

Impact of dissolved organic carbon, phosphorus, and grazing on phytoplankton biomass and production in experimental lakes

Stephen R. Carpenter

Center for Limnology, University of Wisconsin, 680 N. Park St., Madison, Wisconsin 53717

Jonathan J. Cole

Institute of Ecosystem Studies, Box AB, Millbrook, New York 12545

James F. Kitchell

Center for Limnology, University of Wisconsin

Michael L. Pace

Institute of Ecosystem Studies

Abstract

Phytoplankton biomass and production in lakes tend to be increased by phosphorus input and decreased by grazing or high levels of colored, dissolved organic carbon (DOC). We estimated and compared the effects of these three factors by using data from three lakes that were manipulated during 1991–1995, and data from a reference lake. Multivariate probability distributions of chlorophyll or primary production, as predicted by P input rate, DOC, and grazer length, were fit to the data. All three factors had substantial effects on chlorophyll, primary production, and their variability. Comparable reductions in the mean and variance of chlorophyll and primary production were achieved by reducing P input rate from 5 to 0.5 mg m⁻² d⁻¹, increasing DOC from 5 to 17 mg C liter⁻¹, or increasing mean crustacean length from 0.2 to 0.85 mm. The negative effect of mean crustacean length (an index of size-selective predation) results from grazing by herbivorous zooplankton. The negative effect of DOC on primary producers could be explained by shading. The results suggest that natural variation in colored DOC concentrations is a major cause of variation in primary production.

Understanding the patterns of phytoplankton biomass and primary production in lakes has been a central concern of limnologists for both theoretical and practical reasons. Among the various factors that influence primary production, phosphorus inputs are emphasized for their role in cultural eutrophication (Schindler 1977). Food-web structure, through its influence on grazing, also affects primary production. Size-selective predation by fishes alters planktonic food-web structure (Brooks and Dodson 1965) and was recognized early on as a potential cause of variance in phosphorus–chlorophyll relationships (Vollenweider 1976). Crustacean zooplankton body size is correlated with chlorophyll (Pace 1984; Carpenter et al. 1991). Food-web manipulations that alter zooplankton size cause changes in primary producers (Gulati et al. 1990; Carpenter and Kitchell 1993). Dissolved organic carbon (DOC), especially colored compounds, may have diverse and powerful effects on lake ecosystem metabolism (Wetzel 1990). DOC potentially limits primary production by shading (Jones 1992). Furthermore,

DOC may interact chemically with iron and phosphorus to limit nutrients available to phytoplankton (Jackson and Hecky 1980; Francko 1986). Analyses of phosphorus–chlorophyll relationships hint that lakes with high DOC may not conform to regressions for unstained lakes (Vollenweider 1976). However, the net effects of DOC on chlorophyll and primary production are not as well known as are those of phosphorus and grazing.

Although a diverse literature documents various effects of these three factors, their relative strengths and interactions are poorly understood. One reason for poor resolution is that it is difficult to obtain data in which the three factors vary independently at the whole-lake scale. We obtained such data by deliberate manipulation of P inputs and the food web in lakes with contrasting DOC concentrations. In this paper, we describe the joint effects of P, DOC, and grazing on chlorophyll and primary production.

It is extremely difficult to predict the interlake and temporal patterns of primary production in our experimental lakes, or in lakes in general. Regressions using multilake data demonstrate strong correlations, but predictions from such models have high variances. Furthermore, the predictions apply to populations of lakes and may not be pertinent to a specific lake of interest. Deterministic simulation models can examine mechanisms in individual lakes, but require many structural assumptions and the estimation of many parameters. Prediction errors of such models are substantial, although they are estimated only rarely.

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Our analysis is closer to the regression approach than to the simulation approach, and offers improvements on both. Like regressions, our models account for key drivers and their interactions by using relatively few parameters that can be estimated directly from the data. The models also account for autocorrelation in the time-series data. The predictions are probability distributions, which explicitly account for the trends in the data as well as the variability. A comparison of probability distributions for contrasting scenarios of interest (say, high vs. low P input rates) provides a complete description of the shifts in chlorophyll or primary production predicted using the data. The predicted probability distributions are obtained by Bayesian analysis of a multiple regression model (Gelman et al. 1995).

Whole-lake experiments

The whole-lake experiments were conducted in small, deep lakes near Land O' Lakes, Wisconsin (89°32'W, 46°13'N; Carpenter et al. 1996; Christensen et al. 1996). Paul Lake has not been manipulated and has served as a reference ecosystem. Its food web is dominated by piscivorous largemouth bass, and large daphnids are its dominant grazers. Peter Lake's food web has been dominated by planktivorous minnows since 1991 and its grazers are predominantly rotifers and small copepods. Beginning in 1993, Peter Lake was enriched with P and N (N:P ≈ 25 by atoms). Long Lake was divided by plastic curtains into east, central, and west basins in 1991. The east and west basins were used for these experiments. The food web of west Long Lake is dominated by piscivorous largemouth and smallmouth bass. Large daphnids are the dominant grazers. After the curtains were installed in 1991, east Long Lake became stained and its DOC concentrations increased (Christensen et al. 1996). Concentrations of DOC in east Long Lake are 7.1–17.1 mg C liter⁻¹, while those of the other three lakes are 3.8–12.6 mg C liter⁻¹. East Long Lake's food web includes planktivorous sticklebacks and bluegill. Grazer body size and species composition have been highly variable, ranging from rotifer dominance in some weeks to daphnid dominance at other times. All basins of Long Lake were enriched with P and N (N:P ≈ 25 by atoms) beginning in 1993.

These experiments have indicated strong effects of P input rate, grazing, and DOC on primary producers (Carpenter et al. 1996; Christensen et al. 1996). Chlorophyll and primary production of Paul Lake have remained relatively low and moderately variable (Fig. 1). Chlorophyll and primary production of Peter Lake (small-bodied grazers and relatively low DOC concentrations) have responded strongly to enrichment. In contrast, chlorophyll and primary production of west Long (large-bodied grazers and relatively low DOC concentrations) and east Long (variable grazers and relatively high DOC concentrations) Lakes showed a modest increase to experimental enrichment.

The July data depicted in Fig. 1 do not include substantial short-term variability that occurred during other summer months. A planktivore dieback in August 1994 caused a brief outbreak of *Daphnia* and temporary reduction in chlorophyll (Carpenter et al. 1996). DOC concentrations in east

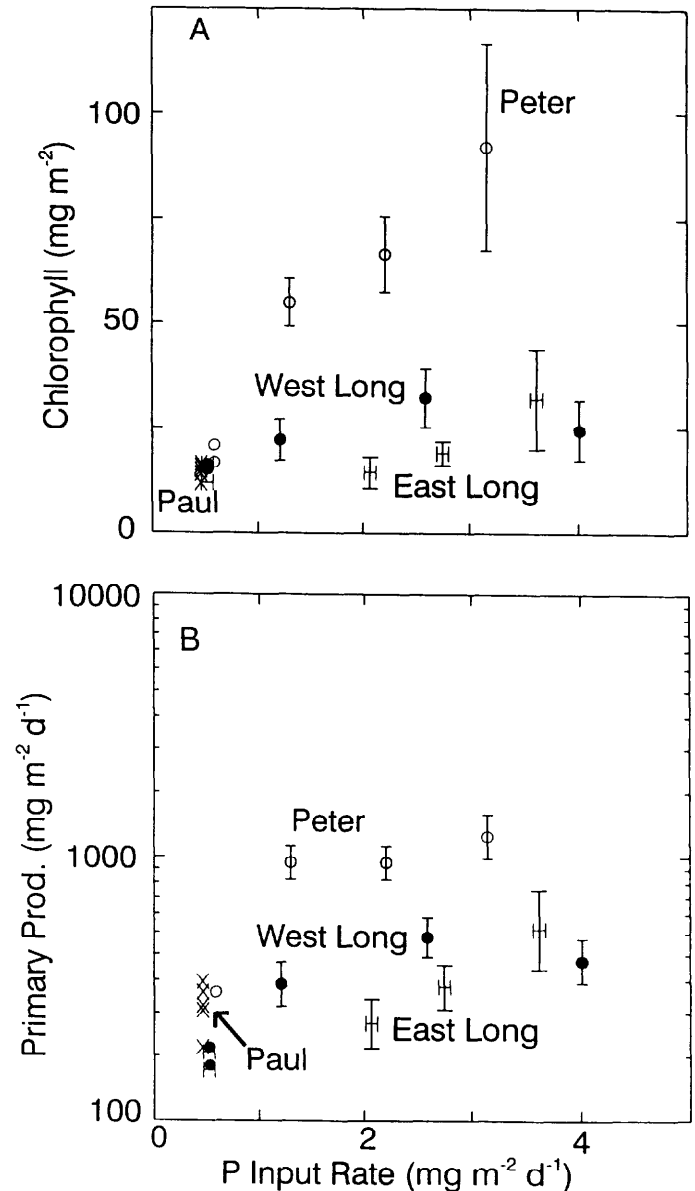


Fig. 1. Chlorophyll (A) and primary production (B) vs. phosphorus input rate for Paul Lake (×, the reference lake), Peter Lake (○), West Long Lake (●), and East Long Lake (H). Data points are means for July during 1991–1995. Error bars (standard errors) are shown for years of experimental enrichment.

Long Lake increased over a 2-year period and were accompanied by considerable variability in grazer size and chlorophyll (Christensen et al. 1996). Such events must be accounted for in a quantitative assessment of P, DOC, and grazer effects. A comprehensive analysis of the entire data, including the unexplainable variability, is the objective of this paper.

Methods

Limnological analyses—This paper is based on weekly data for chlorophyll, primary production, light extinction, P

input rate, DOC, and the grazer community for summer stratification (approximately mid-May to early September) during 1991–1995 in Paul, Peter, east Long, and west Long lakes. Details of our methods are available elsewhere (Carpenter and Kitchell 1993).

Each week in each lake a temperature profile was measured at a central station. A light profile was measured using a submersible spherical quantum sensor and a deck cell. Extinction coefficients (k) for epilimnetic water were calculated by regression. Chlorophyll was measured fluorometrically at depths corresponding to 100, 50, 25, 10, and 5% of surface irradiance (Carpenter and Kitchell 1993). DOC was measured on a pooled epilimnetic sample using either an Astro 2001 TOC analyzer with persulfate and UV oxidation (1991–1993) or a Shimadzu model 5050 high-temperature TOC analyzer (1994–1995). Zooplankton were collected by vertical hauls of a calibrated 80- μm mesh net, preserved in cold sugared formalin, and measured and enumerated by species. Here we use mean crustacean body length as an index of size-selective predation and grazing intensity (Pace 1984; Carpenter et al. 1991). Primary production was measured in situ by the ^{14}C method at the same depths sampled for chlorophyll. Primary production was calculated as described in Carpenter and Kitchell (1993). Briefly, primary production rates were regressed against chlorophyll, irradiance, dissolved inorganic carbon (DIC) concentration, and temperature. The regressions were used to calculate daily predictions of primary production from continuous measurements of surface irradiance and interpolated values of chlorophyll, DIC, and temperature. Daily values were averaged by week to yield time series with the same frequency of observation as chlorophyll.

Statistical analyses—We described the data (3 experimental lakes \times 5 years \times 16 profiles per year) as probability distributions of chlorophyll or primary production predicted from P input rate, DOC, and grazer size. The distributions provide a full description of the data, including the trends and all of the variability that we observed. This description makes it possible to visualize and compare the outcomes of specific scenarios of interest by plotting the predicted distributions of chlorophyll or primary production for particular combinations of P input rate, DOC, and grazer size.

The distributions were calculated by Bayesian analysis of a multiple regression model that includes a term to correct for autocorrelation in the errors. The analysis yields distributions of response variates (chlorophyll or primary production) that result from specified combinations of predictors (P input rate, DOC concentration, and grazer size). Gelman et al. (1995) provided a complete account of the Bayesian methods used in this paper. Our analyses assumed that the predicted probability distributions depended on our data alone, and did not depend on any additional or external information. This assumption is termed a noninformative prior distribution (Gelman et al. 1995).

The analysis resembles a multiple regression but the interpretation is completely different (Ellison 1996; Gelman et al. 1995). The Bayesian analysis yields probability distributions for predicted values of chlorophyll or primary production. These distributions give the probability that a par-

ticular predicted value will be in fact observed (Gelman et al. 1995). In contrast, conventional multiple regression analyses used most commonly in limnology predict confidence intervals that include the true value of the response variate in a given percentage of independent, identical studies (Ellison 1996).

Probability distributions of chlorophyll and primary production were calculated using the model

$$Y_{t+1} = \phi Y_t + \mathbf{b}'\mathbf{X}_t + E_t, \quad (1)$$

where the subscript t denotes time, ϕ is an autoregression parameter, Y is the response variate (chlorophyll or primary production, log-transformed). E is an independently, identically and normally distributed prediction error with mean 0 and variance s^2 . \mathbf{X} is a vector of predictors

$$\mathbf{X}_t = [1 P_t C_t Z_t P_t \times C_t P_t \times Z_t C_t \times Z_t P_t \times C_t \times Z_t]'. \quad (2)$$

P is phosphorus input rate, C is DOC concentration, and Z is mean crustacean length. The regression coefficients corresponding to the predictors in \mathbf{X} comprise the column vector \mathbf{b} . Eq. 1 and 2 are a multiple regression that includes all predictors and their interactions, along with an autoregressive parameter to correct for autocorrelation. Point predictions of this model explained a substantial amount of the variation in the data (*see results*). Residuals were approximately normally distributed, had no significant autocorrelations, and had no apparent trends over time.

For any specified set of predictor values, Eq. 1 converges to a steady-state distribution for which $Y = Y_{t+1} = Y_t$:

$$Y = [1/(1 - \phi)](\mathbf{b}'\mathbf{X} + E). \quad (3)$$

Here \mathbf{X} is a vector of predictor values (conforming to Eq. 2) for which the probability distribution of Y is to be calculated. The probability distribution of Y conditional on \mathbf{X} is a t -distribution with $n - 9$ degrees of freedom where n is the number of observations and 9 is the number of parameters (ϕ plus the eight elements of \mathbf{b}) (Gelman et al. 1995). The mean of the t -distribution is

$$\text{mean}(Y) = [1/(1 - \phi)]\mathbf{b}'\mathbf{X} \quad (4)$$

The variance of the t -distribution is

$$\text{var}(Y) = \mathbf{Q}'\mathbf{C}\mathbf{Q} + [s^2/(1 - \phi)^2], \quad (5)$$

where \mathbf{Q} is a vector composed of the partial derivatives of Y with respect to each of the 9 parameters. The first 8 elements of \mathbf{Q} are $\mathbf{X}'/(1 - \phi)$ and the ninth element is $(\mathbf{b}'\mathbf{X})/(\phi - 1)^2$. The 9×9 covariance matrix of parameters, \mathbf{C} , and the residual variance s^2 are calculated by regression analysis of Eq. 1 (Draper and Smith 1981).

In summary, the steady-state probability distribution of log chlorophyll or log primary production resulting from specified levels of P input rate, DOC concentration, and grazer size is a t -distribution with mean and variance calculated by Eq. 4 and 5, and degrees of freedom $n - 9$. Because our data provide high degrees of freedom (210), we substituted normal distributions for t -distributions. For high degrees of freedom, these curves cannot be distinguished graphically, but the normal curve is much easier to compute. Distributions of chlorophyll and primary production in the

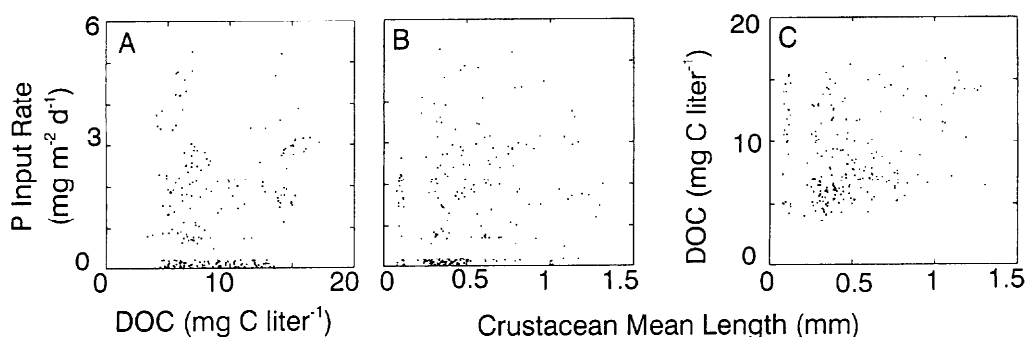


Fig. 2. Independent variates for the ecosystem experiments. A. P input rate vs. DOC ($r = 0.140$). B. P input rate vs. mean length of crustacean zooplankton ($r = 0.219$). C. DOC vs. mean length of crustacean zooplankton ($r = 0.238$). For all plots, $n = 219$.

untransformed units were computed as log-normal distributions (Gelman et al. 1995).

Results

In the experimental lakes, data were obtained at a wide range of combinations of the predictors—P input rate, DOC concentration, and grazer length (Fig. 2). The predictors were weakly correlated. Perfectly uncorrelated predictors are desirable for statistical analysis (Draper and Smith 1983) but are generally not found in field data.

Chlorophyll and primary production show weak bivariate correlations with the predictors (Fig. 3). P input rate is positively correlated with chlorophyll and primary production, while DOC and grazer length are negatively correlated with

primary production. There is considerable scatter in the bivariate plots.

Multiple regression using all three predictors and the autoregressive term, however, successfully explained variations in mean chlorophyll (Fig. 4A) and primary production (Fig. 4B). Week-to-week predictions depend in part on autoregressive terms (for chlorophyll, $\phi = 0.51$, $s = 0.06$; for primary production, $\phi = 0.54$, $s = 0.06$). Significant effects of P, DOC and grazer length remained after autoregressive effects were removed statistically.

The multiple regression models are highly significant by conventional statistical standards, yet the predictions have substantial scatter on log-transformed axes (Fig. 4). The Bayesian analysis depicts that variability as probability distributions for scenarios within the range of the data.

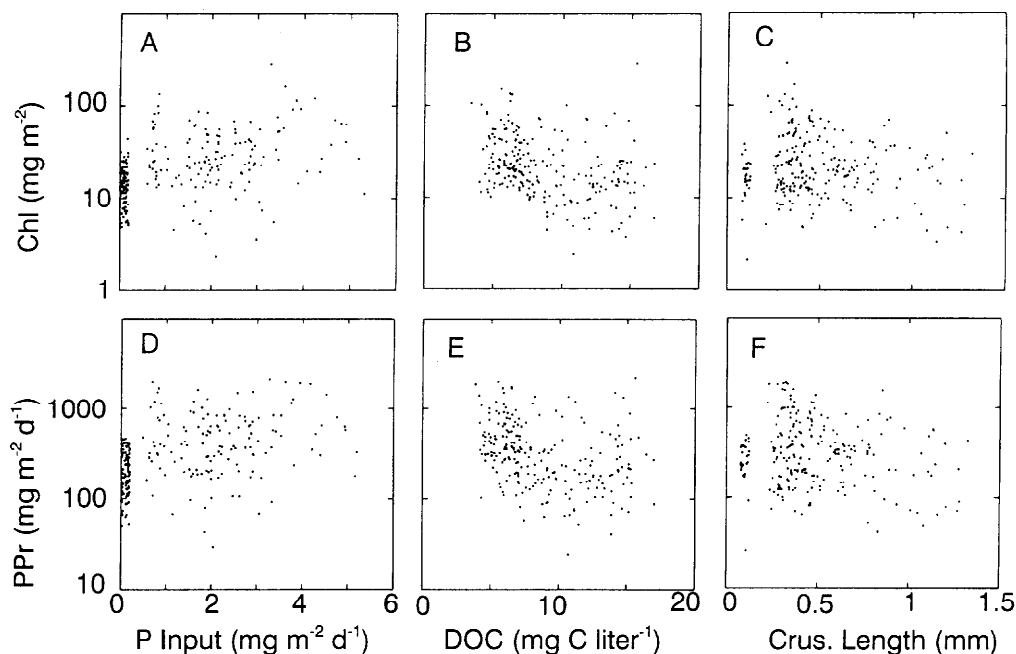


Fig. 3. Scatter plots of response variates (note logarithmic axes) and independent variates. A. Chlorophyll vs. P input ($r = 0.431$). B. Chlorophyll vs. DOC ($r = -0.337$). C. Chlorophyll vs. mean crustacean length ($r = -0.116$). D. Primary production (PPr) rate vs. P input ($r = 0.429$). E. Primary production vs. DOC ($r = -0.327$). F. Primary production vs. mean crustacean length ($r = -0.150$). For all plots, $n = 219$.

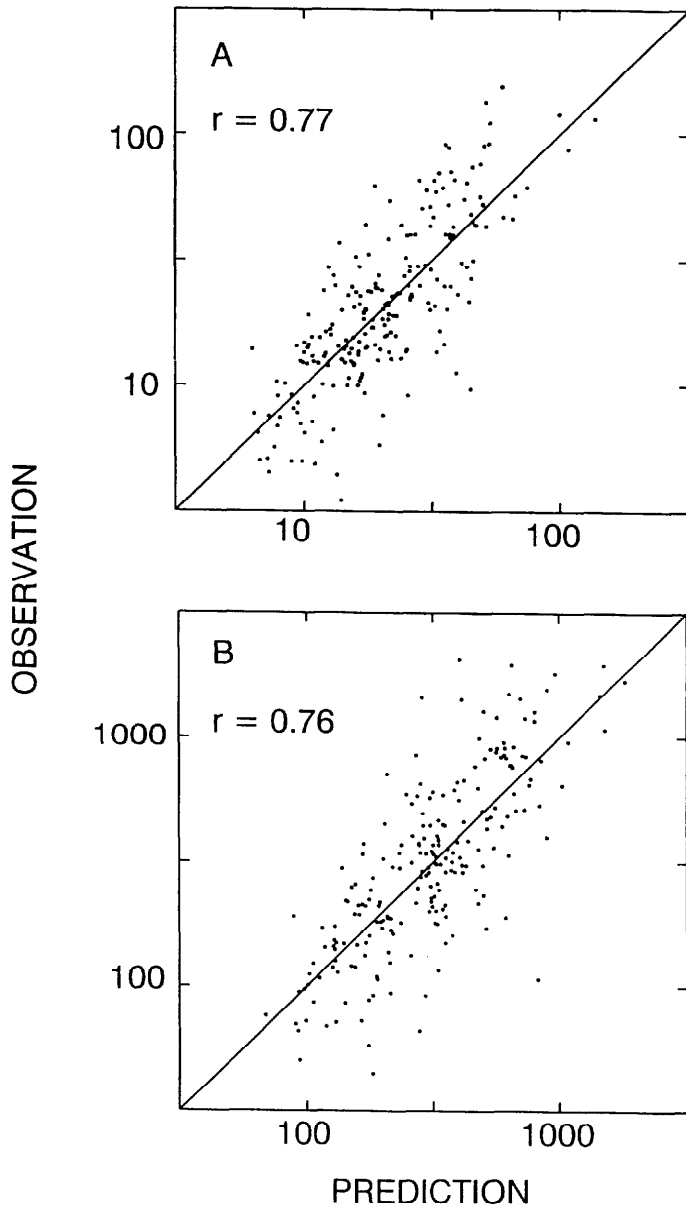


Fig. 4. Scatter plots of observations vs. predictions of the mean for (A) chlorophyll (mg m^{-2}) and (B) primary production ($\text{mg m}^{-2} \text{d}^{-1}$). Note logarithmic axes. For both plots, $n = 219$.

Probability distributions indicate the responses of chlorophyll (Fig. 5) or primary production (Fig. 6) to selected combinations of P input rate, DOC concentration, and grazer length. A sharply peaked distribution indicates a narrowly defined response with low variance, whereas a low, flat distribution indicates a highly variable response. For given values of DOC and grazer length, P enrichment generally causes chlorophyll and primary production to increase and become more variable. For example, when DOC is $5 \text{ mg C liter}^{-1}$ and crustacean mean length is 0.3 mm , P input of $1 \text{ mg m}^{-2} \text{d}^{-1}$ yields moderately variable chlorophyll with a mode of $\sim 15 \text{ mg m}^{-2}$ (Fig. 5A). If P input is increased to $3 \text{ mg m}^{-2} \text{d}^{-1}$, chlorophyll becomes highly variable (indi-

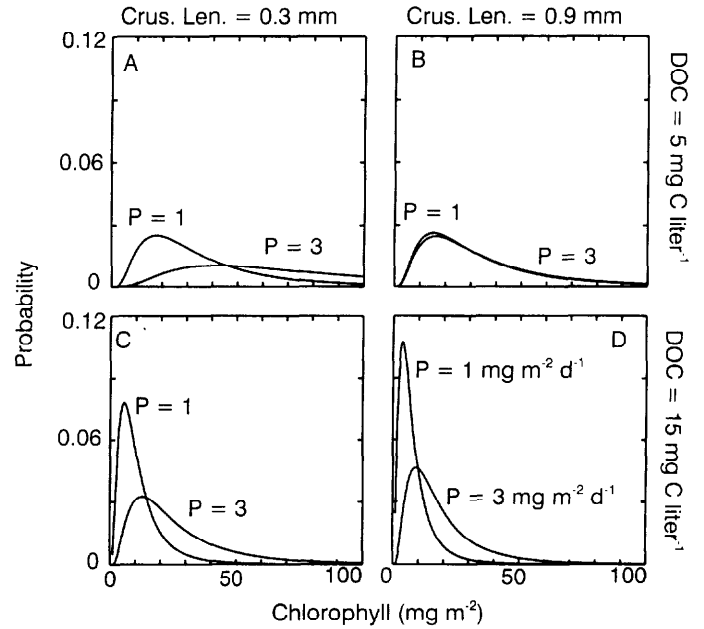


Fig. 5. Steady-state probability distributions for chlorophyll in eight scenarios: all combinations of low and high values for P input rate, DOC concentration, and crustacean mean length. The area under each curve is 1. Low, flat distributions indicate that chlorophyll is highly variable; sharply peaked distributions indicate that chlorophyll has low variability.

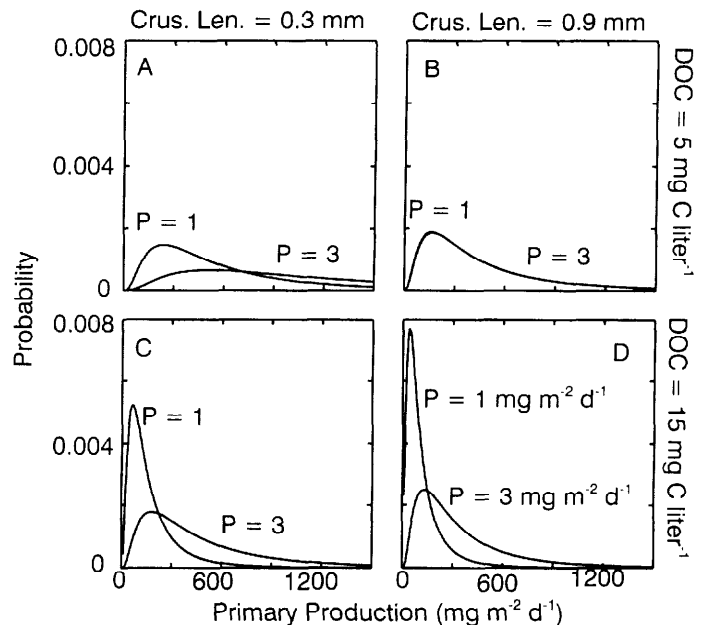


Fig. 6. Steady-state probability distributions of primary production for eight scenarios: all combinations of low and high values for P input rate, DOC concentration, and crustacean mean length. The area under each curve is 1. Low, flat distributions indicate that primary production is highly variable.

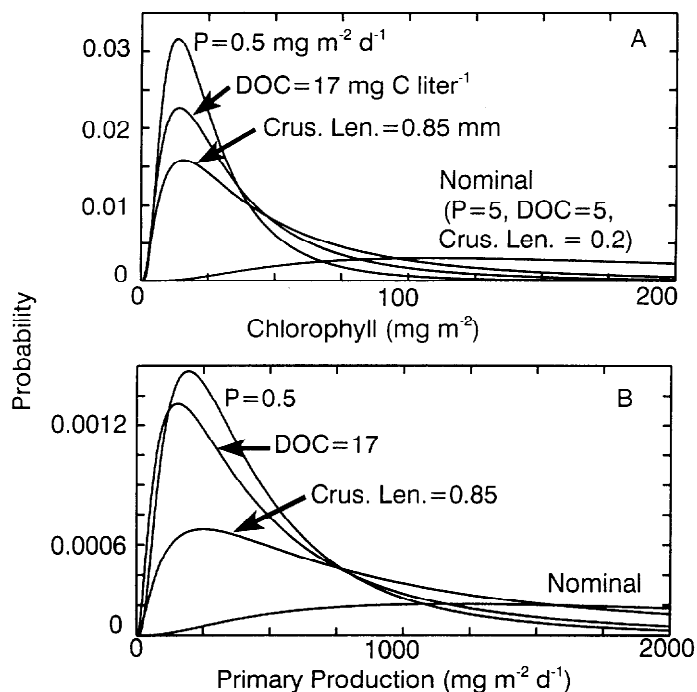


Fig. 7. Steady-state probability distributions of (A) chlorophyll and (B) primary production for a nominal, eutrophic scenario and scenarios in which only one factor is changed while the other factors are held at the nominal values. The changes were chosen to reduce chlorophyll and primary production. P input rate was reduced to one-tenth of the nominal value. Increases of DOC and crustacean length were chosen to yield chlorophyll distributions with the same mode as the chlorophyll distribution that resulted from P reduction.

cated by the low, flat distribution) with a modal value of $\sim 40 \text{ mg m}^{-2}$.

Increasing DOC concentrations or grazer lengths generally decrease the mean and the variability of chlorophyll and primary production. Consequently, P enrichment has much weaker effects when DOC concentrations are high or grazers are large. Consider the scenario with DOC of $15 \text{ mg C liter}^{-1}$ and crustacean mean length of 0.9 mm (Fig. 5D). When P input rate is $1 \text{ mg m}^{-2} \text{ d}^{-1}$, chlorophyll variability is very low (indicated by the sharply peaked distribution), with a modal value of $\sim 3 \text{ mg m}^{-2}$. If P input rate is increased to $3 \text{ mg m}^{-2} \text{ d}^{-1}$, chlorophyll variability increases and the mode shifts to $\sim 10 \text{ mg m}^{-2}$. However, the increase in variability and mean chlorophyll with enrichment is far less than occurred at low DOC and crustacean length (compare Fig. 5D and 5A).

The interactive effects of DOC and grazers on the response to P inputs in lakes were complex (Figs. 5, 6). For example, P enrichment had little effect when DOC was $5 \text{ mg C liter}^{-1}$ and crustacean length was 0.9 mm (Figs. 5B, 6B).

Eutrophication increases the variance as well as the mean of phytoplankton biomass and production (Fig. 7). The probability distribution for a typical eutrophic condition (nominal scenario in Fig. 7) has modal chlorophyll of $\sim 120 \text{ mg m}^{-2}$ and high variability as indicated by the low, flat distribution. Such high variability is known from many eutrophic lakes

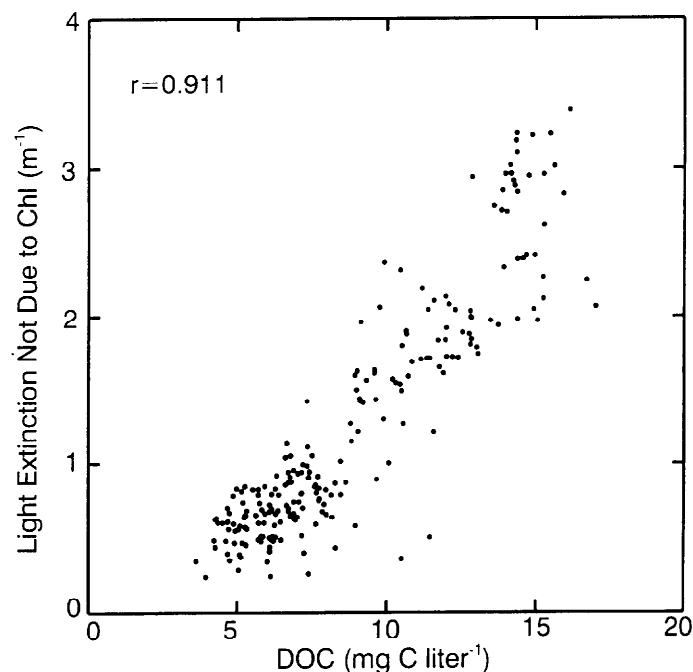


Fig. 8. Scatter plot of light extinction that is not explainable by chlorophyll vs. DOC concentration ($n = 219$).

where phytoplankton blooms develop and decline repeatedly. The modal chlorophyll can be shifted to $\sim 15 \text{ mg m}^{-2}$, with substantial reductions in variability, by reducing P input rate to $0.5 \text{ mg m}^{-2} \text{ d}^{-1}$, increasing DOC concentration to $17 \text{ mg C liter}^{-1}$, or increasing crustacean mean length to 0.85 mm . These changes also reduce primary production and decrease its variability relative to the nominal, eutrophic scenario.

The negative effect of DOC on chlorophyll and primary production is explainable by light extinction by DOC. To compare light extinction by chlorophyll and DOC, we fit the regression

$$\Delta k = b_0 + b_1 \Delta \text{Chl} + b_2 \Delta \text{DOC}. \quad (6)$$

Time series for the light extinction coefficient (k), chlorophyll (Chl) and DOC were used to estimate the parameters b_0 , b_1 , and b_2 by ordinary least squares. Week-to-week differencing, denoted by the Δ s, was necessary to eliminate autocorrelation and the parameter bias that it causes (Box et al. 1994). Residuals were approximately normal and had no significant autocorrelations.

The parameter estimates showed that both chlorophyll and DOC had strong and significant effects on light extinction. Parameter estimates (standard errors in parentheses, $n = 219$) are $b_0 = 0.0213 \text{ m}^{-1}$ (0.0164), $b_1 = 0.0177 \text{ m}^2 \text{ mg}^{-1}$ (0.00177), and $b_2 = 0.0514 \text{ m}^2 \text{ g}^{-1}$ (0.0190). The extinction coefficient for chlorophyll, $0.0177 \text{ m}^2 \text{ mg}^{-1}$, is close to values found by others. A review by Bannister (1974) concluded that chlorophyll extinction coefficients in natural waters averaged $0.016 \text{ m}^2 \text{ mg}^{-1}$ (range, 0.013–0.020).

Light extinction that cannot be explained by chlorophyll is highly correlated with DOC concentration (Fig. 8). Light extinction not attributable to chlorophyll was calculated us-

ing the mean extinction coefficient of Bannister (1974) and subtracted from extinction coefficients measured in the field to estimate the light extinction not explainable by chlorophyll.

Discussion

Although chlorophyll and primary production are often correlated, we were uncertain whether they would respond in parallel to our manipulations. Models and bag experiments have suggested that grazing affects chlorophyll and primary production differently (Carpenter and Kitchell 1993). Shading by DOC could potentially stimulate increased chlorophyll production by cells while reducing carbon fixation. However, the responses of chlorophyll and primary production in these whole-lake experiments were very similar. This finding corroborates other whole-lake experiments that document parallel responses of chlorophyll and primary production to nutrients (Schindler et al. 1978) and grazing (Carpenter and Kitchell 1993). DOC suppressed both primary production and chlorophyll in similar ways.

These data demonstrate strong effects of DOC on primary producers. Similar responses have occurred in earlier studies (Jackson and Hecky 1980; Jones 1992). Shading by DOC can explain, in the statistical sense, the negative effects on primary producers in our experimental lakes. However, the responses we observed may also involve more complex chemical mechanisms (Francko 1986; Juttner and Faul 1984) that were not examined in this study.

P input rate, DOC, and grazing have substantial effects on primary producers in our experimental lakes. Primary production rate could be reduced ~20% by decreasing P input rate $1 \text{ mg m}^{-2} \text{ d}^{-1}$, increasing DOC concentration $4 \text{ mg C liter}^{-1}$, or increasing grazer mean length by 1 mm. How do these shifts compare with the ranges known from the world's lakes? P input rates of most natural lakes with relatively undisturbed watersheds are $<2\text{--}3 \text{ mg m}^{-2} \text{ d}^{-1}$, although values as large as several hundred $\text{mg m}^{-2} \text{ d}^{-1}$ are known from culturally eutrophic lakes (Canfield and Bachman 1981). The wide range of P input rates among lakes, caused in part by human activities, accounts for the statistical power of P as a predictor of chlorophyll and primary production. Mean crustacean lengths vary by ~1.2 mm among the world's lakes (Carpenter et al. 1996). This range is large enough to have substantial effects on primary producers. However, the potential for control of primary producers by crustacean grazers is limited by this range of grazer sizes. Thus, the scope for regulation of primary production by grazing is less than that for regulation by P or DOC. The range of DOC concentrations among lakes is ~50 mg C liter^{-1} (Perdue and Gjessing 1990). This range is more than threefold greater than that observed in our experiments. DOC is a potentially powerful cause of variation among lakes in primary production.

The relationship of colored DOC concentrations to phytoplankton production may be nonlinear beyond the range of our data. At very low DOC concentrations, high UV transmission may have negative effects on phytoplankton (Morris et al. 1995). Through UV attenuation, DOC, and

phytoplankton production may be positively related at relatively low DOC concentrations. At the DOC concentrations of our experimental lakes, UV transmission is negligible (Morris et al. 1995) and increasing DOC concentrations have negative effects on primary producers. These patterns suggest the hypothesis that primary production is maximized at an intermediate DOC concentration near or below the lower range of our data (~4 mg C liter^{-1}).

Regulation of phytoplankton by colored DOC may have important functional differences from regulation by P or grazing. Both P and grazers have strong feedbacks with phytoplankton. Phytoplankton growth reduces P standing stocks and leads to sedimentation of P. Predator-prey interactions between phytoplankton and zooplankton also involve strong negative feedbacks. Colored DOC, however, has negative effects on phytoplankton whereas negative effects of phytoplankton on colored DOC may be weak (Carpenter and Pace 1996). Thus, phytoplankton may lack feedback mechanisms for overcoming limitation by humic substances.

Our analysis shows that three key factors, P input, grazing, and DOC, account for much of the variability in chlorophyll and primary production. Because of the broad variations in P input caused by human activity, the effects of P are strong in multilake comparisons, despite fluctuations in DOC and grazing. If cultural eutrophication had not produced an enormous range of P input rates among lakes, comparative limnologists would conclude that DOC and grazing were the most important factors controlling lake productivity. Interlake differences in grazing derive from complex interactions in the food web, and can vary substantially from year to year (Carpenter and Kitchell 1993). Interlake variation in DOC is correlated with the extent of wetlands in the watershed (Hemond 1990, Kortelainen 1993). Wetlands are thought to mitigate eutrophication by nonpoint pollution, but the capacity of riparian wetlands to retain P is variable (Gilliam 1994). Our results suggest that DOC production by wetlands may be as important as P retention in the regulation of lake productivity and eutrophication. The extent of wetlands in the watershed and their contribution of colored DOC to lakes are likely a key driver of variation in productivity.

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