Creating a Concentration Translator to Link Chlorophyll and Phosphorus

The central tenet behind development of nutrient criteria 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 therefore becomes a focal point for nutrient criteria development because it establishes the potential for impairment of uses. Chlorophyll concentration is a widely-used surrogate for the abundance of algae, and it is the parameter used as the water quality standard. From a regulatory perspective, however, setting standards for chlorophyll is only part of the task.

In the parlance of nutrient criteria, chlorophyll is a "response variable." The abundance of algae reflects the net effect over time of the various growth and loss processes operating on the algal species resident in a lake. For practical purposes, the response (i.e., the growth of algae) occurs entirely within the lake; there are no significant watershed sources of chlorophyll. On the other hand, the causal variables (i.e., nutrients) come chiefly from the watershed. In order to effect control of algal abundance in a lake, the supply of nutrients from the watershed must be managed. Development of nutrient criteria therefore depends on targeting cause (nutrients) and response (algal abundance) in tandem.

Linking causal and response variables in 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 control 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. Controlling BOD is necessary, but 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. The linkage between chlorophyll and nutrients must be quantified if there is to 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. Any quantitative linkage between chlorophyll and nutrients will be referred to as a "concentration translator."

Defining the linkage between chlorophyll and nutrients has been the object of many basic and applied research studies, and some very sophisticated mechanistic models have been 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 for regulatory purposes where the focus is on attainment, based on frequency of exceedance. Predicting how often the chlorophyll standard might be exceeded is a simpler task that places emphasis on locating an upper bound for algal abundance in a lake with a particular nutrient concentration. In other words, presence of unexplained variability can be acknowledged without attempting to quantify the sources.

The premise for linking chlorophyll and nutrients in criteria development is that the nutrient supply sets an upper bound on algal abundance, and that upper bound is affected by physical factors (chiefly light and temperature) prevailing in a particular lake. Other factors such as grazing by herbivores may depress algal abundance below the upper bound, but there are no factors other than nutrients that can augment algal abundance beyond this upper bound. Creating the quantitative linkage 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, it is necessary to develop several supporting concepts and arguments, beginning with a review of the limiting nutrient concept and a rationale for targeting phosphorus. Next is a characterization of the factors that can suppress algal abundance below the upper bound expected on the basis of physical factors and nutrient concentrations. 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 both 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 the conditions of 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 species at a time. Natural communities are composed of many algal species, each of which has slightly different nutrient requirements and different growth responses to light and temperature.

Moreover, the species composition can change dramatically over the course of the summer. The result is that the amount of chlorophyll produced in response to a given supply of nutrients will vary depending on light, temperature, and the species present, all of which change throughout the growing season. The point is that the potential 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 advantages to placing the primary focus on phosphorus rather than nitrogen, which is the only other nutrient with a strong claim for controlling algal abundance. Control of phosphorus sources in the watershed can reduce loads in a predictable manner. Similar controls on nitrogen can be circumvented by algae able to fix atmospheric nitrogen, which is essentially inexhaustible.

In general, there appears to be no special disadvantage incurred by ignoring 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 ratios (low values of the ratio are often taken as indirect evidence for nitrogen limitation). Nitrogen could, of course, be used on a site-specific basis if some special regulatory advantage were conferred, but in general phosphorus alone appears to be as good or better than nitrogen. 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).

Phosphorus also offers some practical benefits with respect to implementation of controls, and it has no particular disadvantages with respect to nitrogen. 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, but it is a moving target insofar as steady-state conditions do not prevail.

Furthermore, 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 algae faster than the algae can reproduce. Changes in any of these or other 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 usually reflects the effect of one or more factors in suppressing abundance below the potential abundance. The degree of suppression varies, but must occasionally be small enough so that the realized abundance approximates the potential. The objective is not to quantify the amount or source of suppression, but to accommodate variability observed in chlorophyll measurements.

Characterizing Chlorophyll-Phosphorus Relationships with Concentration Translators

The scientific literature is replete with studies exploring relationships between phosphorus and algal abundance in a wide variety of lakes. Typically, these studies produce empirical relationships (regression lines) that predict chlorophyll as a function of phosphorus. These quantitative relationships are examples of concentration translators as defined for this document. One widely cited equation, derived by Jones and Bachmann (1976), has been applied in the development of control regulations in Colorado. Many such empirical relationships exist, and a few examples highlighting regional variations are shown in Figure 1.

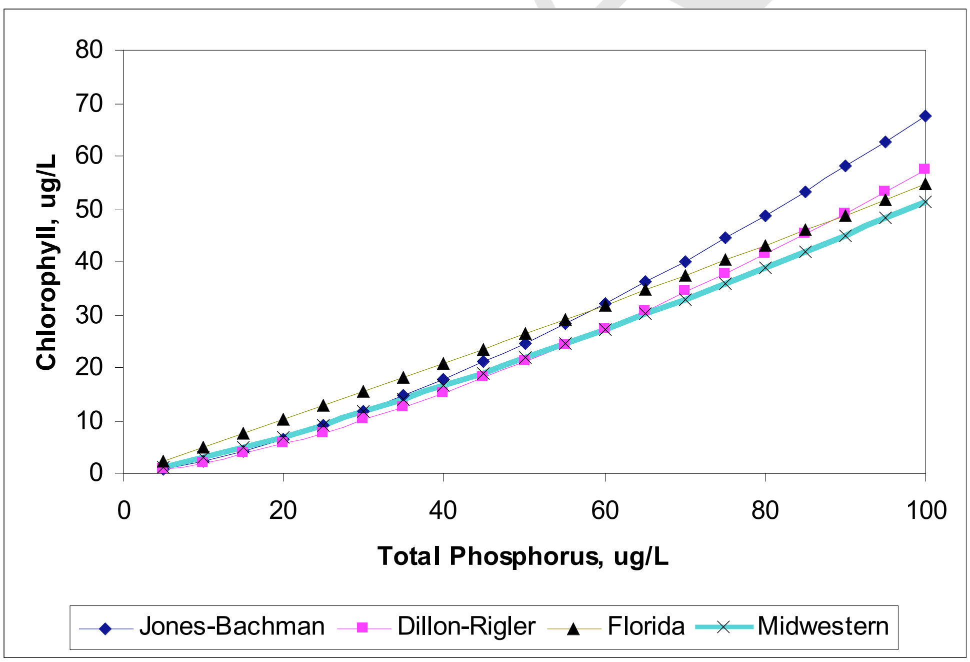

Figure 1. A selection of equations predicting chlorophyll as a function of phosphorus. Sources include Jones and Bachman (1976), Dillon and Rigler (1974), Hoyer and Jones (1983), and Brown et al. (2000).

Factors that Suppress Algal Abundance

Light and temperature affect the potential abundance of algae for a given level of phosphorus. An example for the role of light is provided by the work of Hoyer and Jones (1983), who have shown the importance of accounting for inorganic suspended solids (ISS), which increase turbidity and decrease the availability of light. Not surprisingly, higher concentrations of ISS decrease the yield of 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.

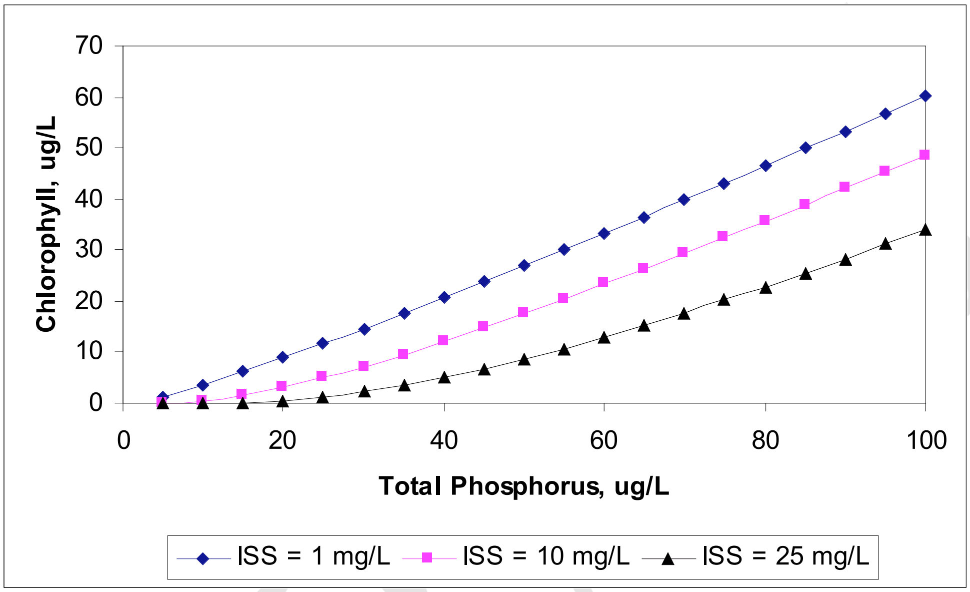

Figure 2. Predictions of chlorophyll as a function of phosphorus, at three levels of inorganic suspended solids (ISS). Higher ISS means less light available for algae. Equation from Hoyer and Jones (1983).

The potential abundance may not be realized at any point in time due to suppression by grazers that feed 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 species have the capacity to consume a significant portion of the algal biomass, and thus to depress realized abundance below the potential expected for a given phosphorus concentration.

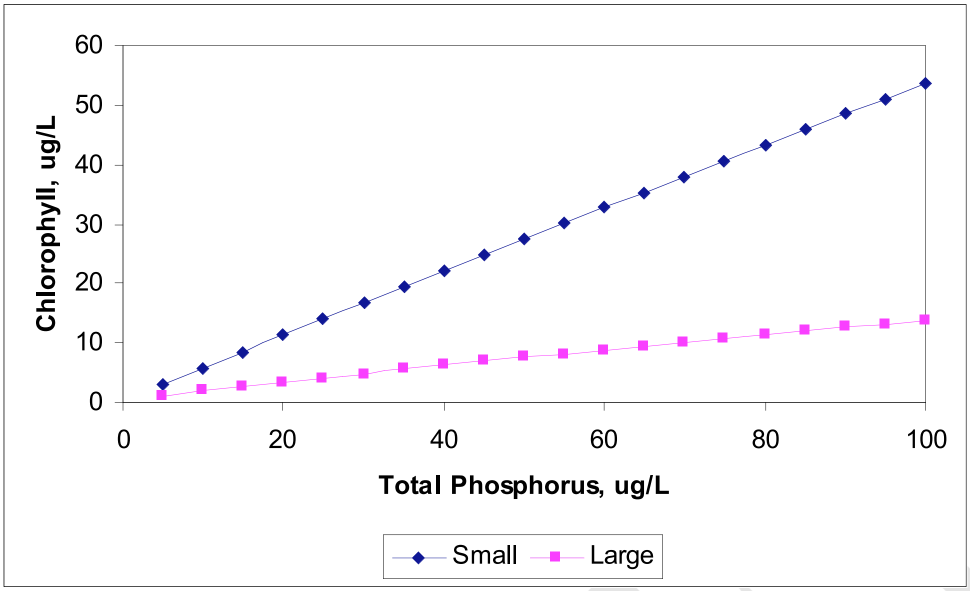

Figure 3. Predictions of chlorophyll as a function of phosphorus, in the presence of large or small zooplankton species. The zooplankton are herbivores that consume algae. Equation from Mazumder and Havens (1998).

The abundance of algae also may be affected by the availability of nitrogen, which may 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 in any lake. 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, albeit briefly, returning control to phosphorus. 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). 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). Thus, for a given concentration of phosphorus, expected chlorophyll concentrations tend to be smaller as the TN:TP ratio decreases, although the effect is seen mainly at phosphorus concentrations above 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 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.

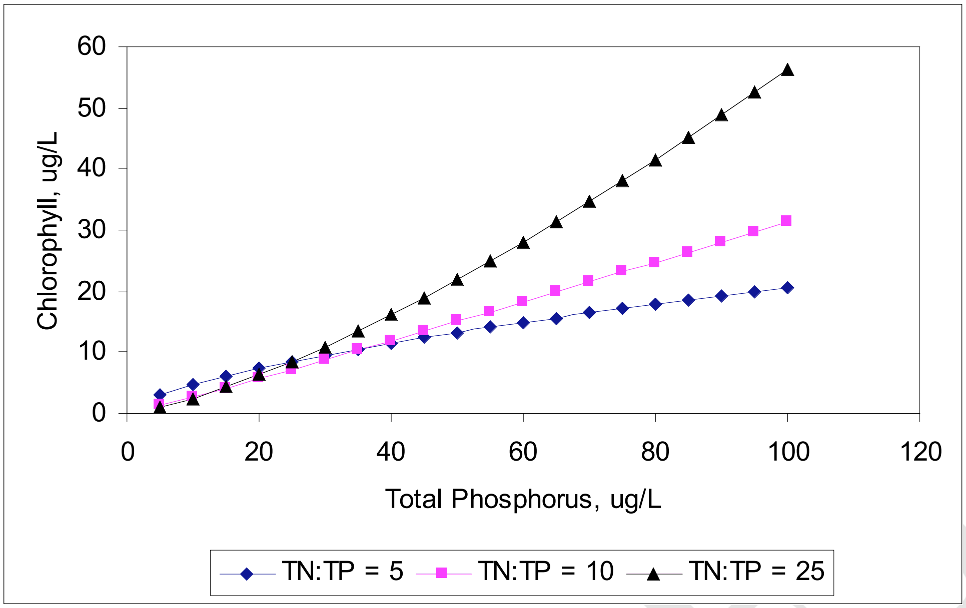

Figure 4. Predictions of chlorophyll as a function of phosphorus for different ratios of nitrogen to phosphorus. A low ratio of TN:TP is often taken as an indicator if nitrogen limitation. Equation from Prairie et al. (1989).

Most studies linking chlorophyll to phosphorus and other independent variables have been based on data from large sets of lakes. This is true of the relationships portrayed in Figures 1-4. 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 an accurate estimate of a seasonal mean. The concept advanced here is that decisions can be based on the 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 outcome tends to be very predictable. In an environment of controlled light and temperature, the growth of the algae depends largely on the abundance of nutrients. When all nutrients are abundant but 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 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 typical assumptions about composition of algal cells, the ratio of chlorophyll to phosphorus would be about 1:1.

Theoretical ratios may be viewed as the asymptote of values expected in the field, but there is no guarantee that they would be realistic for most lakes. Rather than setting expectations based on theoretical ratios, field data can be used to establish the potential abundance of algae (chlorophyll) for different amounts of phosphorus. Hern et al. (1981) employed this concept to define a "response ratio" that was used for evaluation of lakes sampled in the National Eutrophication Survey of the 1970s.

A ratio of 1:1 is consistent with the upper bound of most observations from lakes in the National Eutrophication Survey (Figure 5), although the average response ratio in the summer was considerably less: 0.29. If nothing else were known, a ratio of 1:1 might be a good starting point for control measures, but it could be unnecessarily stringent for many lakes.

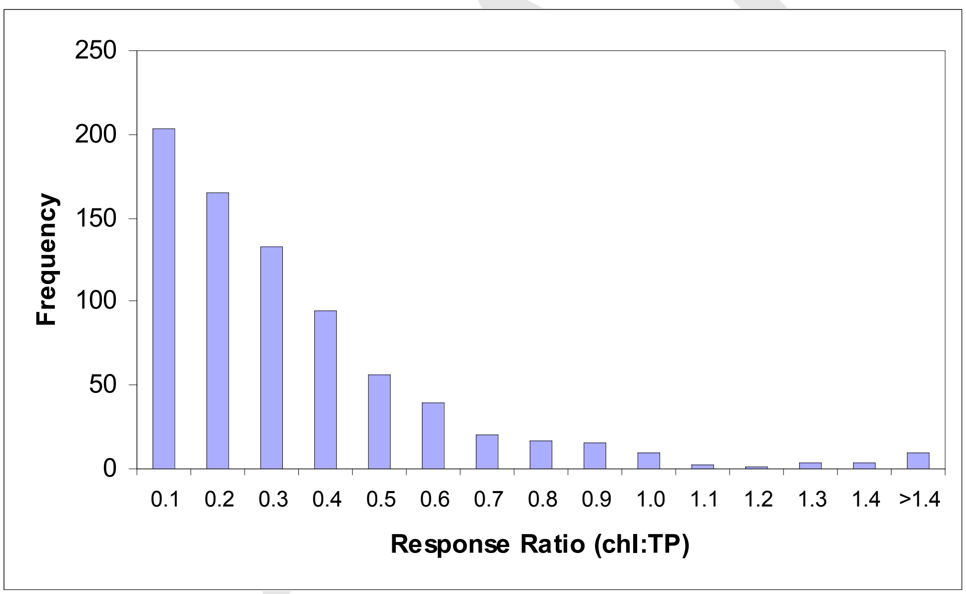

Figure 5. Frequency histogram of response ratios recorded during the National Eutrophication Survey (Hern et al. 1981).

In any large collection of chlorophyll measurements from a lake, the potential can be approximated with an operational definition based on some percentile selected from the distribution of realized abundances. The response ratio observed on a particular date represents realized abundance that may be less than the potential expected for a particular amount of phosphorus. The role of factors other than phosphorus determines suppression of the ratio below the potential. For a cross section of lakes, typical ratios can be extracted from published regression equations characterizing chlorophyll as a function of phosphorus.

The effect of increasing ISS concentration is like a discount factor applied to the responsiveness of the algal community to the availability of 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). Presumably, the difference occurs because large herbivores are much more efficient grazers able to suppress the response ratio by removing evidence of algal growth. Finally, the effect of altering the TN:TP ratio is, not surprisingly, to make chlorophyll more responsive to phosphorus at higher TN:TP ratios (Figure 8); the effect is inconsistent at low phosphorus concentrations, however.

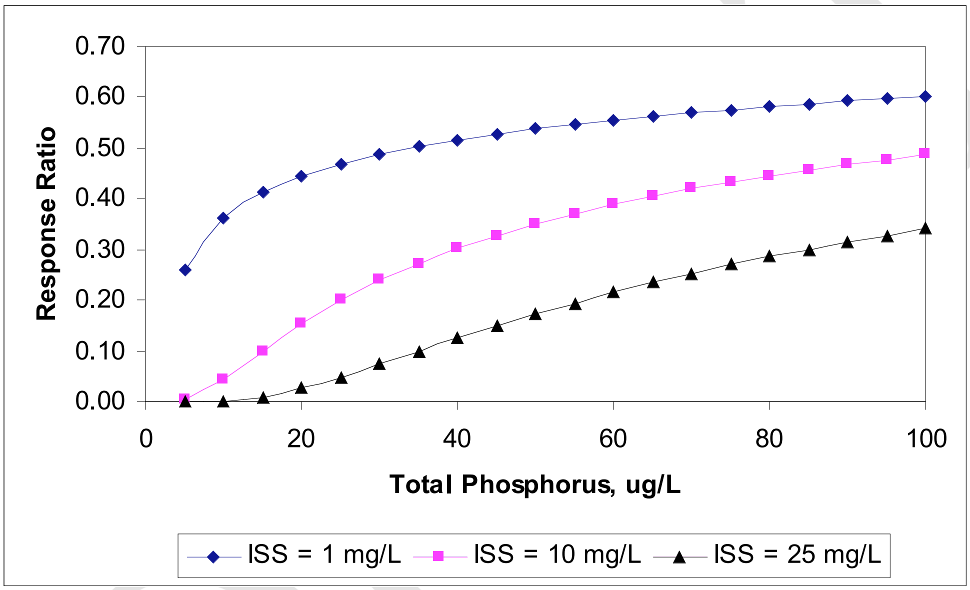

Figure 6. Response ratios implied by an equation that predicts chlorophyll as a function of phosphorus and inorganic suspended solids (from Hoyer and Jones 1983). Each line represents predictions where inorganic suspended solids is held constant at 1, 10, or 25 mg/L. Higher ISS means less light available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

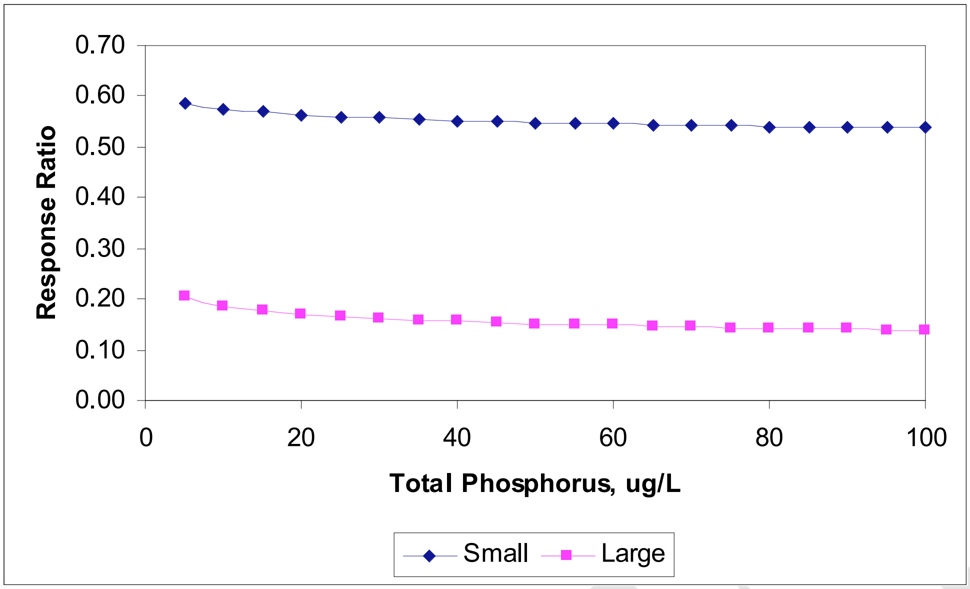

Figure 7. Response ratios implied by a equations that predict chlorophyll as a function of phosphorus. Each line represents predictions for lakes where the zooplankton community is comprised of small or large herbivores (from Mazumder and Havens 1998). Larger herbivores have the capacity to remove a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

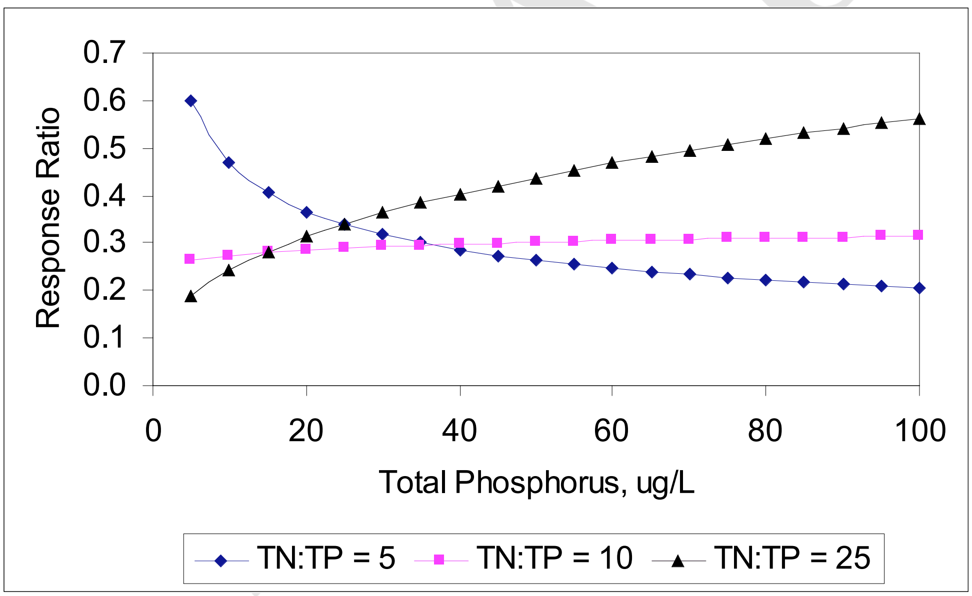

Figure 8. Response ratios implied by an equation that predicts chlorophyll as a function of phosphorus and nitrogen. Each line represents predictions for a fixed nitrogen concentration.

In each case where phosphorus is supplemented with an additional control factor, more variance in chlorophyll concentration can be explained. Each time another factor becomes important relative to phosphorus, the response ratio is depressed below the potential for a given lake. This was evident 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. 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 implementation procedures for chlorophyll standards. Part of the attraction resides in the potential for developing regional approaches for defining the amount of phosphorus consistent with a particular chlorophyll standard. Characteristics of the response ratio in a range 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 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 have been omitted where enough samples were taken, but most of the phosphorus concentrations were below detection limit (e.g., Granby, Carter, Shadow Mountain). In these cases, the response ratio could not be determined reliably.

	Response Ratio Percentile				**Years Exceeding Percentile**		
Lake	**50th**	**75th**	**90th**	**Years Sampled**	**50^{th}**	**75^{th}**	**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 50^{th}, 75^{th}, and 90^{th} percentiles in each lake, as well as the 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 clear 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 above the detection limit. It was assumed that the set of 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 National Eutrophication Survey 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 included in Table 1, yielding a total of 152 lake-years for the next step in the analysis.

An expected value for summer median chlorophyll in a lake can be derived from the summer median phosphorus and the response ratio distribution. The expected value represents potential algal abundance defined empirically based on exceedance frequency. Data from Lake Loveland are used to illustrate the procedure (Figure 9). Chlorophyll and phosphorus have been measured during the summer months in eight years, plotted individually on the graph. The median response ratio (0.290), which was calculated from all summer observations, is applied to the observed summer median phosphorus concentrations to produce the lowest of three lines on the graph. Four of the observed summer median chlorophyll concentrations exceed the line based on the median response ratio. The same kind of line is generated with the 75th percentile response ratio (0.390), and only two of the eight chlorophyll values lie above that line. The third (uppermost) line is generated with the 90th percentile response ratio (0.459), and only one chlorophyll value falls above the line.

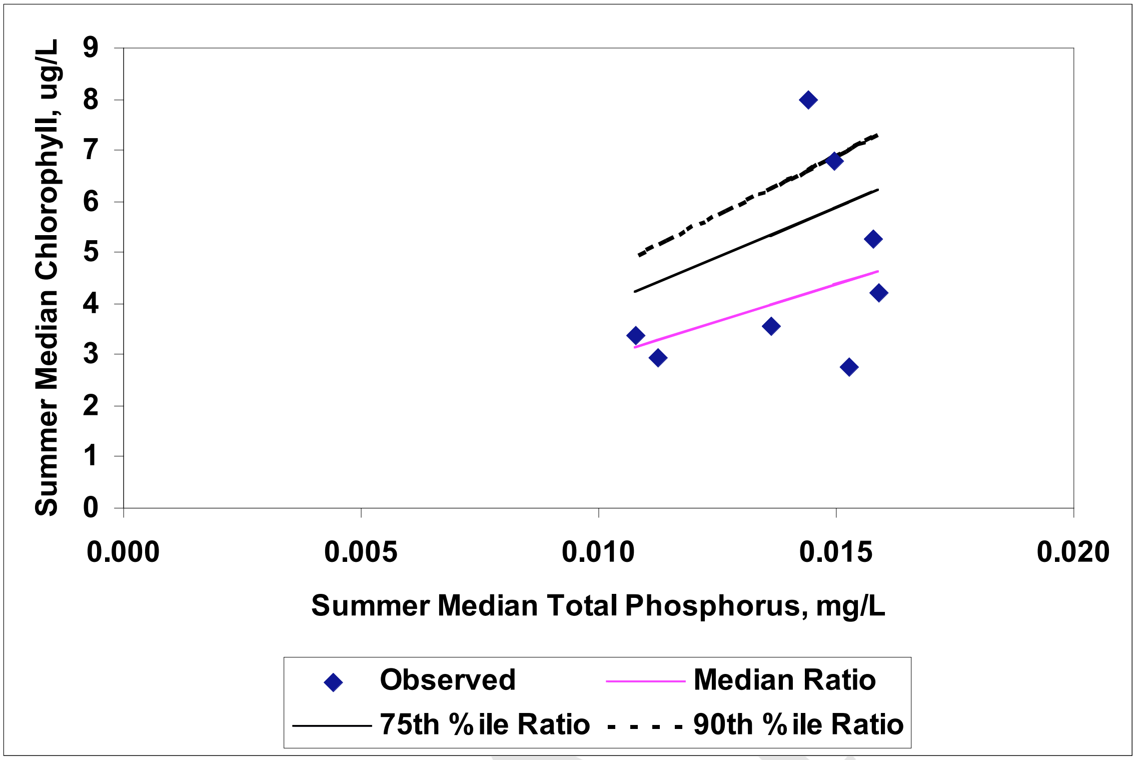

Figure 9. Plot of summer median chlorophyll vs. summer median total phosphorus in Lake Loveland. The three lines represent chlorophyll expected based on the observed phosphorus and one of three percentiles from the distribution of response ratios.

A sample size of eight is too small for estimating a general exceedance frequency, but Lake Loveland is just one of the lakes included in the analysis. 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 expected chlorophyll, the expected is exceeded by the observed about half of the time (81/152 lake-years), which makes sense for the median. 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 strictly 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 the 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 ratios 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 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 wrong and the unexplained variance in chlorophyll 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, the 75th percentile value of the response ratio can be used to generate the corresponding concentration for total phosphorus.

References Cited

Brown, CD, MV Hoyer, RW Bachmann, and DE Canfield, Jr. 2000. Nutrient-chlorophyll relationships: an evaluation of empirical nutrient-chlorophyll models using Florida and north-temperate lake data. Canadian Journal of Fisheries and Aquatic Sciences 57: 1574-1583.

Chapra, SC. 1997. Surface Water-Quality Modeling. McGraw-Hill, Boston. 844 p.

Dillon, PJ and FH Rigler. 1974. The phosphorus-chlorophyll relationship in lakes. Limnology and Oceanography 19: 767-773.

Golterman, HL. 1975. Physiological Limnology. Elsevier, Amsterdam. 489 p.

Hern, SC, VW Lambou, LR Williams, and WD Taylor. 1981. Modification of models predicting trophic state of lakes. Environmental Monitoring Systems Laboratory Final Report EPA-600/3-81-001.

Hoyer, MV and JR Jones. 1983. Factors affecting the relation between phosphorus and chlorophyll a in midwestern reservoirs. Canadian Journal of Fisheries and Aquatic Sciences 40: 192-199.

Jeppesen, E et al. 2005. Lake responses to reduced nutrient loading – an analysis of contemporary long-term data from 35 case studies. Freshwater Biology 50: 1747-1771.

Jones, JR and RW Bachmann. 1976. Prediction of phosphorus and chlorophyll levels in lakes. Journal of the Water Pollution Control Federation 48: 2176-2182.

Mazumder, A and KE Havens. 1998. Nutrient-chlorophyll-Secchi relationships under contrasting grazer communities of temperate versus subtropical lakes. Canadian Journal of Fisheries and Aquatic Sciences 55: 1652-1662.

Morris, DP and WM Lewis, Jr. 1988. Phytoplankton nutrient limitation in Colorado mountain lakes. Freshwater Biology 20: 315-327.

Prairie, YT, CM Duarte, and J Kalff. 1989. Unifying nutrient-chorophyll relationships in lakes. Canadian Journal of Fisheries and Aquatic Sciences 46: 1176-1182.

Reynolds, CS. 2006. Ecology of Phytoplankton. Cambridge University Press, Cambridge. 535 p.

Smith, VH. 1982. The nitrogen and phosphorus dependence of algal biomass in lakes: an empirical and theoretical analysis. Limnology and Oceanography 27: 1101-1112.

Smith, VH and J Shapiro. 1981. Chlorophyll-phosphorus relations in individual lakes. Their importance to lake restoration strategies. Environmental Science & Technology 15: 444-451.