correlation between general nutrient fertility and N:P. Because rich nutrient sources are often depleted in N relative to P through biological uptake or denitrification, N:P generally declines as lakes become nutrient enriched (Downing 1997). Previous studies have shown strong collinearity between P concentrations and ambient N:P ($0.74 \leq r \leq 0.90$), making it difficult to discriminate the effects of these variables.

A main role of predictive models of Cyanobacteria dominance is to allow lake and watershed managers to manipulate nutrients to avoid conditions under which Cyanobacteria become dominant. The protection of human and ecosystem health is best served by a model that indicates conditions of highest risk of Cyanobacteria dominance with minimal misclassification of low risk conditions. This criterion is best satisfied by models that include only measurements of single limiting nutrients (e.g., total P or total N in Figs. 1a, 1b) because the right-hand sides of these graphs show few lakes with little Cyanobacteria. The N:P model does not discriminate waters where Cyanobacteria are likely to dominate from those where they do not.

The relationships shown in Table 1 provide insights of practical value. Lake managers have gained significant capa-

bilities in managing watersheds to decrease lake water nutrient concentrations. Until now, Cyanobacteria dominance was thought to be a function of ambient N:P, with Cyanobacteria rare above N:P = 29 (by mass) but more often dominant at N:P < 29. Figure 1 shows that the relative contribution of Cyanobacteria to total phytoplankton biomass follows nonlinear relationships with phytoplankton biomass, N:P stoichiometry, and nutrient concentrations. The most potentially useful of these relationships is that with total P, because total P predicts phytoplankton biomass (Watson et al. 1992) and discriminates incisively the lakes dominated by Cyanobacteria (Fig. 1b). As total P increases, Cyanobacteria represent an increasing percentage of the phytoplankton biomass, rising from a minimal fraction in nutrient-poor oligotrophic lakes to an asymptotic average of 60% above total P of 80–90 $\mu\text{g}\cdot\text{L}^{-1}$.

Of greatest management importance, however, is the prediction of risk of water bodies developing phytoplankton dominated by Cyanobacteria. The risk of Cyanobacteria dominance is only 0–10% between 0 and 30 $\mu\text{g}\cdot\text{L}^{-1}$ of total P, rising abruptly to about 40% between 30 and 70 $\mu\text{g}\cdot\text{L}^{-1}$, then asymptoting at around 80% near 100 $\mu\text{g}\cdot\text{L}^{-1}$. When risk levels rise to >10%, chlorophyll *a* concentrations in the water column are >10 $\mu\text{g}\cdot\text{L}^{-1}$ (Fig. 1d) which often leads to a reduction in transparency to <1 m (Canfield and Bachmann 1981) and is a known breakpoint where nuisance algae blooms occur at high frequency. Therefore, there is a high likelihood that Cyanobacteria will yield a visible bloom impairment of the water body, even at P levels where the average risk of Cyanobacteria dominance is fairly low ($\approx 20\%$). Lake management for minimal risk of Cyanobacteria dominance (e.g., for body-contact recreation, esthetic resources, or drinking water) requires lake total P concentrations below 30 $\mu\text{g}\cdot\text{L}^{-1}$, whereas a 40% risk of Cyanobacteria dominance (e.g., for non-contact recreation) could allow total P to rise as high as 70 $\mu\text{g}\cdot\text{L}^{-1}$. Average summer concentrations above 70 $\mu\text{g}\cdot\text{L}^{-1}$ provide an 80% guarantee of phytoplankton dominated by Cyanobacteria.

Although N:P impacts on Cyanobacterial dominance are well founded in resource-ratio theory, the stoichiometric model is of less practical value than a simpler approach based on

single nutrients or algae biomass. This is consistent with algal biology because not all Cyanobacteria are nitrogen fixers or efficient nitrogen competitors. We show that nutrient stoichiometry plays less of a role in establishing Cyanobacteria dominance in lakes than was previously believed, and our empirical analysis suggests that we should be testing alternative explanations for dominance of Cyanobacteria. Instead, Cyanobacteria may be superior light or CO₂ competitors under turbid, CO₂-depleted conditions prevalent in nutrient-rich lakes; their photosystem and buoyancy regulation may allow them to photo-adapt to the extreme light conditions present in these systems. High temperature tolerance may allow better survival in warm, shallow, nutrient-rich environments. Avoidance by herbivores may allow them longer persistence under the intense herbivory of eutrophic lakes, or efficient ammonium-nitrogen use may allow uptake superiority in ammonium-rich eutrophic lakes. It is even possible that allelopathic exudates may favor Cyanobacteria dominance when enriched nutrients yield dense phytoplankton biomass. Studies examining ways in which combinations of these mechanisms lead to Cyanobacteria dominance are therefore of great value (Reynolds 1999).

Given the increased awareness of water quality and public safety impairment by Cyanobacteria, aquatic scientists need to emphasize prediction of their dominance in freshwater ecosystems. Although it is likely that nutrient stoichiometry influences the structure of phytoplankton communities, our analysis of temperate zone lake data shows that the key mechanisms leading to Cyanobacteria dominance may be most closely related to the physical and biological constraints accompanying a simple increase in nutrient supply.

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