Creating a Concentration Translator to Link Chlorophyll and Phosphorus

The central tenet of nutrient criteria development is that enriching the supply of nutrients to aquatic systems leads to an over-abundance of algae, which can result in impairment of uses. Setting a standard for algal abundance (as measured by chlorophyll concentration) is therefore a necessary component of nutrient criteria because chlorophyll concentration establishes the potential for impairment of uses. Regulating chlorophyll alone is not a sufficient basis for nutrient criteria because algal abundance is a response to enrichment and not its cause. The distinction between causal and response variables is an important facet of EPA recommendations and both must be included in nutrient criteria.

Chlorophyll concentration in a lake is determined largely by the nutrient concentration, which is controlled by the nutrient supply from the watershed. (There are no significant watershed sources of chlorophyll.) In order to control algal abundance in a lake and guard against impairment, the supply of nutrients from the watershed must be managed. Therefore, nutrient criteria should target cause (nutrients) and response (algal abundance) in tandem.

Linking causal and response variables for development of water quality criteria is not unprecedented. In streams, for example, the concentration of dissolved oxygen reflects in part the effect of biochemical oxygen demand (BOD) contributed by external sources. Attaining the DO standard requires management of the BOD load to the stream, a linkage that has been understood for decades. BOD is the causal variable and DO is the response variable. Managing BOD is necessary, albeit not always sufficient, for ensuring attainment of the DO standard.

Nutrient criteria are similar in the sense that managing the nutrient supply is necessary for controlling the abundance of algae. Only when the linkage between chlorophyll and nutrients is quantified can there be a common understanding of the benefits (in terms of reduced algal abundance) that can be expected from the cost of implementing a reduction in the nutrient supply. A quantitative linkage between chlorophyll and nutrients will be referred to as a “concentration translator.”

Defining a concentration translator to link chlorophyll and nutrients has been the objective of many basic and applied research studies. The quest has produced some very sophisticated mechanistic models developed for the purpose of explaining variability in algal abundance. While these models may provide well-deserved satisfaction from a scientific perspective, they may not be practical or necessary from a regulatory perspective.

A model capable of explaining all temporal variation in algal abundance is not necessary in order to focus on the regulatory goal of attaining the standard. It is sufficient to understand the conditions that could jeopardize attainment. Predicting how often the chlorophyll standard might be exceeded is a simpler task than explaining all variation. It places emphasis on locating an upper bound for algal abundance in a lake with a particular nutrient concentration. In other words, unexplained variability can be acknowledged without attempting to quantify the sources.

The nutrient supply sets an upper bound on algal abundance, and that upper bound is affected by the physical factors (chiefly light and temperature) prevalent in a particular lake. Other factors such as non-algal turbidity or grazing by herbivores may depress algal abundance below the upper bound, but there are no factors other than nutrients that can augment the upper bound for algal abundance. Defining the upper bound for chlorophyll in terms of nutrient concentration is the task of a concentration translator.

Before describing a concentration translator for Colorado, several supporting concepts and arguments are needed, beginning with a review of the limiting nutrient concept, a rationale for targeting phosphorus, and expectations for algal abundance. Next is a characterization of concentration translators and the factors that can suppress algal abundance below the upper bound expected on the basis of physical factors and nutrients. A candidate concentration translator, the response ratio, is defined as it relates to expectations for algal abundance, and it is examined in terms of its capacity to reflect the operation of factors that may suppress algal abundance. Finally, data are presented from Colorado lakes and a sample application of the response ratio is given.

Limiting Nutrient Concept

Algae require nutrients to grow. Increasing the supply of nutrients can increase algal growth in the same way that fertilizer increases the growth of crops in a field. Although many nutrients are required for growth, the limit on growth that is reached at one point in time is determined by just one nutrient, as stated in Liebig's Law of the Minimum:

> *"Under conditions of equal temperature and light, the nutrient available in the smallest quantity relative to the requirement of the plant will limit productivity."*

There are two qualifiers, one explicit and one implicit, in Liebig's Law, and both have contributed to misconceptions about expectations for algal abundance in lakes. Light and temperature are subject to significant temporal and spatial variation, which is contrary to the explicit qualifier in Liebig's Law ("Under conditions of equal temperature and light…."). Temperature in the mixed layer of a lake varies seasonally, and light varies seasonally and with depth. Furthermore, temperature and light regimes differ among lakes. In practical terms, when algae do not experience steady-state growth conditions, it weakens expectations for a strong relationship between chlorophyll and nutrients. For example, there may be a time lag between a change in temperature (or light) and the response of the algae as measured by chlorophyll concentration.

The implicit qualifier is that the "law" applies, strictly speaking, to one algal species at a time. Natural communities are composed of many algal species, each of which has slightly different nutrient requirements and different growth response to light and temperature. Moreover, species composition can change dramatically over the course of a summer. Thus, for each lake, the amount of chlorophyll produced in response to a given supply of nutrients will vary depending on light, temperature, and the algal species present, all of which change throughout the growing season; potential algal abundance (i.e., upper bound for chlorophyll) is subject to change throughout the year.

Reasons to Focus on Phosphorus

It has been common practice, based on an extensive scientific literature, to assume that phosphorus is the nutrient most likely to be effective in controlling algal abundance in lakes. There are many studies showing a strong statistical linkage between chlorophyll and phosphorus. In addition, a recent review of lake restoration efforts (Jeppesen et al. 2005) found that a reduction in total phosphorus loads led to a reduction in chlorophyll in most lakes. This is not the same things as saying that phosphorus is always the limiting nutrient in a strict sense, but it is encouraging to note the concordance.

There are practical reasons for placing the primary focus on phosphorus rather than nitrogen, which is the only other nutrient with a strong claim for controlling algal abundance. One reason is that control of phosphorus sources in the watershed can reduce loads and in-lake concentrations in a predictable manner. Similar controls on nitrogen can be circumvented by algae able to fix atmospheric nitrogen, which is essentially inexhaustible. Another reason is related to the statistical linkage between chlorophyll and nitrogen. Prairie et al. (1989) found that the correlation between chlorophyll and total nitrogen is about the same as that between chlorophyll and total phosphorus for a wide range of nitrogen to phosphorus (N:P) ratios. Low values of the N:P ratio are often taken as indirect evidence for nitrogen limitation. It is also worth noting that the occurrence of nitrogen limitation may often simply be the consequence of pre-existing over-enrichment with phosphorus (cf. Golterman 1975).

Although Colorado does not see a need to incorporate nitrogen in nutrient criteria for lakes in general, it could be included on a site-specific basis if there were sufficient justification. In general, phosphorus appears to the only indispensable causal variable for lakes. Golterman’s (1975) observation made more than 30 years ago remains relevant today:

> *“It is not important whether [*phosphorus*] is currently the limiting factor or not, or even that it has ever been so; it is the only essential element that can easily be made to limit algal growth.”*

Expectations for Algal Abundance

The upper bound on expectations for chlorophyll in a particular lake will be referred to as *potential abundance* in this document. For the purpose of discussion, potential abundance is defined as the steady-state amount of chlorophyll expected with the observed nutrient concentrations, under the ambient light and temperature regime. The supply of nutrients creates a potential for growth of the algal species present in the community. The potential may not be realized if abundance is suppressed by other factors. For example, if grazers are abundant, they may be able to consume algal biomass faster than the algae can reproduce. Changes in these factors can occur on a scale of days within a lake and the relative importance of factors will vary among lakes.

The chlorophyll that is measured in a lake is referred to as *realized abundance* and it reflects suppression of abundance below the potential. The degree of suppression varies, but must occasionally be small enough so that the realized abundance approximates the potential. The objective is capture in a relative sense the variability observed in chlorophyll measurements.

Characterizing Chlorophyll-Phosphorus Relationships with Concentration Translators

The scientific literature is replete with studies exploring relationships between phosphorus and chlorophyll in a wide variety of lakes. Typically, these studies produce empirical relationships (regression lines) that predict chlorophyll as a function of phosphorus (Figure 1). These quantitative relationships are examples of concentration translators as defined here. One widely cited equation, derived by Jones and Bachmann (1976), has been applied previously in Colorado for development of control regulations. Although these relationships were derived from a set of lakes, they are often applied to individual lakes, especially where there is an interest in estimating chlorophyll for phosphorus concentrations outside the range of experience.

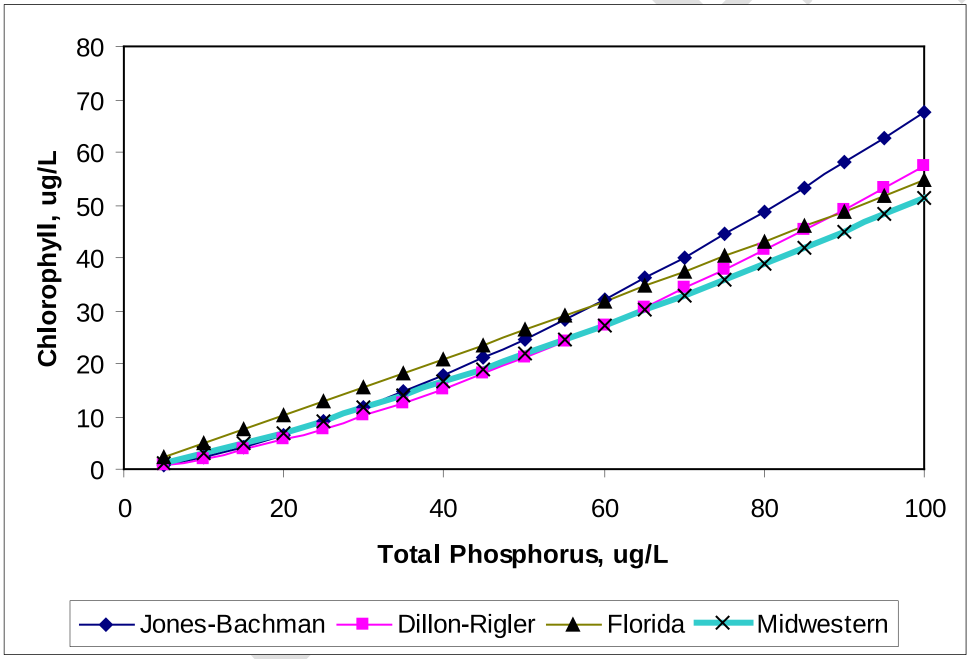

Figure 1. A selection of equations predicting chlorophyll as a function of phosphorus. Sources include Jones and Bachman (1976), Dillon and Rigler (1974), Hoyer and Jones (1983), and Brown et al. (2000).

Factors that Suppress Algal Abundance

The full potential for algal abundance often is not achieved because one or more factors are operating to suppress growth or remove biomass. For example, transitory changes in light regime, as might be expected with a large input of sediment following a storm event, might reduce growth rates as long as the sediment remains in suspension. A study by Hoyer and Jones (1983) highlights the effect of inorganic suspended solids (ISS) on the amount of chlorophyll expected at specific phosphorus concentrations. Higher concentrations of ISS decrease the effective light climate and lead to lower chlorophyll per unit total phosphorus (Figure 2). Other things being equal, manipulating the availability of light affects the potential abundance of algae across the spectrum of phosphorus concentrations.

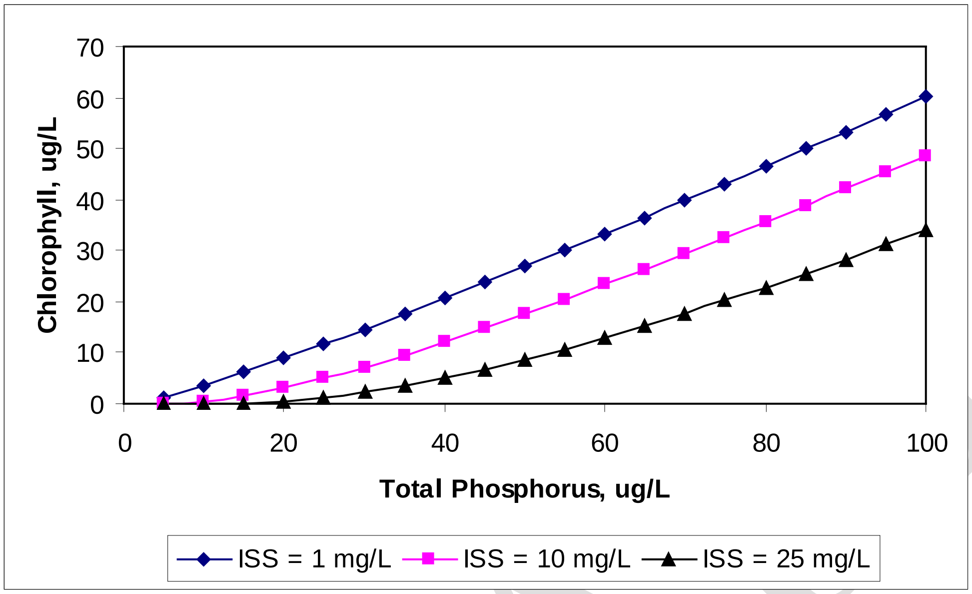

Figure 2. Predictions of chlorophyll as a function of phosphorus, at three levels of inorganic suspended solids (ISS). Higher ISS means less light available for algae. Equation from Hoyer and Jones (1983).

Potential abundance may be suppressed by grazers feeding on algae. When large grazers (chiefly zooplankton species such as *Daphnia*) are abundant, their feeding can remove a significant portion of algal biomass. Mazumder and Havens (1998) captured this effect by contrasting the chlorophyll-phosphorus relationships derived when the zooplankton community is dominated by large or by small species (Figure 3). In general, only the large zooplankton species have the capacity to consume a significant portion of the algal biomass, and thus to depress abundance below the potential expected for a given phosphorus concentration. Because the generation time of large herbivores is on the scale of weeks, the impact of grazing can wax and wane in a relatively short period of time.

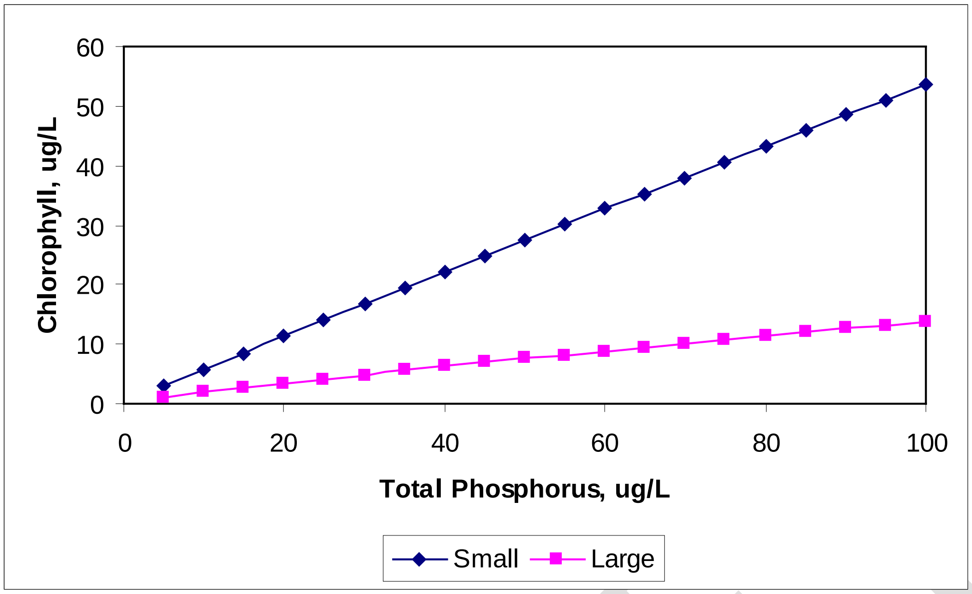

Figure 3. Predictions of chlorophyll as a function of phosphorus, in the presence of large or small zooplankton species. The zooplankton are herbivores that consume algae; large herbivores have a much greater capacity to consume algae than do small herbivores. Equation from Mazumder and Havens (1998).

The abundance of algae also may be affected by the availability of nitrogen, which can supplant phosphorus as the limiting nutrient. Nitrogen limitation is known to occur seasonally in some Colorado lakes (Morris and Lewis 1988), although it is unlikely to be limiting at all times. Even in Cherry Creek Reservoir, where nitrogen limitation probably applies for most of the summer months, disruption of the intermittent stratification may relieve nitrogen limitation, returning control to phosphorus, albeit briefly. It is not uncommon for predictions of chlorophyll to be improved by including both phosphorus and nitrogen as independent variables (e.g., Brown et al. 2000, Smith 1982). What has been surprising about investigations of nitrogen-limited lakes is that nitrogen alone has not emerged as a stronger predictor of chlorophyll.

A conventional, but indirect, indicator of nitrogen limitation is the ratio of total nitrogen to total phosphorus (TN:TP). When the ratio is less than 14, nitrogen limitation is sometimes inferred (Downing and McCauley 1992). Prairie et al. (1989) show that the TN:TP ratio affects the abundance of chlorophyll expected on the basis of the phosphorus concentration (Figure 4). For a given concentration of phosphorus, expected chlorophyll concentrations tend to be smaller as the TN:TP ratio decreases, although the effect seems to disappear at phosphorus concentrations less than 30 ug/L (Figure 4). They also found that for the full range of TN:TP values, from nitrogen limitation to phosphorus limitation, “TN and TP correlated equally well with chlorophyll….” The TN:TP ratio varies within and among lakes, and that variability should influence the abundance of algae. At a given phosphorus concentration, the [phosphorus-based] potential abundance of algae is more likely to be achieved when the TN:TP ratio is high. As the ratio decreases (i.e., the concentration of nitrogen is reduced relative to the amount of phosphorus), the realized abundance is suppressed relative to the potential.

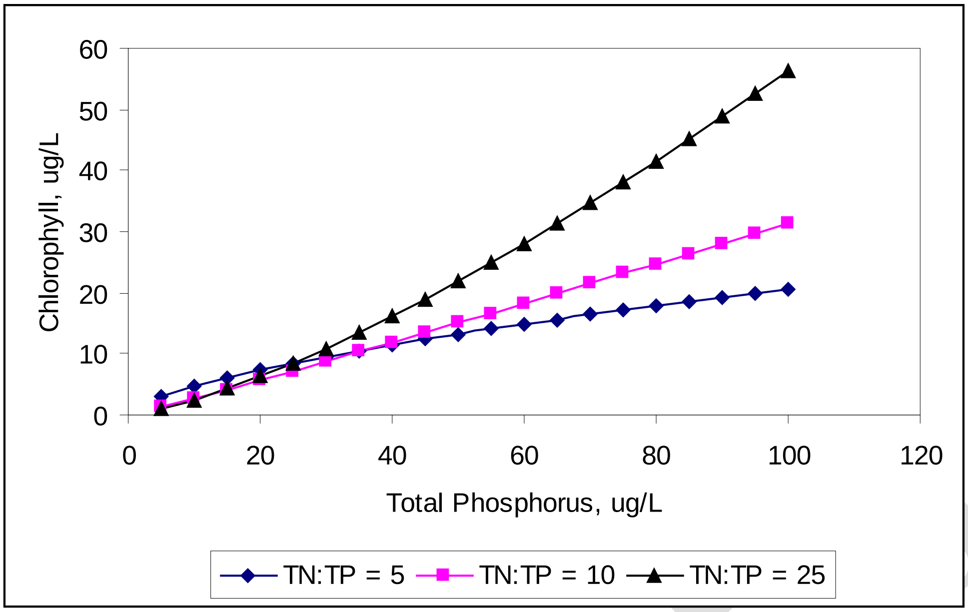

Figure 4. Predictions of chlorophyll as a function of phosphorus for different ratios of nitrogen to phosphorus. A low ratio of TN:TP is often taken as an indicator if nitrogen limitation. Equation from Prairie et al. (1989).

What can be said generally is that the responsiveness of the algal community, as indicated by the chlorophyll concentration, is affected by the nature and relative importance of the various growth and loss processes, which operate largely independently of each other. It is easy to envision seasonal variation in each of the factors with the potential for additive suppression, resulting in the observed seasonal pattern of algal abundance. It is very difficult to predict such a pattern, or even the contribution of a single factor, in a single lake.

Most studies linking chlorophyll to phosphorus and other independent variables have been based on data from large sets of lakes. The relationships portrayed in Figures 1-4, for example, were developed from large sets of lakes. These "global" studies are often used to predict response in a single lake, but there are good reasons why individual lakes may not respond exactly as predicted (Smith and Shapiro 1981). While it is certainly possible to improve predictions of chlorophyll by adding more independent variables, and by treating each lake individually, these steps may not be necessary when the primary objective is to forecast frequency of exceedances rather than to estimate accurately the seasonal mean. The concept advanced here is that decisions can be based on site-specific responsiveness of algal abundance (chlorophyll) when scaled to phosphorus alone.

The Response Ratio as a Tool for Defining Lake-Specific Potential Abundance

When algae are grown in culture, the growth of the populations tends to be very predictable. In an environment of controlled light and temperature, growth depends largely on the abundance of nutrients. When all nutrients are abundant except one (phosphorus, for example), the abundance of algae in a closed culture can be controlled by manipulating the concentration of that one limiting nutrient (e.g., Golterman 1975). The endpoint in terms of chlorophyll produced per unit phosphorus varies for physiological reasons among algal species and even within a species. The ratio of chlorophyll to phosphorus may vary about an order of magnitude from the minimum cell quota to the full extent of “luxury consumption” (cf. Reynolds 2006). Moreover, the ratio declines as the “bioavailable” phosphorus increases. The ratio could be as high 6 when phosphorus concentrations are very low.

Another way to consider the expected ratio of chlorophyll to phosphorus is by reference to the chemical composition of phytoplankton. According to the widely-cited Redfield ratio ($C_{106}H_{263}O_{110}N_{16}P_1$), phosphorus constitutes about 2.4% (by weight) of the carbon content of algae. Chlorophyll is often estimated to be about 2% of cellular carbon (e.g., Chapra 1997). With these assumptions about composition of typical algal cells, the ratio of chlorophyll to phosphorus would be about 1:1.

Field data can be used to assess the actual response of resident algae to different amounts of phosphorus. Hern et al. (1981) employed this concept to define a “response ratio” (mass of chlorophyll per unit mass of phosphorus) that was used for evaluation of lakes sampled in the National Eutrophication Survey (NES) during the 1970s. The response ratio varies widely among the NES lakes (Figure 5). The average response ratio in the summer was 0.29, and the upper bound was in the vicinity of 1:1 (i.e., the typical assumptions in the preceding paragraph appear to represent asymptotic conditions).

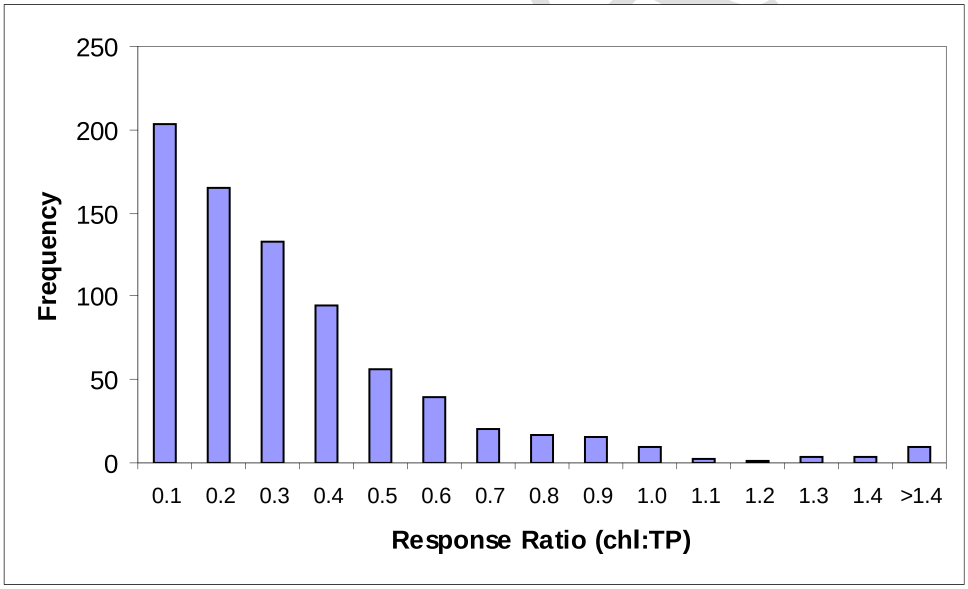

Figure 5. Frequency histogram of response ratios recorded from lakes sampled during the National Eutrophication Survey (Hern et al. 1981).

For a cross section of lakes, typical ratios can be extracted from published regression equations characterizing chlorophyll as a function of phosphorus. The relationships are useful for showing general patterns, even though these ratios are defined in terms of average chlorophyll rather than potential. For example, increasing ISS concentration diminishes the responsiveness of the algal community to the available phosphorus (Figure 6). Higher ISS means less chlorophyll per unit phosphorus. Effective grazing also reduces the apparent yield of chlorophyll per unit phosphorus (Figure 7) because large herbivores are more efficient grazers able to suppress the response ratios by removing evidence of algal growth. Finally, the effect of altering the TN:TP ratio is to make chlorophyll more responsive to phosphorus at higher TN:TP ratios (Figure 8); the effect is inconsistent at low phosphorus concentrations, however (as noted previously by Downing and McCauley 1992).

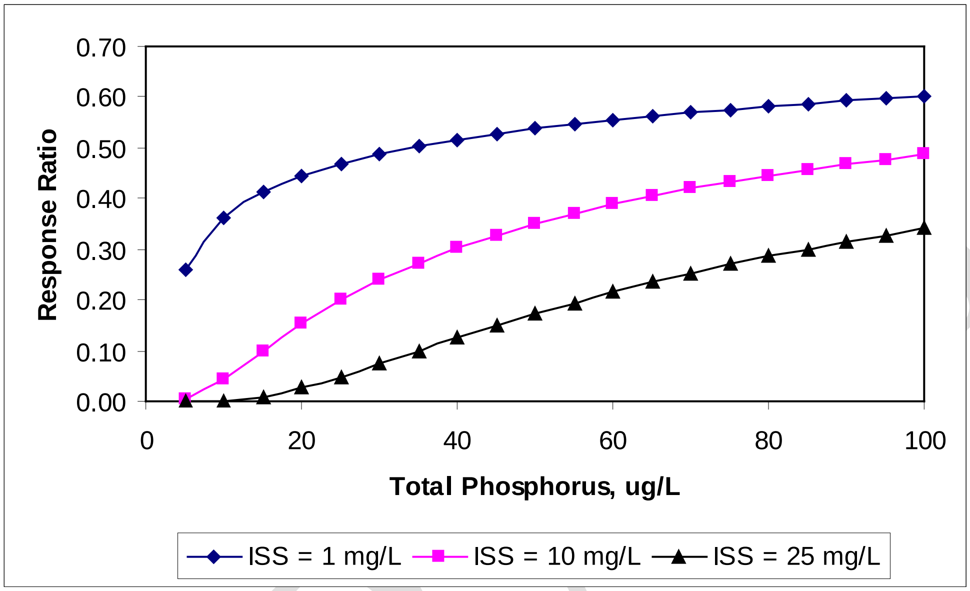

Figure 6. Response ratios implied by an equation that predicts chlorophyll as a function of phosphorus and inorganic suspended solids (from Hoyer and Jones 1983). Each line represents predictions where inorganic suspended solids is held constant at 1, 10, or 25 mg/L. Higher ISS means less light available for algae.

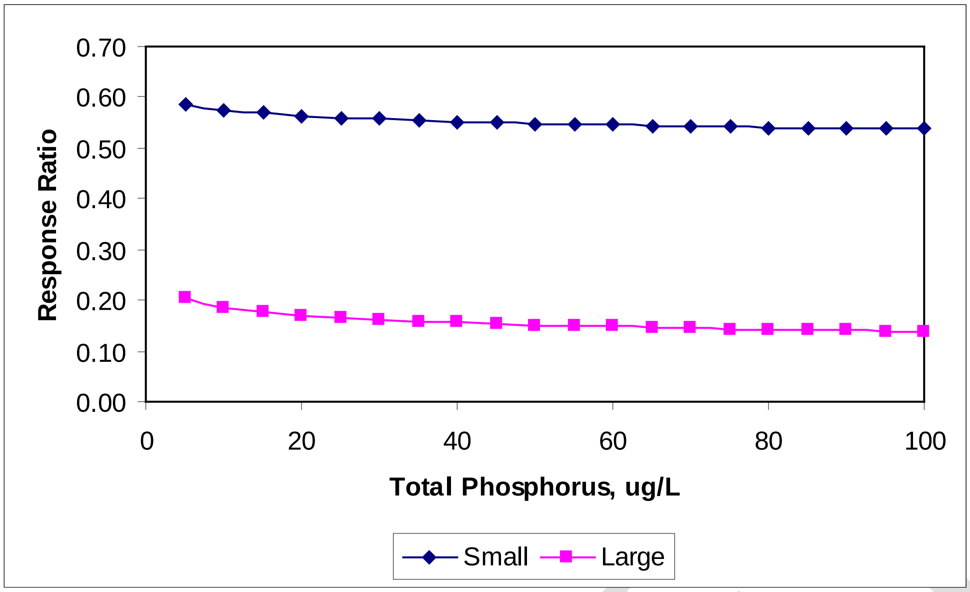

Figure 7. Response ratios implied by a equations that predict chlorophyll as a function of phosphorus. Each line represents predictions for lakes where the zooplankton community is comprised of small or large herbivores (from Mazumder and Havens 1998). Larger herbivores have the capacity to remove a significant portion of algal biomass.

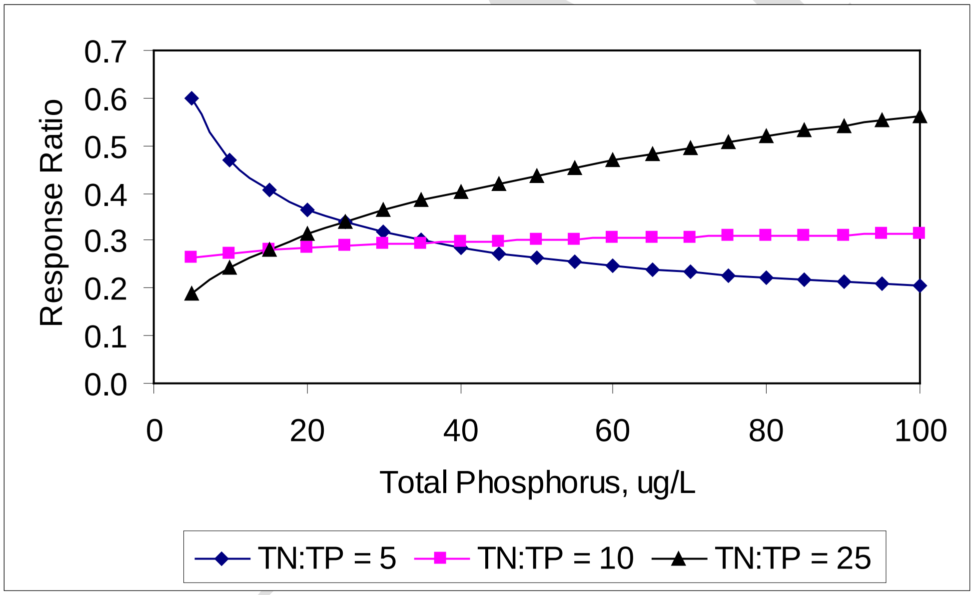

Figure 8. Response ratios implied by an equation that predicts chlorophyll as a function of phosphorus and nitrogen. Each line represents predictions for a fixed nitrogen concentration.

Each time a control factor becomes important relative to phosphorus, the response ratio is depressed below the potential expected for that phosphorus concentration in that lake. This expectation is based on patterns documented for increasing suspended solids, increasing grazing pressure, and decreasing nitrogen-phosphorus ratios. It is not difficult to imagine a sequence of events in a lake where variations in nitrogen concentrations or the wax and wane of grazer populations could alter the response of algal populations to phosphorus concentration at any point in time. It would be difficult to incorporate all relevant variables in a predictive equation, but it is relatively easy to capture the aggregate effect of all factors on algal abundance by means of the response ratio. The response ratio observed in one sample from one lake represents realized abundance that is probably less than the potential expected for a particular amount of phosphorus in that lake. The role of factors other than phosphorus determines the extent to which the ratio is suppressed relative to the potential for a lake. In the next section, real data are used to show how potential abundance can be defined in terms of the response ratio.

Survey of Response Ratios in Colorado Lakes

The response ratio offers an attractive basis for developing site-specific linkages between chlorophyll and phosphorus. Part of the attraction resides in the potential for generalizing from a site-specific to a regional basis for defining the amount of phosphorus consistent with a particular chlorophyll standard. This approach depends on using site-specific data for the response ratio to define potential algal abundance at any phosphorus concentration. Characteristics of response ratios in a set of Colorado lakes can help establish the means of defining potential abundance.

Chlorophyll and phosphorus have been sampled in many lakes throughout the state, but there are relatively few lakes with many samples from the summer averaging period. Attention is restricted to lakes where at least 20 samples have been taken during the summer averaging period (Table 1). A few lakes with large data sets have been omitted because most of the phosphorus concentrations were below detection (e.g., Granby, Carter, Shadow Mountain), precluding reliable determination of the response ratio.

	Response Ratio Percentile				**Years Exceeding Percentile**		
Lake	**50th**	**75th**	**90th**	**Years Sampled**	**50th**	**75th**	**90th**
Arvada	0.304	0.403	0.498	9	6	3	1
Aurora	0.219	0.260	0.309	9	4	1	0
Barr	0.101	0.223	0.428	5	2	0	0
Bear Creek*	0.285	0.555	1.041	11	8	2	0
Boulder	0.275	0.346	0.441	12	5	4	1
Boyd	0.234	0.325	0.548	8	4	2	1
Chatfield	0.236	0.371	0.518	13	8	4	1
Cherry Creek	0.239	0.305	0.364	10	5	1	0
Dillon	0.682	0.857	1.097	22	11	3	0
Green Mt	0.304	0.402	0.617	13	8	3	1
Loveland	0.290	0.390	0.459	8	4	2	1
Milton	0.049	0.144	0.303	5	2	1	0
Quincy	0.316	0.411	0.532	8	3	1	1
Seaman	0.341	0.569	1.043	7	5	2	0
Standley	0.233	0.322	0.554	12	6	1	0
Overall	**0.275**	**0.371**	**0.518**	**152**	**81**	**30**	**7**
* - after 1995							

Table 1. Characteristics of response ratios observed during the summer months (Jul-Sep) in Colorado lakes. Ratios are shown for the 50th, 75th, and 90th percentiles in each lake, as well as the

overall median across all lakes. The number of summer seasons sampled is indicated for each lake. The final three columns indicate the number of years in which the observed summer median concentration of chlorophyll exceeds the concentration calculated from the observed summer median phosphorus and a particular percentile of the response ratio. Bear Creek Reservoir data prior to 1996 were omitted due to presence of a strong trend in phosphorus concentrations.

For each lake, at least 20 pairs of chlorophyll and phosphorus measurements were available from the summer months; all such pairs were used to calculate response ratios, provided that the component concentrations were both above the detection limit. It was assumed that all summer response ratios for one lake were representative of a single distribution, from which percentiles could be drawn. The percentiles chosen for this study were the 50th (median), 75th, and 90th as shown in Table 1. The median response ratio ranged from 0.049 in Milton Reservoir to 0.682 in Lake Dillon. The typical (median) value from the set of lakes was 0.275, which is close to the average from the NES lakes. A response ratio of 0.275 indicates that an increase of nearly 4 ug/L of phosphorus is needed to produce an increase of 1 ug/L in chlorophyll.

In separate calculations, the median summer chlorophyll and phosphorus concentrations were determined for each year in the period of record for each lake. The period of record included from 5 to 22 years for the lakes in Table 1. For each lake, chlorophyll concentrations vary among years, but the variation cannot be explained solely on the basis of variation in the phosphorus concentration. By the logic in the response ratio concept, the unexplained variation in chlorophyll reflects suppression by factors other than phosphorus. What is needed is a way to estimate the chlorophyll expected if there is little or no suppression by the other factors, because this is the scenario most likely to compromise attainment of the standard.

Data from Lake Loveland are used to illustrate the procedure for site-specific estimation of potential chlorophyll (Figure 9). Summer median concentrations of chlorophyll and phosphorus are plotted for eight years (symbols on Figure 9). Separately, the 23 summer samples collected during those eight years are used to calculate the median response ratio (0.290) for the algal community in Lake Loveland. The median response ratio is applied to the range of values recorded for the summer median phosphorus concentration; the resulting line is an exceedance threshold for summer median chlorophyll concentration based on typical (median) responsiveness on the part of the algal community. Half of the observed summer median chlorophyll concentrations exceed the chlorophyll expected based on the median response ratio. From a regulatory perspective, defining the potential on the basis of the median response ratio is not very desirable because it will be exceeded about half of the time. The same logic can be used to develop exceedance thresholds based on response ratios representing the 75th and 90th percentiles of the distribution. The exceedance threshold based on the 75th percentile response ratio is exceeded by two of the eight observed values, and the threshold based on the 90th percentile is exceeded only once. Clearly, associating potential with a high percentile shows promise.

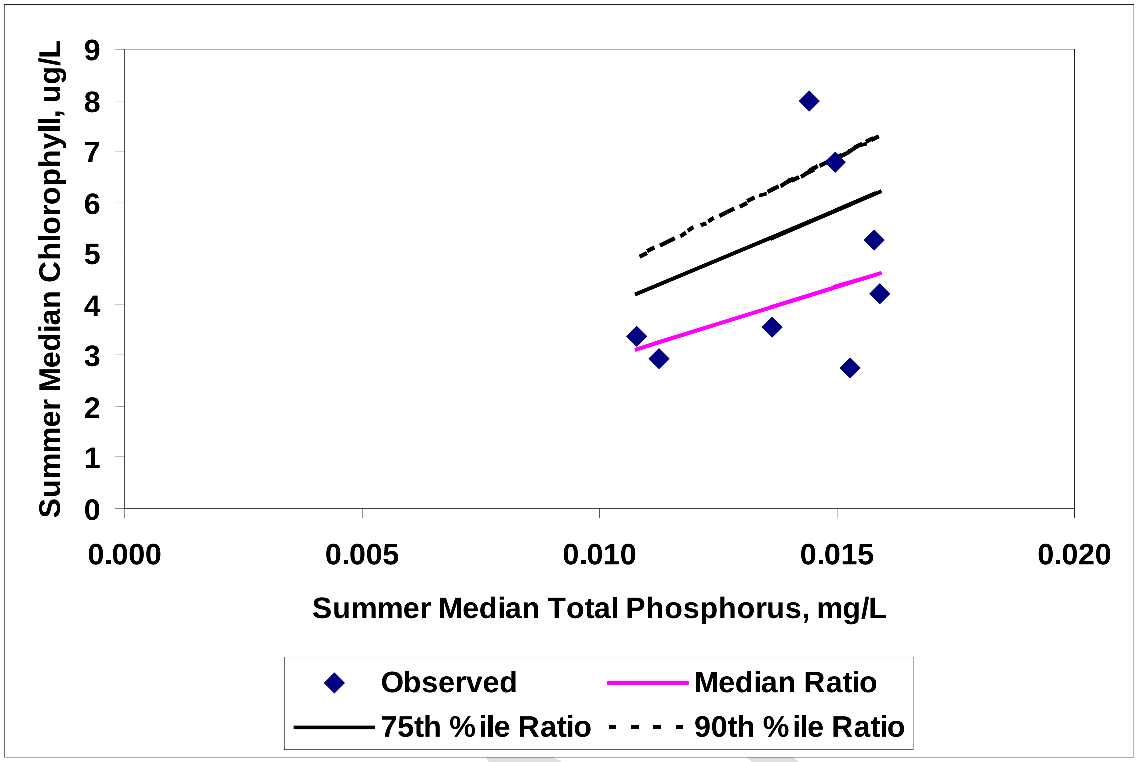

Figure 9. Plot of summer median chlorophyll vs. summer median total phosphorus in Lake Loveland. The three lines represent chlorophyll expected based on the observed phosphorus and one of three percentiles from the distribution of response ratios.

A sample size of eight is too small for estimating a general exceedance frequency, but Lake Loveland is just one of the 15 lakes available. The sample size can be expanded greatly by aggregating information from the set of 15 lakes (Table 1). When the 50th percentile response ratio is used to generate the exceedance threshold (done separately for each lake), the expected chlorophyll is exceeded by the observed about half of the time (81/152 lake-years), as would be expected when the threshold is based on the median response ratio. When the 75th percentile response ratio is used, the expected chlorophyll is exceeded by the observed much less frequently (30/152 lake-years), which can be interpreted as a once-in-five year exceedance frequency. Finally, the expected chlorophyll generated with the 90th percentile response ratio is exceeded rarely (7/152), for an exceedance frequency of approximately once-in-20 years.

While it is easy to conceptualize the exceedance frequency associated with use of the median response ratio, the other two exceedance frequencies must be viewed as empirical in origin. One advantage of an empirical approach is that it avoids some of the statistical complications related to defining and generalizing about distributions. For the purpose of discussion, an allowable exceedance frequency of once in five years seems reasonable for a chlorophyll standard.

The response ratio provides the basis for linking phosphorus to chlorophyll in criteria development. For lakes with sufficient data, the 75th percentile response ratio from the set of all summer values for the ratio is applied to the chlorophyll standard to generate the phosphorus concentration consistent with a once-in-five year exceedance frequency for the chlorophyll standard (TP=chl/ratio). It is likely that default values of the potential response ratio will be established for lakes of a particular region or basin, but more work is needed before those are proposed.

Conclusions

1) The linkage between chlorophyll and phosphorus is central to development of nutrient criteria for Colorado lakes.
2) Conventional regression analysis does not yield a suitable basis for developing criteria because the objective of the analysis is not consistent with present needs for the concentration translator and because the unexplained variance in the chlorophyll-phosphorus relationship is high.
3) An alternative procedure is described using a response ratio (chlorophyll: phosphorus) to characterize potential abundance on a site-specific basis.
4) Analysis of a set of Colorado lakes indicates that the 75th percentile value for the response ratio is consistent with a once-in-five year exceedance frequency.
5) Given a chlorophyll standard and the 75th percentile value of the response ratio distribution, the corresponding concentration for total phosphorus can be derived.

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