

COMMENT

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Determining trophic state in experimental lakes

Carpenter et al. (1998) investigated how nutrients (i.e., phosphorus [P] input), dissolved organic carbon (DOC), and grazing are related to phytoplankton biomass and production in four manipulated lakes intensely sampled during five summers. Multivariate probability distributions of algal biomass and production were constructed for varying data on P input rates, DOC, and grazer length, where DOC was used as a surrogate for humic and fulvic acids (also called colored DOC by Carpenter et al.). It is important to study the joined effects of these three predictor variables to improve predictability of lake trophic state (Nürnberg and Shaw 1999). However, as happens frequently in science, specialization has progressed so far that related disciplines use different expressions and methods, hindering the exchange of ideas and comparison of results. In this context I do not mean to diminish the value of the study by Carpenter et al. (1998) on the effect of trophic interactions and biological components on nutrient–phytoplankton relationships. My purpose is to caution against overgeneralization of these results and to suggest the usage of more appropriate measures.

In particular, Carpenter et al. (1998) used several concepts that may be misleading: (1) areal instead of volumetric measures of algal biomass and productivity in correlations with volumetric measures of DOC concentrations, (2) nutrient load instead of lake concentration to assess the effects of P on lake trophic state, and (3) transfer of results from small, potentially meromictic lakes that experienced various types of manipulations to trophic state interactions in natural lakes.

Using areal measures of algal biomass

Typically, average summer epilimnetic concentrations of nutrients and chlorophyll (in $\mu\text{g liter}^{-1}$) or secchi disk transparency (in m) are used to determine the trophic state in lakes (reviewed by Cooke et al. 1993; Nürnberg 1996). Categories that are used to determine whether a lake is oligotrophic, mesotrophic, eutrophic, or hypereutrophic are based on volumetric expressions of these variables in the epilimnion. However Carpenter et al. (1998) used areal measures (mg m^{-2} chlorophyll and $\text{mg m}^{-2} \text{d}^{-1}$ primary production). Although areal measures are often used in ecosystem studies to describe whole lake biomass or productivity, it is misleading to use these measures in the context of trophic state. Indeed, the clear waters of oligotrophic lake 228 in the Experimental Lakes Area in northwestern Ontario (Table 1) have higher areal chlorophyll values than the shallow eutrophic green Rice Lake in southern Ontario, where self-shading restricts phytoplankton to the upper layer (Table 1). The

use of areal biomass is not consistent with the trophic state concept.

Because Carpenter et al. (1998) used areal measures of phytoplankton biomass, they found a negative effect of DOC on algae (Fig. 3B,E in Carpenter et al. 1998) due to decreased light penetration in stained lakes. This phenomenon is well known and has been described repeatedly (*see* Jones 1992). It would be interesting to determine whether the negative effect of DOC persists if volumetric expressions such as epilimnetic chlorophyll concentration were used instead. Carpenter and Kitchell (1993) found that highly stained Tuesday Lake (phototrophic depth = 3.3 m) had chlorophyll and primary production similar to those of Peter Lake (phototrophic depth = 7.2 m) when expressed on an areal basis but had higher chlorophyll and primary productivity when those values were expressed volumetrically.

In a study of many worldwide lakes, Nürnberg and Shaw (1998) found that average summer epilimnetic chlorophyll concentrations (in $\mu\text{g liter}^{-1}$) were positively correlated with DOC ($n = 188$, $r = 0.41$, $P < 0.0001$) or color ($n = 264$, $r = 0.56$, $P < 0.0001$). Furthermore, maximum rates of primary productivity expressed on a volumetric basis (PP, $\text{mg C m}^{-3} \text{d}^{-1}$), were positively correlated with color, but when expressed on an areal basis, as in annual areal primary productivity (PA, $\text{g C m}^{-2} \text{yr}^{-1}$), rates of productivity were negatively correlated with color (Fig. 1). DOC was also positively correlated with PP ($n = 60$, $r = 0.41$, $P < 0.0001$), but its correlation with PA was not significant ($n = 31$). The positive effect of color and DOC on volumetric measures of algal biomass can be explained by the occurrence of highly significant positive correlations of color and DOC with P concentrations ($r = 0.49$, $n = 207$; $r = 0.52$, $n = 320$; Nürnberg and Shaw 1998). Even so, color had a significant, although small, positive effect on the chlorophyll–P regression ($P < 0.003$, randomization test, Manly 1991).

Using nutrient load

Carpenter et al. (1996) investigated the effect of nutrient load on lake trophic state. Although P load is ultimately used to manage eutrophication, its effect on lake trophic state depends on several variables, in particular morphometric and hydrological characteristics as in areal water load ($q_s = \bar{z}/\tau$, where \bar{z} is the mean depth in meters and τ is the annual water residence time in years; Dillon and Rigler 1974; Volenweider 1976). Furthermore, lake P concentration and hence lake trophic state, is controlled by sedimentation of incoming P, which is offset by internal P release from the

Table 1. Comparison of chlorophyll expressed volumetrically as concentration with chlorophyll expressed areally as standing stock (computed from the product of chlorophyll concentration and the depth of more than 1% light penetration or twice the Secchi disk depth) for two lakes with different trophic states (according to Nürnberg 1996).

Lake	Area (ha)	\bar{z} (m)	Phosphorus ($\mu\text{g liter}^{-1}$)	Secchi disk (m)	Chlorophyll		Trophic state
					Volume ($\mu\text{g liter}^{-1}$)	Areal (mg m^{-2})	
ELA 228*	1,677	55	7	10.7	2.4	51.4	oligotrophic
Rice†	10,010	2.4	35	1.2	16	40	eutrophic

* Fee 1979.

† Tzaras and Pick 1994.

sediments. Therefore, steady-state P budget models can have the form of

$$P = (L_{\text{ext}}/q_s)(1 - R) \quad (1)$$

(Nürnberg 1984), where L_{ext} is the annual external areal P load ($\text{mg m}^{-2} \text{yr}^{-1}$), and R is P retention, either measured in mass balance studies as $R_{\text{obs}} = (\text{in} - \text{out})/\text{in}$ (in this case an annual average P is predicted) or predicted as the fraction of external load that sediments out, $R_{\text{pred}} = 15/(18 + q_s)$ (in this case average epilimnetic early summer concentration is predicted; Nürnberg 1998). When internally derived P (as gross annual internal P load, L_{int} , $\text{mg m}^{-2} \text{yr}^{-1}$) entrains into the epilimnion during late summer and fall, it then can be added to the equation (in this case, a maximum fall P concentration is predicted; Nürnberg 1998):

$$P_{\text{max}} = (L_{\text{ext}}/q_s)(1 - R_{\text{pred}}) + L_{\text{int}}/q_s \quad (2)$$

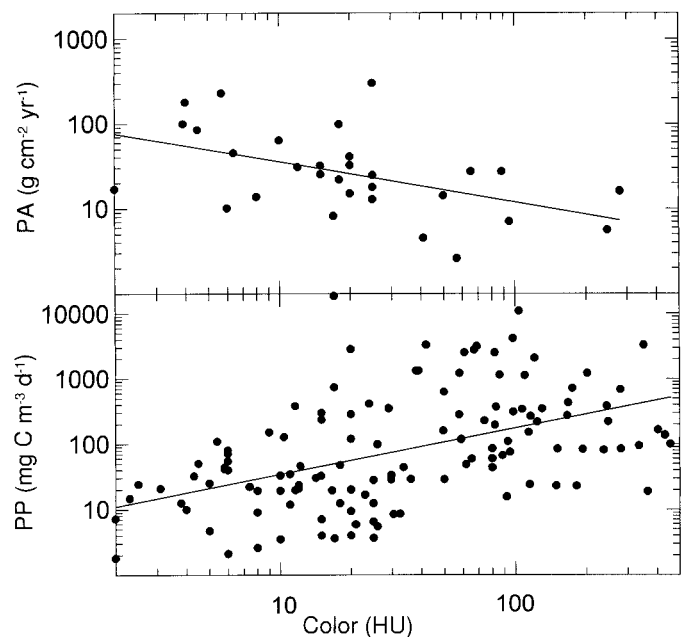


Fig. 1. Primary productivity versus color for epilimnetic summer averages from worldwide lakes. Data from Nürnberg and Shaw (1998). For lakes where productivity was expressed on an areal basis (PA), the correlation is negative ($n = 30$, $r = -0.49$, $P < 0.01$). Where productivity was expressed on a volumetric basis (PP), the correlation is positive ($n = 125$, $r = 0.48$, $P < 0.0001$). Regression lines are shown.

The study lakes of Carpenter et al. (1998) are strongly stratified during summer but experience some P entrainment from their anoxic hypolimnia, which is probably the reason for the metalimnetic chlorophyll maxima (Christensen et al. 1995). Failure to consider the effect of flushing and internal P load may contribute to unexplained variation in the regressions obtained. Replacing P loads with lake P concentration (unless loads are corrected for q_s and internal load) and areal biomass with volumetric biomass would improve their regressions and thus benefit our understanding of the mechanisms involved.

Generalization

Carpenter et al. (1998) generalized their findings to culturally eutrophied lakes. However, the study lakes are small and potentially meromictic. Their small areas and large depths result in large morphometric ratios of 25–35 m km^{-1} ($\bar{z}/A^{0.5}$, Osgood 1988). Such high ratios indicate stable thermal conditions and meromictic tendencies. Meromixis can also be inferred from thermoclines and oxyclines (maximum depth of oxygenation) that in Long and Paul Lakes remained well above the maximum depth in 1990–1993 (Figs. 5, 7 in Christensen et al. 1996). Such thermally stable lakes are not typical of culturally eutrophic lakes and lakes in general, which usually have much lower morphometric ratios (only 4 of 75 North American lakes had values $>25 \text{ m km}^{-1}$; Nürnberg 1995; and the medians of large data sets were $<8 \text{ m km}^{-1}$; Nürnberg and Shaw 1998) and are usually di- or monomictic and occasionally polymictic. The chemical cycle including P budgets of the study lakes is different because of entrainment from the meromictic layer, as manifested by metalimnetic oxygen maxima and algal blooms that represent half of total integral primary productivity (Carpenter and Kitchell 1993). Such high metalimnetic productivity is not typical for eutrophic lakes.

If the lakes are typical of culturally eutrophied lakes, general relationships of water quality variables should apply to the study lakes, at least for control conditions (before or without manipulation). Phosphorus models using empirically derived retention coefficients and P–chlorophyll regressions are such relationships. To investigate whether general relationships hold, I have summarized published data on these lakes in Table 2. No long-term average P or chlorophyll values and estimates of their variation could be found; therefore, I could not statistically evaluate any deviations from

Table 2. Observed summer chlorophyll and phosphorus concentration in the study lakes before and after manipulation. Because the observed chlorophyll data of Carpenter et al. (1995) were used in their own comparison of phosphorous–chlorophyll relationships, these data are probably the most applicable. Approximate expected phosphorus concentrations that reflect average relationships found between phosphorus and chlorophyll of world wide lakes (phosphorus–chlorophyll regression equations, Nürnberg 1996) are indicated.

Lake	Observed phosphorus ($\mu\text{g liter}^{-1}$)*		Chlorophyll ($\mu\text{g liter}^{-1}$)			
			Observed		Predicted	
	Before	After	Before	After [†]	Before	After
Paul (control)	15	NA [‡]	12 (5)	12 (5)	5.7	NA
Peter	12	26	9 (5)	29 (20–30)	4.7	9.1
West Long	NA	24	9.5 (6)	19 (11)	NA	8.6

* Carpenter and Kitchell 1993; Carpenter et al. 1995.

[†] Values from Figs. 2 of Carpenter et al. (1995, 1996) given in parentheses.

[‡] NA = not available.

general relationships. Carpenter et al. (1995) computed mean annual whole-lake P concentrations from external input and outflow measurements of the three study lakes using the Vollenweider (1976) P model with its implied retention model. These predictions were four and six times higher than values actually observed in the epilimnion (ca. $100 \mu\text{g P liter}^{-1}$ instead of $26 \mu\text{g liter}^{-1}$ in planktivore Peter Lake and ca. $160 \mu\text{g liter}^{-1}$ instead of $24 \mu\text{g liter}^{-1}$ in piscivore West Long Lake; no observed values were given for the control lake). Such high average whole-lake P concentrations would imply severely elevated hypolimnetic P concentrations, which have not been reported.

Nonetheless, these annual whole-lake P predictions were used to estimate summer chlorophyll concentrations based on the Vollenweider (1976) P–chlorophyll relationship, and a reasonable agreement was obtained (fig. 2 in Carpenter et al. 1995). However, if the observed epilimnetic P concentrations are used, the Vollenweider relationship underestimates observed chlorophyll concentrations drastically. Newer P–chlorophyll regression equations for North American or worldwide lakes (Nürnberg 1996) also underestimate the observed chlorophyll concentrations when predicted from observed epilimnetic P concentrations (Table 2). Conversely, much higher P concentrations are expected from the observed chlorophyll values. Therefore, large differences between observed P and chlorophyll values and those predicted from P budget models or P–chlorophyll regressions appear to disprove the assumption that the study lakes are representative of lakes in general.

Usually, high chlorophyll per unit of P is due to increased P availability. High availability may be a consequence of fertilization with phosphate in the nutrient addition experiments, of entrainment of highly available P from the monim- or hypolimnion during periods of cooling in late summer and fall, or of inefficient grazing in these lakes. However, only Peter Lake was manipulated to be dominated by planktivores, whereas West Long Lake was dominated by piscivores and should have had comparably low algal biomass.

The lakes may not be representative also because they have been exposed to numerous experimental manipulations starting in 1951. It is not clear how the more recent treatments (i.e., fish kill in 1988–1991 and fertilization of the epilimnion in 1993 in Peter Lake and the division of Long

Lake in 1991, disrupting water flow and changing DOC concentration (Carpenter and Kitchell 1993) might have influenced the interaction of the variables studied from 1991 to 1995. Although the lakes may have reached equilibrium after the early manipulations, the more recent DOC increases in West Long Lake may have induced biological changes that take longer to equilibrate, especially changes and increases in mixotrophic biomass and bacteria (Jansson et al. 1996).

The comparison of such intensively studied lakes to lakes in general would be facilitated if basic data such as average concentrations of nutrients and phytoplankton biomass and background data on hydrology (e.g., q_s or τ) were available. Also, basic lake characteristics expressed in units used routinely by other researchers, e.g., annual areal P load, would facilitate the comparison with other lakes. For example, I found no reference to values of total P load added in the enrichment study or any natural internal or external loads. Such data would make it easier to determine whether results from certain experimental whole lake studies apply to certain groups of lakes only (e.g., small, potentially meromictic, or manipulated lakes) or are typical of lakes in general.

My intention is not to diminish the value of Carpenter et al.'s (1998) study. However, I want to caution against generalizing its results to culturally eutrophied lakes without testing first whether established relationships for such lakes apply (e.g., P–chlorophyll regressions, P retention models). Furthermore, when results are to be used to assess the trophic state of these lakes, they should be expressed in volumetric units that are used in the trophic state context rather than (or in addition to) integral or areal units. Otherwise, incorrect conclusions, such as “colored DOC . . . has negative effects on phytoplankton,” may be drawn. In general, DOC is positively correlated with chlorophyll concentration but negatively correlated with integral algal biomass because of light limitation (not because of an inhibiting effect of DOC).

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Predicting responses of chlorophyll and primary production to changes in phosphorus, grazing, and dissolved organic carbon (Reply to comment by Nürnberg)

Carpenter et al. (1998) showed that the dynamics of primary producers in experimental lakes are predictable from phosphorus (P) input rate, grazer body size, and concentration of colored dissolved organic carbon (DOC). The negative effect of colored DOC on areal chlorophyll could be explained by light limitation alone. Nürnberg (1999) objected to our (1) use of areal chlorophyll rather than surface water concentration, (2) use of P input rate instead of surface water P concentration, and (3) extrapolation of results from experimental lakes to a larger population of lakes. In this rejoinder, we show that (1) areal measures of primary producers are more appropriate for ecosystem analysis and more relevant to analysis of algal blooms, (2) prediction of chlorophyll from P input rates links lakes to the surrounding landscape and provides models that are useful for management focused on control of P input, and (3) these experimental lakes conform to published relationships between P input rate and chlorophyll and that Nürnberg's characterization of the lakes as outliers is incorrect.

Areal biomass and production measures

We chose areal measures of chlorophyll and primary production because they are most relevant to total ecosystem production, the focus of our paper. This important topic is central to understanding the roles of lakes relative to other ecosystems. For example, in comparing gas exchange between ecosystems and the atmosphere, it makes most sense to express lake data in areal units, comparable to those used by terrestrial ecologists for wetlands and forests.

When our data are analyzed in volumetric units, we obtain a weak positive relationship between chlorophyll concentration and DOC that is comparable to the scatterplots of Nürnberg (1999). Volumetric chlorophyll concentration is positively correlated with DOC ($r = 0.243$, $n = 219$). If the effects of autocorrelation, P, and grazing are removed by regression, the correlation is lower and nonsignificant ($r = 0.086$, $n = 219$) yet positive.

Nürnberg (1999, table 1) compared a shallow lake and a