

- grazing on phytoplankton biomass and production in experimental lakes. *Limnol. Oceanogr.* **43**: 73–80.
- , AND J. F. KITCHELL. 1993. The trophic cascade in lakes. Cambridge.
- , AND OTHERS. 1995. Biological control of eutrophication in lakes. *Environ. Sci. Technol.* **29**: 784–786.
- , J. F. KITCHELL, K. L. COTTINGHAM, D. E. SCHINDLER, D. L. CHRISTIANSEN, D. M. POST, AND N. VOICHICK. 1996. Chlorophyll variability, nutrient input and grazing evidence from whole-lake experiments. *Ecology* **77**: 725–735.
- CHRISTENSEN, D. L., S. R. CARPENTER, AND K. L. COTTINGHAM. 1995. Predicting chlorophyll vertical distribution in response to epilimnetic nutrient enrichment in small stratified lakes. *J. Plankton Res.* **17**: 1461–1477.
- , ———, ———, S. E. KNIGHT, J. P. LEBOUTON, D. E. SCHINDLER, N. VOICHICK, J. J. COLE, AND M. L. PACE. 1996. Pelagic responses to changes in dissolved organic carbon following division of a seepage lake. *Limnol. Oceanogr.* **41**: 553–559.
- COOKE, G. D., E. B. WELCH, S. A. PETERSON, AND P. R. NEWROTH. 1993. Restoration and management of lakes and reservoirs. Lewis.
- DILLON, P. J., AND F. H. RIGLER. 1974. A test of a simple nutrient budget model predicting the phosphorus concentration in lake water. *J. Fish. Res. Board Can.* **31**: 1771–1778.
- FEE, E. J. 1979. A relation between lake morphometry and primary productivity and its use in interpreting whole-lake eutrophication experiments. *Limnol. Oceanogr.* **24**: 401–416.
- JANSSON, M., P. BLOMQUIST, A. JONSSON, AND A.-K. BERGSTRÖM. 1996. Nutrient limitation of bacterioplankton, autotrophic and mixotrophic phytoplankton, and heterotrophic nanoflagellates in Lake Östräsket. *Limnol. Oceanogr.* **41**: 1552–1559.
- JONES, R. I. 1992. The influence of humic substances on lacustrine planktonic food chains. *Hydrobiologia* **229**: 73–91.
- MANLEY, B. F. J. 1991. Randomization and Monte Carlo methods in biology. Chapman and Hall.
- NÜRNBERG, G. K. 1984. The prediction of internal phosphorus load in lakes with anoxic hypolimnia. *Limnol. Oceanogr.* **29**: 111–124.
- . 1995. Quantifying anoxia in lakes. *Limnol. Oceanogr.* **40**: 1100–1111.
- . 1996. Trophic state of clear and colored, soft- and hard-water lakes with special consideration of nutrients, anoxia, phytoplankton and fish. *Lake Reserv. Manag.* **12**: 432–447.
- . 1998. Prediction of annual and seasonal phosphorus concentrations in stratified and polymictic lakes. *Limnol. Oceanogr.* **43**: 1544–1552.
- , AND M. SHAW. 1998. Productivity of clear and humic lakes: Nutrients, phytoplankton, bacteria. *Hydrobiologia* **382**: 97–112.
- OSGOOD, R. A. 1988. Lake mixis and internal phosphorus dynamics. *Archive Hydrobiol.* **113**: 629–638.
- TZARAS, A., AND F. R. PICK. 1994. The relationship between bacterial and heterotrophic flagellate abundance in oligotrophic to mesotrophic temperate lakes. *Mar. Microb. Foodwebs* **8**: 347–355.
- VOLLENWEIDER, R. A. 1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. *Mem. Ist. Ital. Idrobiol.* **33**: 53–83.

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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

deep lake to support her argument that volumetric chlorophyll is a better index of eutrophication than is areal chlorophyll. This example is irrelevant to the study of changes in chlorophyll and production over time in a single lake. Lake depth changes on geological, not ecological, time frames and is not subject to human impact (with the exception of dredging projects or construction of dams). Although the relationships of lake depth to limnological variates are of interest to comparative limnologists, they are not relevant to the problem of predicting temporal variation of individual similar lakes over time, which was the topic of our paper.

Although agencies often assess water quality from a sample of epilimnetic chlorophyll concentration, this is not always an appropriate index of eutrophication. The public reacts to surface blooms of cyanobacteria that contain pseudovacuoles. Such blooms are related only loosely to concentrations. Blooms occur when calm conditions allow most of the cyanobacteria to rise to the surface, forming a scum (Soranno 1997). In effect, buoyant cyanobacteria vertically integrate the chlorophyll to produce a surface bloom.

High chlorophyll concentrations found in the epilimnions of humic lakes with high nitrogen (N):P ratios, such as those we studied, are not generally derived from nuisance algae. More commonly, these phytoplankton are chrysophytes, dinoflagellates, and chlorophytes (Sandgren 1988; Cottingham and Carpenter 1998). In fact, the high chlorophyll concentrations found in epilimnia of some humic lakes have quite different implications for management than do the high concentrations found in eutrophic lakes. Areal chlorophyll is generally low for humic lakes and high for eutrophic lakes, as we would expect for an indicator of eutrophication.

Nürnberg's argument against areal measures of primary producers is overly narrow. Investigators should have the latitude to choose the approach that is most appropriate for their research question. The use of an areal metric is consistent with the goals of our paper and with a significant body of ecological research. Although volumetric units are advantageous for some questions, we see no reason why they should be the only appropriate choice for limnology.

### P input rates versus concentrations

Nürnberg suggested that internal loading of P is an important but ignored component of our results. We have measured diffusion of solutes across the thermocline during summer and demonstrated that it is negligible (Cole and Pace 1998). Entrainment of P by deepening of the thermocline is a minor source of P compared with experimental enrichments (McTigue 1992; Christensen et al. 1995). Schindler et al. (1978) also found that chlorophyll and primary production could be predicted accurately by models that did not include a term for P flux from sediments. Studies of P cycling at the Experimental Lakes Area support our decision to focus on external inputs of P rather than recycling from sediments (Schindler et al. 1977; Levine et al. 1986).

Nürnberg stated that we should adjust P loads for flushing rates. We have measured flushing rates in these lakes (Cole and Pace 1998). There are minor differences in flushing rate among lakes and among years (Carpenter et al. 1995; Cole and Pace 1998). Based on 11 lake-years of data, residence

times averaged 2.5 yr (SE = 0.3 yr; Cole and Pace 1998). In contrast, P input rates were varied about 30-fold by experimental enrichment (Carpenter et al. 1998). Flushing rates were not measured in each lake each year. Instead of extrapolating flushing rates for years in which they were not measured, we chose not to correct the P input rates for water load. Because variation in flushing rates is small compared with that created by experimental enrichment, we find strong effects of P input on chlorophyll and primary production (Carpenter et al. 1998).

Nürnberg argued that estimates of P concentration are sufficient and that knowledge of P input rates is not necessary. We disagree. Control of P inputs is the primary means by which lake managers control eutrophication. Thus, prediction of effects of P input rates has applied as well as fundamental importance. Comparative limnologists use P concentrations as a surrogate when input and/or flushing rates are unknown or difficult to measure. We have measured both and have no need to resort to surrogates.

An important reason to use P input rates instead of concentrations to predict chlorophyll and primary production is that in P-limited lakes during summer total P concentration and chlorophyll concentration are both measures of algal biomass. In other words, the majority of the P is in the algae and will, of course, be highly correlated with chlorophyll. This often-overlooked fact creates a circularity that makes prediction of chlorophyll from P concentrations noninformative. Further, the original theoretical and empirical models developed for eutrophication analysis center on the fundamental concept of P loading (Vollenweider 1976). Thus, our approach is consistent with theory and practice, whereas the use of P concentrations as advocated by Nürnberg is, at best, merely a surrogate for loading.

### Generalization among lakes

The P-chlorophyll relationship for our study lakes (Fig. 1) is similar to that recorded by Canfield and Bachmann (1981). They addressed the situation in both reservoirs and natural lakes. Figure 1 presents only their data for natural lakes ( $n = 189$ ). The Canfield and Bachmann data set includes a diverse assemblage of lakes from Canada, Europe, and the United States, spanning a wide range of mean depths (0.5–307 m) and water residence times (0.005–500 yr). The experimental lakes of Carpenter et al. (1998) appear consistent with the pattern found by Canfield and Bachmann.

There is additional evidence that dynamics of the experimental lakes are similar to the patterns found in many diverse lakes. Preenrichment P input rates measured using sediment cores are close to estimates calculated from Vollenweider's (1976) model (Houser 1998). Peter Lake hews closely to the Vollenweider (1976) model, but intensive grazing in West Long lake causes its chlorophyll concentrations to fall below predictions from the Vollenweider (1976) relationship (Carpenter et al. 1995). In a multilake comparison of primary producers and herbivory, these experimental lakes were within the range of variability displayed by unmanipulated lakes (Carpenter et al. 1991).

The data presented in Nürnberg's (1999) table 2 are deceptive because variances are not presented. Our study lakes

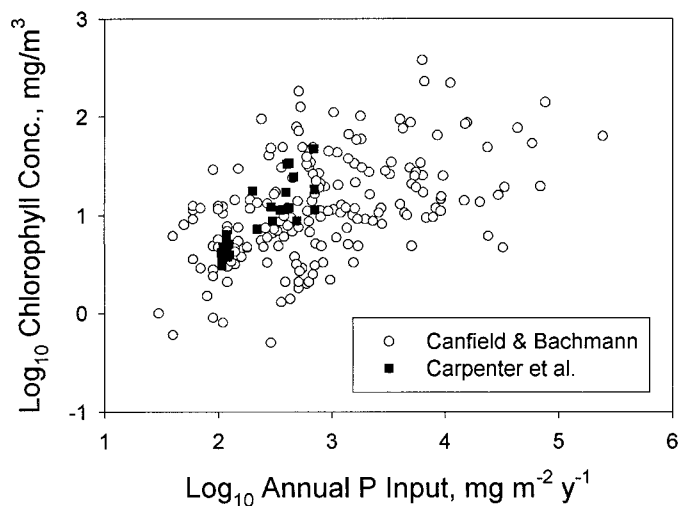


Fig. 1.  $\text{Log}_{10}$  chlorophyll concentration versus  $\text{log}_{10}$  annual P input for 189 natural lakes studied by Canfield and Bachmann (1981) and our experimental lakes. The Canfield and Bachmann data were obtained on microfilm in tabular format. For our study, each point represents a lake in 1 yr. Chlorophyll concentrations are means for the summer stratified season. P input is the sum of natural input and experimental fertilizations (Houser 1998).

appear to be well within the range of the order-of-magnitude scatter exhibited by the data of Nürnberg (1996). Her table 2 provides no support to the suggestion that these lakes are dissimilar from those studied by Nürnberg (1996).

Our experimental lakes are not meromictic. Whole-lake tracer studies have shown that the lakes mix at least once a year (Cole and Pace 1998). Annually laminated sediments support this observation, suggesting annual changes in redox potential at the sediment surface (Leavitt et al. 1993). Conductivity profiles in summer are not suggestive of meromixis (Carpenter unpubl. data). Nürnberg's suggestion that the lakes are meromictic is contradicted by our direct measurements and illustrates the danger of overinterpreting noisy general relationships.

Nürnberg's suggestion that these lakes had metalimnetic algal maxima after fertilization is incorrect. Prior to enrichment, the lakes supported metalimnetic algal populations typical of those found in many oligotrophic and dystrophic lakes (Fee 1976; St. Amand and Carpenter 1993). Chlorophyll concentrations near the bottom of the photic zone typically exceeded surface concentrations by several fold (Fig. 2). After enrichment, chlorophyll profiles showed little vertical structure, differing by only a few percentage points from the surface to the bottom of the photic zone. Enrichment decreased the relative abundance of metalimnetic algae, leading to vertical profiles typical of eutrophic lakes, as predicted by Christensen et al. (1995). These responses simply reinforce the value of areal data as an integrative measure of ecosystem response.

Nürnberg's claim that our experimental lakes are outliers is not supported by any information that she presented or by any data known to us. All lakes are individualistic in some respects, and limnologists have a long history of argument about how things are "in my lake" (Carpenter 1988). Such

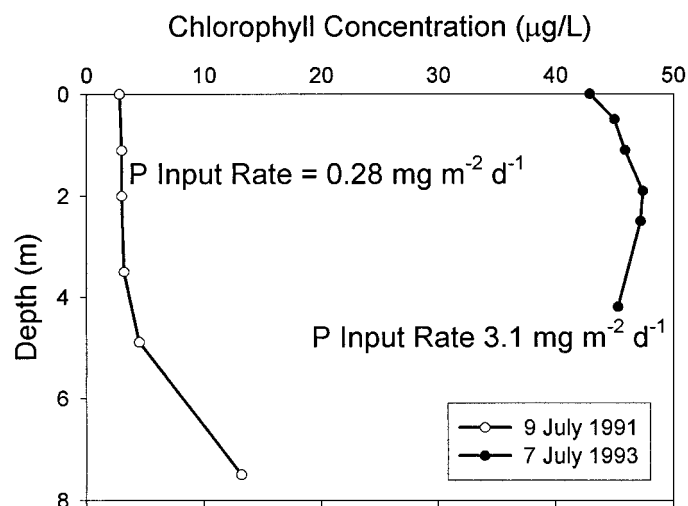


Fig. 2. Chlorophyll profiles in Peter Lake prior to enrichment (1991) and after enrichment (1993). Each profile presents measurements made at depths of 100%, 50%, 25%, 10%, 5%, and 1% of surface irradiance to provide a comparison across a uniform light gradient at low and high nutrient loads.

statements foster the balkanization of limnology by implying that generalizations and predictions are impossible because of the individual nature of lakes. We deny this viewpoint. Instead, we affirm and share with Nürnberg (e.g., Nürnberg 1995) the view that the search for predictive power, both among lakes on the landscape and over time in a single lake, is both feasible and a powerful foundation for our science.

## Conclusion

Too often in limnology, prediction is narrowly construed as meaning interpolation of a lake's condition from a comparative analysis of many lakes. This definition focuses on the average behavior of a population of lakes. The comparative approach is useful to scientists attempting to understand or predict broad patterns among lakes and to managers charged with designing regional policies that apply to many lakes. Often, however, managers are asked to deal with conditions in individual lakes. In that case, interpolation from comparative data can lead to large uncertainties. Consider Nürnberg's fig. 1 as a means for predicting productivity on a volumetric basis. If color is 100 HU, then primary production could be  $20 \text{ mg C m}^{-3} \text{ d}^{-1}$  or it could be  $10,000 \text{ mg C m}^{-3} \text{ d}^{-1}$ . Both are observed, and both appear equally likely. The regression through the centroid of the data, which is highly significant by conventional statistical criteria, forecasts a production rate of  $200 \text{ mg C m}^{-3} \text{ d}^{-1}$ . If a manager knows the color of a lake is 100 HU, what does she know of its primary production?

There are other types of predictions. We focused specifically on forecasting future dynamics of a specified ecosystem after manipulation. Our analysis was designed to predict the responses through time of individual lakes to manipulations, either inadvertent ones or management interventions. This approach is useful to scientists attempting to understand or predict how lakes change over time. Prediction of tem-

poral change is necessary when managers must focus on the restoration of a single specified lake. In fact, that is a frequent challenge for managers.

The problem of predicting a lake's response to manipulation has received limited attention from limnologists. However, this problem is among the most important frontiers of the discipline. Because the future is unknowable in advance, we must forecast probability distributions rather than certainties. This requirement adds to the technical difficulty of the challenge. In management, variance from predictions may be far more influential than mean values (Lindley 1985; Walters 1986; Carpenter et al. 1999). For example, if the variance in limnological predictions is underestimated, economic models lead to P loading decisions that increase the likelihood of eutrophication (Carpenter et al. 1999). Carpenter et al. (1998) showed how probability distributions of primary producers could be predicted for scenarios of changing P input, grazing, and colored DOC. This approach added an important new dimension to limnological prediction and provided new insights into lake dynamics. Our analysis also revealed that wetland losses that reduce levels of colored DOC may make lakes more susceptible to eutrophication by increased P input. Further research on predicting long-term dynamics of lakes holds the potential for many additional important insights and is essential for forecasting future aquatic resources in a changing world.

S. R. Carpenter  
J. F. Kitchell

Center for Limnology  
University of Wisconsin  
Madison, Wisconsin 53706

J. J. Cole  
M. L. Pace

Institute of Ecosystem Studies  
Box AB  
Millbrook, New York 12545

### References

- CANFIELD, D. E., AND R. W. BACHMANN. 1981. Prediction of total phosphorus concentrations, chlorophyll *a*, and Secchi depths in natural and artificial lakes. *Can. J. Fish. Aquat. Sci.* **38**: 414–423.
- CARPENTER, S. R. [ED.]. 1988. Complex interactions in lake communities. Springer-Verlag.
- , J. J. COLE, J. F. KITCHELL, AND M. L. PACE. 1998. Impact of dissolved organic carbon, phosphorus and grazing on phytoplankton biomass and production in experimental lakes. *Limnol. Oceanogr.* **43**: 73–80.
- , AND OTHERS. 1991. Patterns of primary production and herbivory in 25 North American lake ecosystems, p. 67–96. *In* J. Cole, S. Findlay, and G. Lovett [eds.], *Comparative analyses of ecosystems: Patterns, mechanisms, and theories*. Springer-Verlag.
- , AND OTHERS. 1995. Biological control of eutrophication in lakes. *Env. Sci. Tech.* **29**: 784–786.
- , D. LUDWIG, AND W. A. BROCK. 1999. Management of eutrophication for lakes subject to potentially irreversible change. *Ecol. Appl.* In press.
- CHRISTENSEN, D. L., S. R. CARPENTER, AND K. L. COTTINGHAM. 1995. Predicting chlorophyll vertical distribution in response to epilimnetic nutrient enrichment in stratified lakes. *J. Plankton Res.* **17**: 1461–1478.
- COLE, J. J., AND M. L. PACE. 1998. Hydrologic variability of small, northern Michigan lakes measured by the addition of tracers. *Ecosystems* **1**: 310–320.
- COTTINGHAM, K. L., AND S. R. CARPENTER. 1998. Population, community and ecosystem variates as ecological indicators: Phytoplankton response to whole-lake enrichment. *Ecol. Appl.* **8**: 508–530.
- FEE, E. J. 1976. The vertical and seasonal distribution of chlorophyll in lakes of the Experimental Lakes Area, northwestern Ontario: Implication for primary production measurements. *Limnol. Oceanogr.* **21**: 767–783.
- HOUSER, J. N. 1998. Food web structure and experimental enrichment: Effects on phosphorus sedimentation and retention. M.S. thesis, Univ. of Wisconsin-Madison.
- LEAVITT, P. R., P. SANFORD, S. R. CARPENTER, J. F. KITCHELL, AND D. BENKOWSKI. 1993. Annual fossil records of food-web manipulation, p. 278–309. *In* S. R. Carpenter and J. F. Kitchell [eds.], *The trophic cascade in lakes*. Cambridge Univ. Press.
- LEVINE, S. N., M. P. STANTON, AND D. W. SCHINDLER. 1986. A radiotracer study of phosphorus cycling in a eutrophic Canadian Shield lake, Lake 227, northwestern Ontario. *Can. J. Fish. Aquat. Sci.* **43**: 366–378.
- LINDLEY, D. V. 1985. *Making decisions*. Wiley.
- MCTIGUE, K. M. 1992. Nutrient pulses and herbivory: Integrative control of primary producers in lakes. M.S. thesis, Univ. of Wisconsin-Madison.
- NÜRNBERG, G. K. 1995. Quantifying anoxia in lakes. *Limnol. Oceanogr.* **40**: 1100–1111.
- . 1996. Trophic state of clear and colored, soft- and hard-water lakes with special consideration of nutrients, anoxia, phytoplankton and fish. *Lake Reserv. Manag.* **12**: 432–447.
- . 1999. Determining trophic state in experimental lakes. *Limnol. Oceanogr.* **44**: 1176–1179.
- SANDGREN, C. D. [ED.]. 1988. *Growth and reproductive strategies of freshwater phytoplankton*. Cambridge Univ. Press.
- SCHINDLER, D. W., E. J. FEE, AND T. RUSZCZYNSKI. 1978. Phosphorus input and its consequences for phytoplankton standing crop and production in the Experimental Lakes Area and in similar lakes. *J. Fish. Res. Board Can.* **35**: 190–196.
- , D. W., R. H. HESSLEIN, AND G. KIPPHUT. 1977. Interactions between sediments and overlying waters in an experimentally eutrophied Precambrian Shield lake, p. 235–243. *In* H. L. Golterman [ed.], *Interactions between sediments and freshwater*. Junk.
- SORANNO, P. A. 1997. Factors affecting the timing of surface scums and epilimnetic blooms of blue-green algae in a eutrophic lake. *Can. J. Fish. Aquat. Sci.* **54**: 1965–1975.
- ST. AMAND, A. L., AND S. R. CARPENTER. 1993. Metalimnetic phytoplankton dynamics, p. 210–224. *In* S. R. Carpenter and J. F. Kitchell [eds.], *The trophic cascade in lakes*. Cambridge Univ. Press.
- VOLLENWEIDER, R. A. 1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. *Mem. Ist. Ital. Idrobiol.* **33**: 53–83.
- WALTERS, C. J. 1986. *Adaptive management of renewable resources*. Macmillan.

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