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ABSTRACT

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Using chlorophyll and phosphorus data from 119 Missouri reservoirs we show how data aggregation – averaging data into seasonal means or long-term lake means – influences our ability to make inferences from large-scale statistical regression analyses. We demonstrate the most obvious phenomenon of data aggregation, that relations between variables estimated from aggregated data are generally stronger than the same relations estimated from unaggregated data. Averaging reduces the often large variation in the response of chlorophyll to phosphorus (Chl-TP) that characterizes measurements of these variables in lakes. We also demonstrate that inferences made from statistical regression analyses apply only to situations that match the level of aggregation used to produce the model. Using lake means we found a strong positive Chl-TP relation. This strong cross-sectional pattern among lakes in the study, however, did not always reflect the relation of these variables to one another in individual lakes. And the cross-sectional pattern has limited value in predicting conditions in unaggregated data. The effect of aggregation on the estimated strength of a regression relation serves as a caution in transferring inferential statements about the effect of TP on Chl between temporal scales and among lakes.

Key Words: chlorophyll, phosphorus, aggregation, models.

Any historical review of scientific achievements in limnology would highlight the impact of large-scale comparative lake studies on our ability to identify key variables that influence lake structure and processes (Peters 1986). The report by Vollenweider (1968) is sometimes considered a starting point for this approach, but studies by Deevey (1940), Rawson (1955), and Edmondson (1961) are earlier examples of its skillful use. In the comparative approach, extensive collections of data from many lakes are evaluated to identify statistical relations between variables that are powerful enough to stand out against other sources of among-lake variation (Collins and Sprules 1983). These general patterns, typically based on averaging and regression analysis, are called empirical models and describe the composite pattern of the response variable and explanatory factor within the population of lakes being studied. These analyses are typically conducted over a range of lakes without regard to lake identity in individual data points, and the effects of unmeasured variables on the relation exist as residual error. Resulting models prompt subsequent work on explanatory theory, and lake managers use them to make predictions and formulate policy (Peters 1986). A key element of this approach is that we assume processes responsible for the large cross-sectional patterns also operate within single systems over time (Prairie and Marshall 1995).

The chlorophyll-phosphorus relation (Chl-TP, Fig. 1) is a familiar empirical model in limnology. Deevey (1940) first described the correlation between these variables in Connecticut lakes, and using data from Japanese lakes, Sakamoto (1966) showed the response of algal biomass to phosphorus was linear on a log-log scale. Both authors averaged chlorophyll and

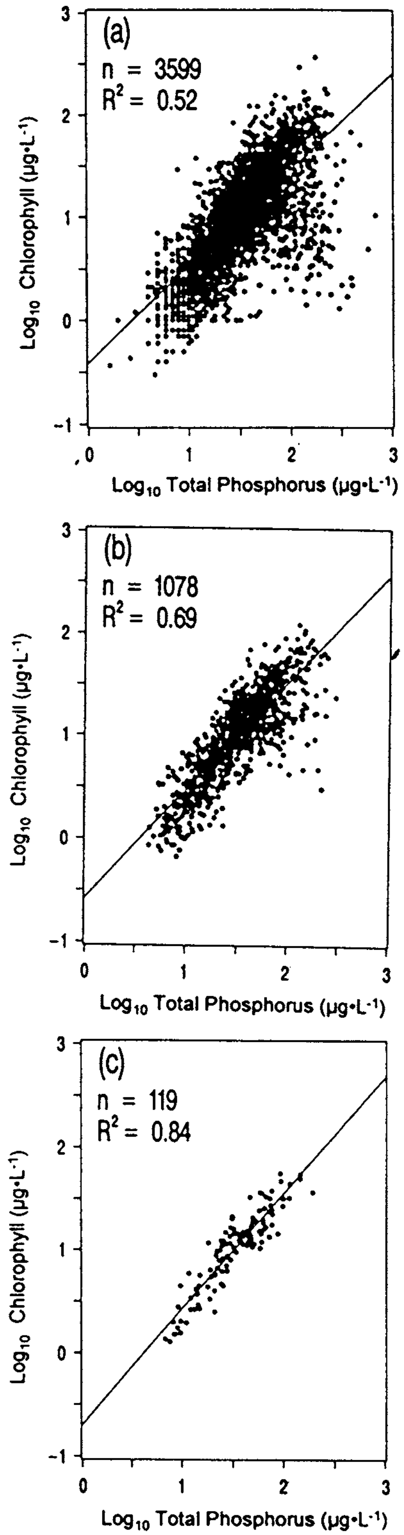


Figure 1.–Chlorophyll-TP relations at different levels of aggregation. a) Individual Observations – data points are from Chl and TP analyses conducted on individual samples of lake water. Fitted regression model is Log_{10} Chl = -0.42 + 0.94 * Log_{10} TP, R^2=0.52. b) Seasonal means – data points are averages of individual observations in a given lake during a particular summer. Fitted regression model is Log_{10} Chl = -0.58 + 1.05 * Log_{10} TP, R^2=0.69. c) Lake means – data points are averages of the seasonal means for each lake. Fitted regression model is Log_{10} Chl = -0.70 + 1.13 * Log_{10} TP, R^2=0.84.

phosphorus measurements from their various study lakes into seasonal mean values prior to statistical treatment. Since then, scores of publications have described models predicting average algal chlorophyll from mean phosphorus values. Among these, there are global models based on lake data from several continents (Dillon and Rigler 1974, Jones and Bachmann 1976, OECD 1982), regional models (Canfield 1983, Quiros 1990, Jones and Knowlton 1993), and models for individual lakes (Edmondson 1972, Smith and Shapiro 1981, Knowlton and Jones 1990). In some data sets, algal biomass responds in a non-linear, or sigmoidal fashion to phosphorus (McCauley et al. 1989, Watson et al. 1992, Knowlton and Jones 1993). Variability in regressions of Chl on TP arises from a variety of physical, chemical, and biotic factors. Light limitation, water residence time, nitrogen limitation, zooplankton grazing, and other conditions have been identified as important (Sakamoto 1966, Shapiro 1980, Straskraba 1980, Hoyer and Jones 1983, Riley and Prepas 1985). Generally ignored, however, is that the practice of data aggregation—averaging data into means—can affect the quantitative features of these models and the perceived influence of other limiting factors (Knowlton et al. 1984).

When an empirical Chl-TP model, formulated using seasonal means or long-term lake means (aggregated data), is used to draw inference or make predictions at finer scales (unaggregated data), there is an implicit assumption that the relation remains the same at these various scales. If the identity of individual lakes is irrelevant in identifying a cross-sectional pattern in regression analysis on aggregated data, then this assumption, and inferences, are appropriate. However, if the Chl-TP relation differs among lakes, or within any given lake over time, then it is inappropriate to ignore scale (level of aggregation) in making inferences or predictions from cross-sectional models. Possible differences in Chl-TP relations among lakes include both differences in the underlying regression equation and differences in the observed ranges of Chl and TP. Both phenomena may cause regressions developed from data at one level of aggregation to differ from those developed at another level or scale.

The 'effects of data aggregation' on the results of regression analysis can be grouped into two broad categories: effects on the strength of Chl-TP relations as judged by the coefficient of determination, and effects on the functional form of regression equations. The impact of data aggregation on the strength of the relation, which impacts our level of confidence in prediction of Chl based on observed TP, is a well-known statistical phenomenon. Yule and Kendall (1950) were among the first to recognize that relations among variables estimated from aggregated data tend to be stronger than the same relations estimated from unaggregated data. The effect of data aggregation on regression equations themselves poses a more difficult problem for statistical treatment, because these effects involve problems of model misspecification (Langbein and Lichtman 1978). If present, both types of aggregation effect have the potential to invalidate inferences about individual lakes made on the basis of models from aggregated data.

The purpose of this paper is to use observations from a large data base on Missouri reservoirs to demonstrate how data aggregation influences our ability to transfer inferences from large-scale comparative analyses of Chl-TP relations to finer scales. It is important in limnology to understand the implication of models based on aggregated data. Inferences from data expressed as seasonal or lake means provide us with functional theories about system characteristics and allow us to predict conditions in unsampled systems. Understanding the conditions under which aggregation is likely important to scientific investigation is a topic of current research (e.g., Cressie 1996). The results presented are also pertinent for a variety of other empirical relations based on data aggregation (Peters 1986).

Database

Data for this analysis come from studies of Missouri reservoirs during 1978 to 1996 in which samples during summer have been used to characterize in-lake conditions and processes (e.g., Knowlton et al. 1984, Jones and Knowlton 1993). This large data set allows us to evaluate the Chl-TP relation at several levels to determine the effect of aggregating data and determine whether aggregate models describe individual lake behavior. Our approach was to screen the historic data set and select reservoirs with from 6 to 14 seasonal means (each with 2 to 14 samples per summer). Analyses were conducted using individual observations (conditions in a reservoir on a given sampling date, n=3599), seasonal means (n=1078), and lake means (average of the seasonal means, n=119). A summary of these data, at the level of the lake mean, is given in Table 1. Unpublished data from Lake Woodrail, located in central Missouri, was used to illustrate the variability of chlorophyll and phosphorus in a single lake. This lake was sampled each day during May through August 1992-96 (n=5 seasons). All measurements are from summer and these data come from a single laboratory and, therefore, minimize the effects of time scale and methodology on the residual variance in these analyses (Nicholls and Dillon 1978).

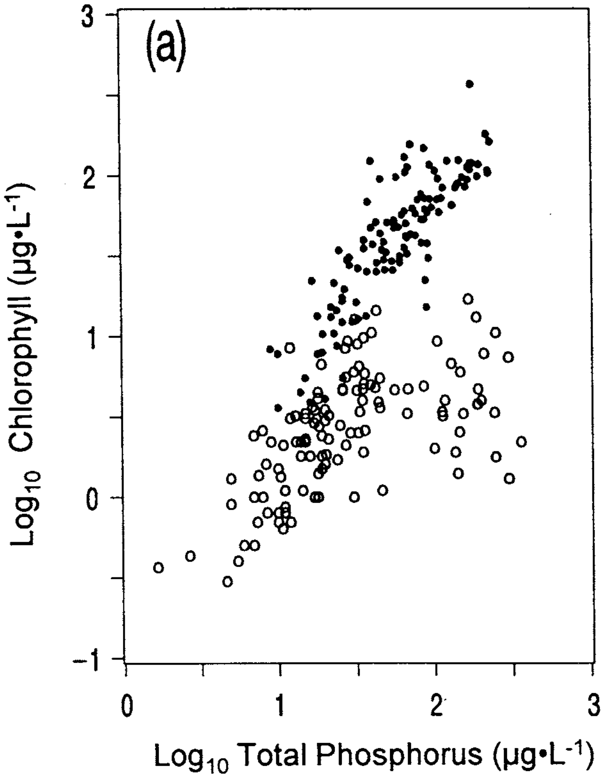
Table 1.–Data set characteristics. Data were collected between 1978 and 1996 from 119 reservoirs in Missouri. Means of CHL and TP are weighted by lake and are back-transformed from the $\log_{10}$ units in which they were calculated.

	Mean	Range
Years per Lake	9.1	6 - 14
Days per Year	3.4	2 - 14
CHL ($\mu g.L^{-1}$)	10.4	0.3 - 368
TP ($\mu g.L^{-1}$)	33.3	1.7 - 692

Results

The effect of data aggregation on Chl-TP in 119 Missouri reservoirs is shown in Fig. 1. Variation about the regression is clearly a function of averaging; the relation strengthens with higher levels of aggregation. Among individual observations there was a 18-fold range in Chl at any given level of TP (Fig. 1a) with a coefficient of determination (R^2) of 0.52. Variation in Chl at fixed levels of TP dropped to ninefold among seasonal means with an R^2 of 0.68 (Fig. 1b). When data were averaged to the level of the lake mean, the range in Chl for given TP value was about fourfold and the R^2 was 0.84. Even though the aggregated data show a stronger relation than unaggregated data, linear regressions fitted to log transformed data in Fig. 1 were similar. The lake mean model did not differ from the other two relations ($p>0.05$, using a standard general linear test). This finding is in keeping with the hypothesis that a cross-sectional pattern between TP and Chl in this population of lakes is the same at each level of aggregation.

To demonstrate variation in Chl-TP in unaveraged data, we plotted the maximum and minimum Chl value from each lake in the data set against the corresponding TP value (selected from an average of 30 values measured during 6 to 14 years of sampling). On average, maximum Chl was some 15 times the minimum. Further, it is likely that the actual range within each lake was much larger than represented in our data. In Lake Woodrail, where samples were collected each day during five summers (n=597), the maximum-minimum fluctuation in Chl was 58-fold. To further illustrate variation within our study lakes, we connected maximum and minimum Chl values from each study lake with straight line (Fig. 2b). In most Missouri reservoirs, maximum Chl values were responsive to increases in TP. However, in about 20% of the study lakes Chl declined with TP; among the data points for these lakes minimum Chl co-occurred with high levels of TP, and



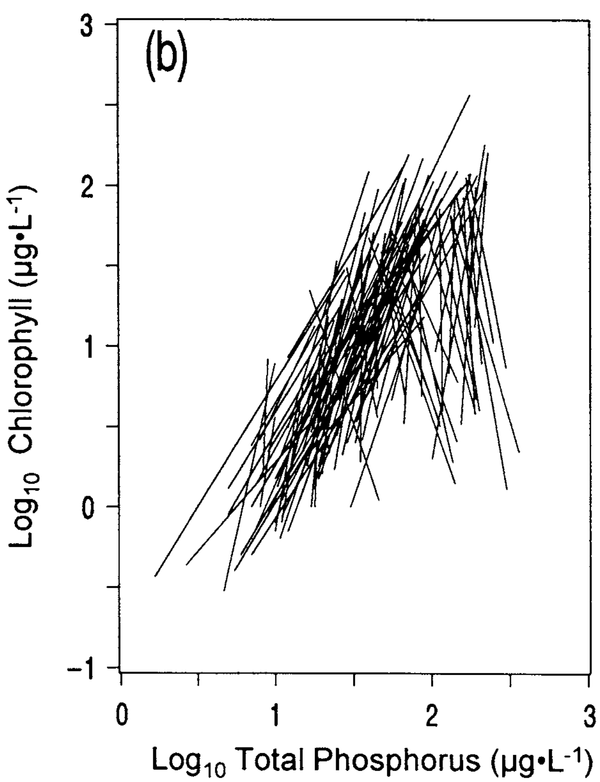


Figure 2.–Minimum and maximum Chl observed in each lake (individual observations) plotted against the TP measured in the same samples. a) Maximum Chl plotted as solid circles, minimum Chl plotted as open circles. b) Maximum and minimum observations from each lake connected by lines.

maximum Chl was measured at moderate TP. This simple example, using only the most extreme values of Chl from each waterbody, shows that response of Chl to TP within individual lakes in the data set is not universal.

Among individual observations in each lake the correlation between Chl and TP ranged between -0.56 and 0.93; some 13% of the r values were <0 and nearly the same proportion were >0.75. In most lakes, Chl and TP track one another (Fig. 3a), and the process operating in the aggregated data seems to apply over time within each, although with a greater level of variability. In these lakes an investigator would identify the Chl-TP relation using individual observations. In some lakes, however, there was little temporal variation in TP resulting in poorly defined, nonsignificant relations between Chl and TP (Fig. 3b). The lack of a clear relation would call into question whether the empirical relation shown in Fig. 1 applies in these cases.

The negative Chl-TP pattern demonstrated with maximum and minimum Chl in Fig. 2b occurs in our most turbid reservoirs (Jones and Knowlton 1993, Knowlton and Jones 1993). Peak TP levels are associated with elevated levels of inorganic suspended solids (Fig. 4a), which increase non-algal light attenuation (Fig. 4b) and reduce algal growth (Knowlton and Jones 1996). Periods of rapid flushing may also be a factor reducing algal response to nutrients (Soballe and Threlkeld 1985, Knowlton and Jones 1990). In these turbid lakes, the cross-sectional Chl-TP relation does not operate. Instead, they represent a second category where Chl-TP is negative as shown in Fig. 3c. And in several lakes we have evidence of a dual response in the Chl-TP relation (Fig. 3d). In wet years when TP inputs are associated with turbidity, the Chl-TP relation is negative, but in dry years the relation is positive and in some cases quite strong. This bifurcated pattern may be present, to a lesser extent, in a number of the study lakes and seems tied to weather and runoff.

The negative Chl-TP relation in some lakes is not obvious from the among-lake patterns in Fig. 1. It certainly is a source of variation in the individual observations and this becomes dampened with aggregation. This effect is most simply demonstrated using lake data from Fig. 3. When individual observations (Fig. 5a) are aggregated to the level of the seasonal mean (Fig. 5b), the orbit of individual points representing the negative Chl-TP relation in Fig. 5a appears as a small number of outliers relative to the general pattern. When reduced to lake means (Fig. 5c), all values closely match the composite pattern with averages from the turbid lakes being displaced slightly below the regression line. At this level, the negative Chl-TP relation is completely masked, and the positive, cross-sectional Chl-TP pattern would wrongly be thought to apply to all lakes in the group.

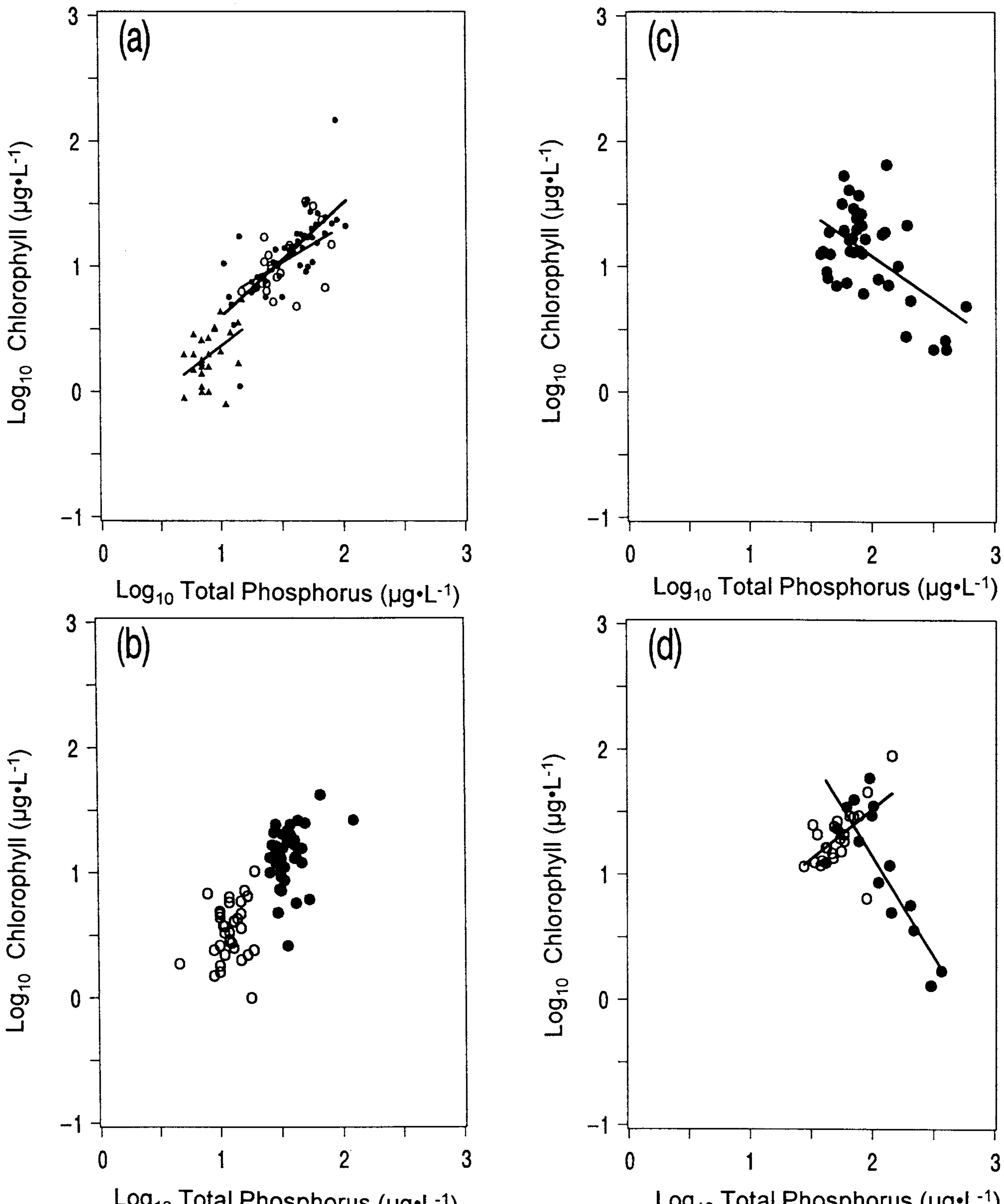


Figure 3.–Unaveraged Chl and TP data from seven representative reservoirs. a) Typical lakes (Council Bluffs Lake – triangles, Tri-City Lake – solid circles, Longview Lake – open circles). These lakes had significant ($p<0.05$) Chl-TP regressions (represented as solid lines for each) with slopes, intercepts and coefficients of determination near the median values for all lakes in the data set. b) Low variation lakes (Lower Taum Sauk Lake – open circles, Smithville Lake – solid circles). These lakes exhibited less temporal variation in TP than most lakes in the data set and had nonsignificant Chl-TP regressions ($p>0.05$). c) Turbid lake (Higginsville Lake). For this lake, the Chl-TP regression (solid line) was significant and negative. d) Lake with a bifurcated Chl-TP pattern (Pape Lake). For this lake, the Chl-TP regression was significant and positive in dry years (open circles – 1978, 1984, 1989, 1991, 1992 and 1994) and significant and negative in wet years (solid circles – 1990, 1993, 1995, and 1996).

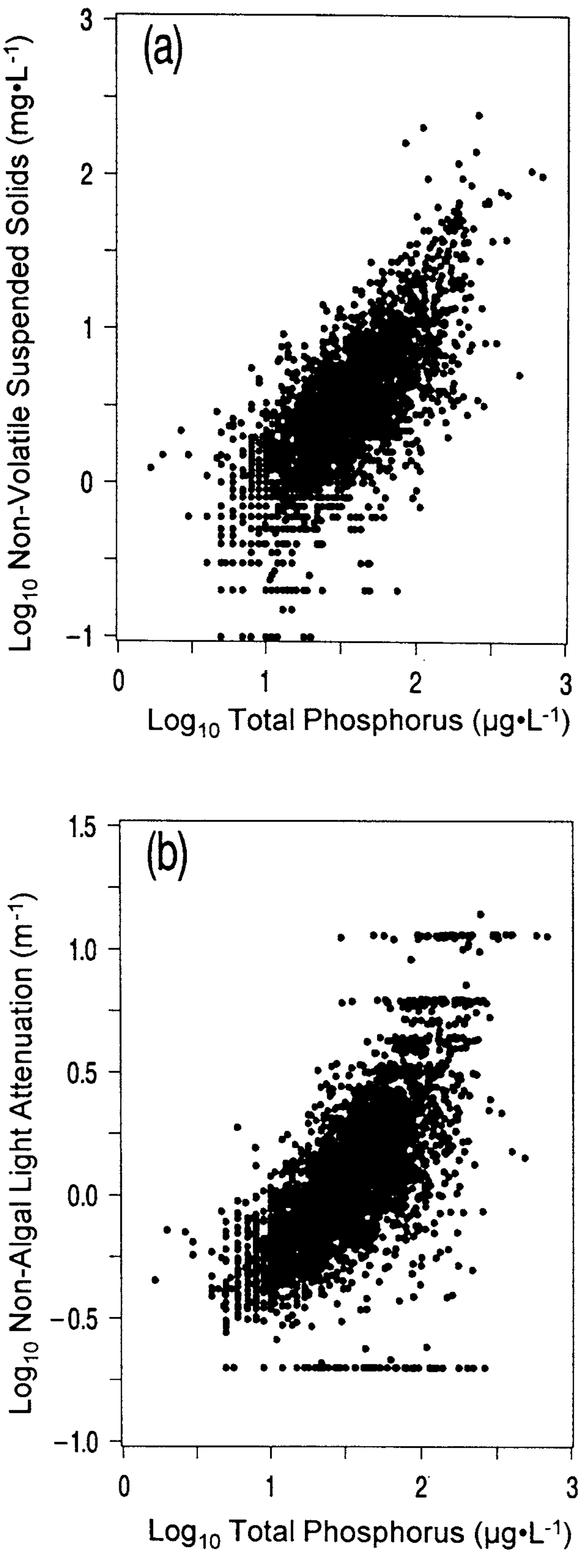


Figure 4.–Panel a. – Plot of non-volatile suspend solids (mg/L) in individual samples against TP in the same sample. Panel b. – Plot of non-algal light attenuation (Kna) against TP.

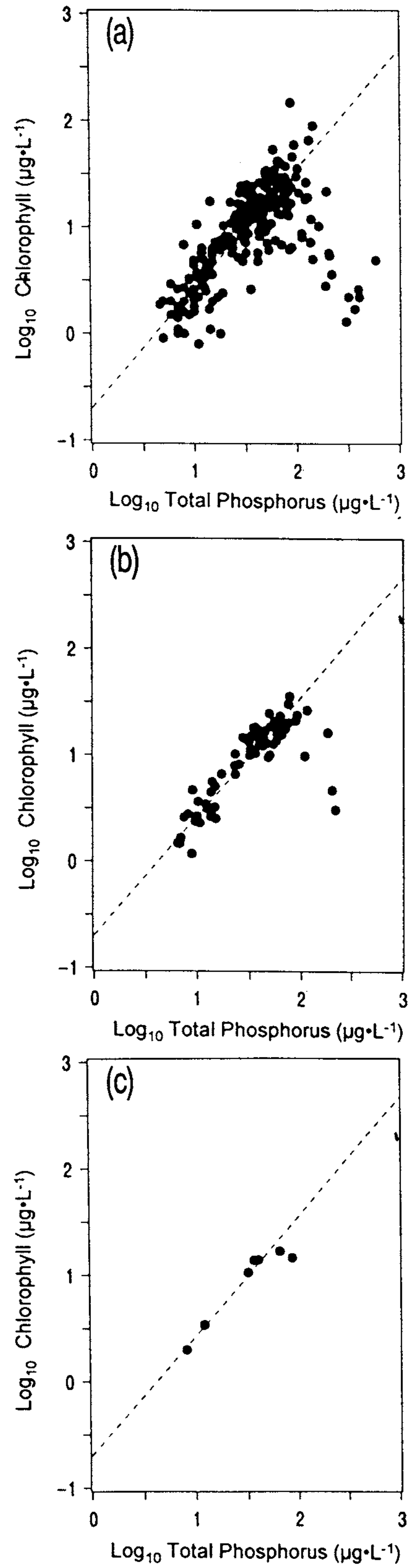


Figure 5.–Effect of data aggregation on the Chl-TP relation using data from Figure 3. a) Individual observations of Chl and TP from each lake. b) Seasonal mean values of Chl and TP for each lake. c) Lake mean values of Chl and TP. The dotted line on each panel is the lake mean regression from Figure 1c.

The underlying assumptions of empirical modeling would lead us to look for the simplest explanation in the cross-sectional pattern. Taking this approach to data in Fig. 1, we would fit a quadratic term (TP^2) to the data and in each case explain some 10% of the variance not explained by the independent variable (Jones and Knowlton 1993). Our interpretation of this composite response would be that in lakes with high levels of phosphorus (>50 ug/L), the yield of Chl per unit of TP would decline. Our analyses of individual lakes (Figs. 2 and 3) indicate this response is present in a subset of the total, but not in all lakes. By fitting a single curve to data containing two functional Chl-TP relations, we are not best representing either one. Doing separate analyses for lakes with positive Chl-TP, and those with negative Chl-TP, patterns would likely reduce unexplained variance. Among lakes with a positive Chl-TP, this approach would increase the response of Chl to TP, the slope of the regression. To take this step, however, requires advanced knowledge about individual lakes which comes with sampling or knowledge about the lakes in the region.

Discussion

Our analysis demonstrated the most obvious phenomenon of data aggregation—the strengthening of correlation at higher levels of aggregation (Fig. 1). Averaging reduces to a single point the often large variation in Chl and TP that characterizes measurements of these variables in lakes (Knowlton et al. 1984). This practice of averaging away the extremes dampens the variable response in Chl per unit TP which is present in the models as residual variance. It may or may not influence our ability to quantify the underlying cross-sectional pattern in these data. However, it nearly always improves its strength relative to nonaggregated data. The mathematical details of why this happens are beyond the scope of this paper, but are partly a function of lake identity. Data used to develop models come from specific lakes with individual characteristics, among which are a range of variation in Chl and TP. If all lakes had the same range in these two variables (similar trophic state), averaging would not have a major effect on the strength of the Chl-TP relation (Figs. 6a and b) because averages for each lake would include data from across the same spectrum. But an inherent aspect of the empirical approach is to include a range of systems to determine cross-sectional patterns; in limnology this implies using lakes across a range of trophic states. Successive levels of averaging restrict the data from each lake in the sample population into increasingly narrow segments of the Chl and TP

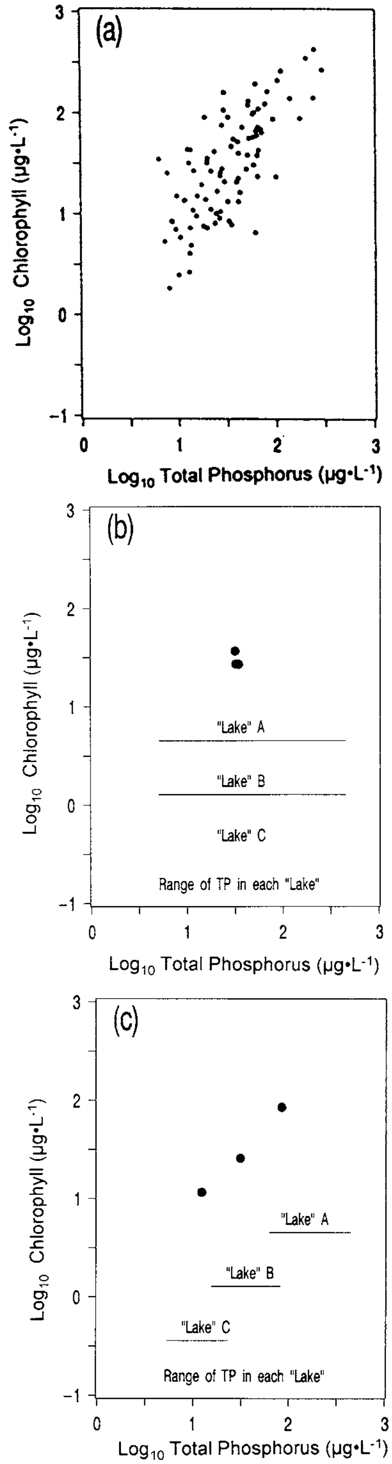


Figure 6.–Hypothetical examples of the effect of data aggregation on the strength of a correlation. a) Hypothetical group of 90 unaveraged Chl and TP measurements with an R^2=0.52 (similar to unaveraged data in Figure 1a). b) Data from Panel-a randomly assigned into three groups and averaged (R^2=0.41). The effect of aggregation is the same as might occur by averaging data from three lakes with the same range of TP. c) Data from Panel-a assigned to three groups each representing one third of the total range of TP and averaged (R^2=0.99). The effect of aggregation is the same as might occur in averaging data from three lakes of differing trophic state and, thus, different ranges of TP.

spectrum. Reducing the extreme values of Chl and TP from each lake by averaging automatically pulls the means closer to the overall central trend (Fig. 6c).

A basic message of our analysis is that inferences made from statistical regression analyses apply only to situations that match the level of aggregation used to produce the model. Simply put, levels of scale should not be mixed when using empirical models. This concept has long been recognized in statistics (Yule and Kendall 1950), and most ecologists recognize that predictions are best when a regression equation is applied to conditions under which the original data were collected (Prairie et al. 1994). The regression of Chl on TP using lake-level data in Missouri indicates a strong positive relation (Fig. 1c). The strength of this relation over the range of conditions in our study lakes, gives us confidence in predicting what the long-term average Chl will be at a given level of TP (on a transformed scale). However, the overall trend in Fig. 1c may or may not accurately reflect the relation of these variables to one another in individual lakes. The central tendency in measurements of Chl and TP, while reflective of lake trophic state, has limited value in predicting conditions in unaggregated data. In our data (Fig. 1), the typical individual observation from any particular lake differs from its overall mean value by 35% for TP and 65% for Chl. Given that the behavior of these variables is highly erratic in any specific sample from a Missouri reservoir, we do not have great confidence in the probable Chl content of a lake on a particular day. However, with knowledge of a seasonal mean or long-term value of TP, we improve our confidence in the probable average Chl content of a given lake (Fig. 1).

The Chl-TP relation was a key component in the paradigm shift from thinking of lakes as unique entities to one in which lakes are viewed in generality, within the context of a continuum. Global Chl-TP relations along with experimental demonstration of phosphorus limitation (e.g., Schindler 1974) helped provide the basis for the empirical approach in limnology. The Missouri example suggests that by aggregating the data into seasonal and lake means to identify average trends we masked the form of the relation in our most turbid lakes. Over time, we have gathered extensive data on each study lake, thereby allowing us to identify atypical patterns where the cross-sectional response does not apply. This is good scientific practice (Peters 1986), which is to compare the response of each system to that of the mean response.

Recognizing that interlake continua exist enables us to understand large-scale patterns in the Chl-TP relation. However, these may not apply to intra-lake or other smaller-scale patterns (Reynolds 1992); Limnologists have long recognized that TP does not account for all of the variation exhibited by measurements of Chl in lakes. The two effects of data aggregation addressed in this paper are important in interpreting the results of statistical construction and analysis of empirical Chl-TP models. The effect of aggregation on the estimated strength of a regression relation serves as a caution in transferring inferential statements about the effect of TP on Chl between temporal scales and among lakes. The potential *effects* of aggregation in masking the functional form of appropriate regression equations indicate that the Chl-TP relation itself may be considered a continuum. The particular relation occurring in a lake or set of lakes over a period of time is influenced by various physical, chemical, and biological factors. With knowlege of these factors, it may be appropriate to view the Chl-TP relation as a variable phenomenon and model it as a function of these other factors. Or, it may be appropriate to shift away from regression analysis as the basic description of Chl-TP relations and similar empirical models (Kaiser et al. 1994). Developing these alternative approaches should be a goal for empirical limnology.

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