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Application of a nutrient-saturation concept to the control of algal growth in lakes

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Abstract

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Either phosphorus or nitrogen can be responsible for nutrient limitation of algae in lakes. Nitrogen limitation can be defeated by heterocystous cyanobacteria through nitrogen fixation, but no comparable mechanism exists for P. Therefore, P is considered the predominant factor limiting phytoplankton biomass in lakes. Even so, increasing numbers of studies show that many lakes are limited by N deficiency because heterocystous cyanobacteria do not become sufficiently abundant to offset N deficiency. Where N limitation prevails, P control over phytoplankton populations can be achieved only if P concentrations are first reduced to a saturation threshold that is determined by the amount of available N. The extent of this reduction, which will typically occur without any suppression of phytoplankton biomass, can be estimated from nutrient chemistry, nutrient enrichment experiments, and information on the stoichiometry of phytoplankton, as illustrated with data for a Colorado reservoir in which a reduction of P of about 50% would be necessary to induce P limitation. Analysis based on stoichiometry could allow managers of water quality in lakes to anticipate the implications of N limitation for P-based management of water quality.

Key words: cyanobacteria, eutrophication, nitrogen, nitrogen fixation, phosphorus, stoichiometry

Phosphorus is generally accepted as the principal nutrient limiting the potential of lakes to produce algal biomass (Wetzel 2001, Kalff 2002), but experimental diagnosis of nutrient limitation in lakes often indicates that nitrogen controls phytoplankton biomass (Elser *et al.* 1990, James *et al.* 2003, Bunting *et al.* 2005). Also, relationships between algal biomass (chlorophyll *a*) and total P among lakes show a notable decline in slope at high concentrations of total P, suggestive of P saturation (Prairie *et al.* 1989, Jones and Knowlton 1993, Cooke *et al.* 2005). High TP concentrations often are associated with low TN:TP ratios, probably because numerous kinds of land use and waste disposal methods produce low N:P ratios in surface water (Downing and McCauley 1992). Colimitation of phytoplankton by N and P is possible (Morris and Lewis 1988, Dodds *et al.* 1989), but is associated with N:P ratios that are near the equilibrium assimilation requirements of phytoplankton. Thus, N limitation can be a significant complication in attempts to manage water quality of eutrophic lakes by control of P.

Phosphorus is treated as predominantly important in control of algal biomass because N deficiency can be offset by nitrogen fixation, whereas P deficiency cannot be offset by any comparable mechanism (Schindler 1977). Numerous examples demonstrate the ability of heterocystous nitrogen fixers to exploit at least a portion of P supplies that would otherwise be unused because of N deficiency (Smith 1982, Howarth *et al.* 1988, Leavitt *et al.* 2006). In many instances, however, N deficiency persists throughout the growing season, presumably because heterocystous cyanobacteria do not become sufficiently abundant to offset N deficiency (James *et al.* 2003). High light requirements of cyanobacteria for N fixation (Lewis and Levine 1984) or for photosynthesis (Walsby *et al.* 2003) indicate that low transparency, which is common in eutrophic waters, could constrain the rate of N fixation or the ability of N fixers to compete on the basis of N fixation alone (Ferber *et al.* 2004). In these cases, N is the dominant control on biomass, and the phytoplankton community remains saturated with P throughout the growing season.

A commonly assumed corollary of the P dominance paradigm for lake management is that reduction of P concentrations in lakes suppresses phytoplankton biomass. While this is true where N:P ratios are such that P depletion occurs, or where N:P ratios favor N limitation but N deficiency is fully offset

by N fixation, it is not true where N:P ratios are low and there is insufficient fixation of N by heterocystous cyanobacteria to allow full use of P. Under these circumstances, reduction of P concentrations will not produce a reduction in algal biomass until P passes below a saturation threshold that is determined by N concentrations (Fig. 1).

Where N fixation does not occur or is insufficient to offset low N:P ratios, the existence of N limitation and the approximate amount of P reduction required to induce P limitation can be estimated from field data and nutrient enrichment experiments. Such an analysis would be useful in establishing the cost and feasibility of controlling phytoplankton by P limitation where phytoplankton communities are initially saturated with P. A strategy for estimating the degree of P saturation for a phytoplankton community and the use of this information for projecting the amount of P reduction that would be required to bring the phytoplankton community under P control are illustrated here for Cherry Creek Reservoir, Colorado.

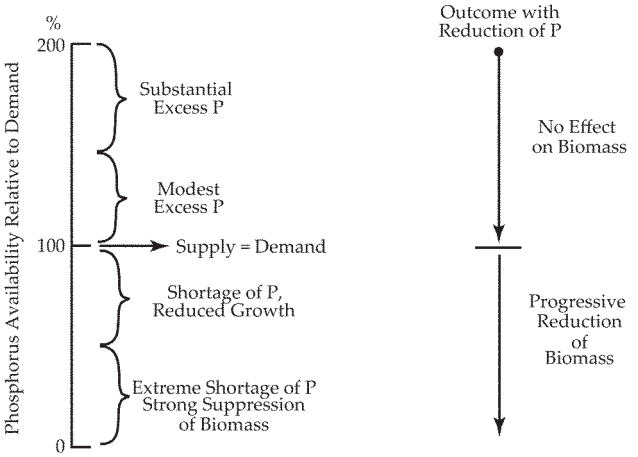

Figure 1.-Conceptual basis for control of algal biomass by restriction of P in a lake that initially is deficient in N.

Study site and methods

Cherry Creek Reservoir was created in 1950 for flood control of Cherry Creek, a tributary of the South Platte River near Denver, Colorado. The reservoir has an area of 3.5 km^2 at its typical pool size, which is held nearly constant; its hydraulic residence time is approximately 2 yr at average inflow, and its mean depth is near 5 m. Because of algal blooms and mass mortality of fish during the late growing season in some years, the State of Colorado has required special control measures, to be identified by the Cherry Creek Basin Authority, that will suppress algal biomass in Cherry Creek Reservoir.

The strategy for suppression of algal biomass in the Cherry Creek Reservoir has been regulation of point and nonpoint sources of anthropogenically generated P. The watershed of Cherry Creek Reservoir (998 km^2) and atmospheric deposition deliver approximately 6500 kg/y of phosphorus to the reservoir (Cherry Creek Basin Authority, unpublished data). A large portion of the upper basin is undeveloped, and the total population size of the basin is relatively small. Point sources of municipal discharge account for only about 15% of the total annual P load. High concentrations of phosphorus in the alluvium of the watershed (about 200 µg/L total dissolved P) above the zone of development indicate intrinsically high phosphorus concentrations in the basin (Cherry Creek Basin Authority, unpublished data), which would suggest the possibility of N limitation. N loading, which has not been studied extensively, probably does not exceed 5 times P loading, as judged from spring N and P concentrations in the lake.

Enrichment experiments of the type described by Morris and Lewis (1988) were conducted on 8 dates between May and October. Water for the experiments was pumped from the mixed layer (~1 m) of the lake into a large plastic drum from which translucent (reduction of photosynthetically available radiation [PAR] <1%) plastic carboys of 10-L capacity were filled. Three replicates were used for each of 4 treatments: control; addition of P; addition of N; or addition of N+P. For P enrichment, potassium phosphate monobasic (KH_2PO_4) was added as necessary to achieve a P increase of 60 µg/L; N was added as ammonium chloride to achieve an increase of 225 µg/L N. The carboys were held in an experimental pond with temperature cycling on a 24-hour basis to match the upper water column of the lake. Irradiance was adjusted by shading to approximately 25% of ambient, which matched PAR irradiance corresponding to the depth of maximum net photosynthesis in the lake. Carboys were agitated periodically. After 2–3 days of incubation, water from each carboy was taken for analysis of chlorophyll, nutrients, and phytoplankton species composition according to methods identical to those used for lake water, as described below. Results of each enrichment were scored through application of an analysis of variance followed by an a posteriori grouping procedure (Bonferroni Multiple Range Test, $p = 0.05$).

On the date of each enrichment experiment, vertical profiles of temperature and dissolved oxygen were obtained with meters, and light penetration was measured with a quantum sensor. A sample from the mixed layer was preserved with Lugol's solution for determination of phytoplankton composition, and water was collected for analysis of P fractions, including soluble reactive P (phosphomolybdate method: Murphy and Riley 1962), total soluble P (persulfate digestion followed by phosphomolybdate method: Lagler and Hendrix 1982), and particulate P (pyrolysis followed by phosphomolybdate treatment: Solorzano and Sharp 1980). Nitrate was measured by ion chromatography, and ammonium was determined by an indophenol blue method (Grashoff 1976).

Table 1.-Nutrients, transparency, and chlorophyll in the mixed layer of Cherry Creek Reservoir on the sampling dates (2003). SRP = soluble reactive P; TSP = total soluble P; PP = particulate P.

Date	Depth of 1% PAR	Phosphorus, µg/L			Nitrogen, µg/L	
		SRP	TSP	PP	NH_4^+-N	NO_3^--N
May 21	3.2	5.6	23	26	10	0
Jun 23	2.8	9.2	28	44	9	0
Jul 14	2.6*	1.6	23	41	11	0
Aug 4	2.7	6.2	30	55	32	51
Aug 18	3.1	-	-	48	15	0
Sep 8	2.1	7.5	25	50	13	0
Sep 29	2.6	1.8	19	50	16	0
Oct 20	2.8	2.1	19	44	19	0

* Estimated from Secchi disk reading.

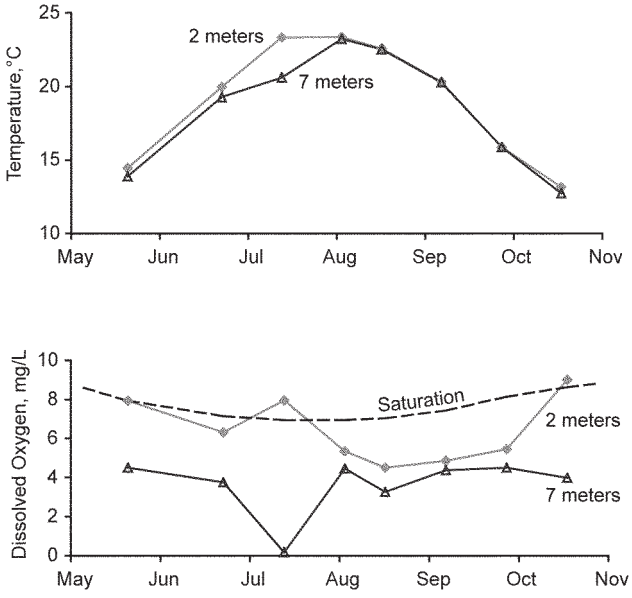

Figure 2.-Temperatures and oxygen concentrations at the top and bottom of the water column in Cherry Creek Reservoir during the growing season of 2003.

Chlorophyll was extracted with hot ethanol and measured spectrophotometrically (Marker *et al.* 1980, Nusch 1980).

On each date when water was taken for enrichment experiments, primary production was measured in the water column by the oxygen-difference method. Glass bottles (330 mL) were filled with water from the mixed layer and were incubated at 0, 0.5, 1, 2, 3, and 5 m in triplicate, along with 5 dark bottles. Incubations lasted about 2 hours, during which time solar irradiance was recorded. Post-incubation samples were analyzed by the Winkler method for dissolved oxygen, as were 5 replicate samples of the water taken just prior to incubation. Volumetric estimates of net production were integrated over depth to provide an areal estimate of primary production per unit time.

Results

The temperature of the upper water column in Cherry Creek Reservoir rose progressively between start of the study in May and the last half of August, 2003, at which time it reached 24 °C and then began to cool (Fig. 2). The bottom of the water column was slightly cooler than the top on some dates, and on other dates there was no detectable difference in temperature with depth, except in the top meter. Thus, the water column was not stably stratified on a seasonal basis. Dissolved oxygen profiles indicate that the stratification at times lasted as much as several days or a week, during which time dissolved oxygen near the bottom of the reservoir declined to concentrations well below saturation. At other times the water column mixed to such an extent that dissolved oxygen concentrations were uniform over depth (Fig. 2). Instability of summer stratification can be explained partly by the low relative depth of the reservoir and partly by withdrawal of water from the deepest part of the water column through the outlet of the reservoir. Depth of 1% PAR varied irregularly between 2.1 and 3.2 m (Table 1), indicating that phytoplankton were commonly being mixed to depths beyond the threshold of positive net primary production.

The upper water column of the reservoir was subsaturated with dissolved oxygen during August and September, 2003 (Fig. 2), but in those same months, net production, as measured in the upper water column, was positive over a 2-hr incubation period (Table 2). Thus, it appears that mixing suppressed primary production in the lake during August and September.

Table 2.-Primary production in Cherry Creek Reservoir. GPP = gross primary production; NPP = net primary production.

	21 May	23 Jun	14 Jul	4 Aug	18 Aug	8 Sep	29 Sep	20 Oct
GPP, $gO_2/m^2/h$ (0-5 m)	0.46	1.27	1.78	1.40	0.79	0.93	0.44	0.96
NPP, $gO_2/m^2/h$ (0-5 m)	0.22	0.81	0.65	1.01	0.21	0.47	0.36	0.45
Incident PAR, $moles/m^2/h$	7.1	6.2	4.8	5.6	2.6	3.8	2.8	3.4
Gross yield, mgO_2/mole PAR	65	204	368	249	307	246	160	287

Table 3.-Average chlorophyll concentrations (µg/L) for experimental treatments at the end of the incubation period for each experiment. Presence of N fixers in the lake is also shown: - = <300 cells/mL; + = 1000–10,000 cells/mL; ++ = >10,000 cells/mL. The nutrient response on each date is characterized on the basis of statistical analyses described in the text.

	21 May	23 Jun	14 Jul	4 Aug	18 Aug	8 Sep	29 Sep	20 Oct
Control	9.7	18.2	61.6	26.0	28.7	23.4	26.8	32.5
Add P	8.0	19.3	77.3	28.9	29.1	28.9	26.8	38.6
Add N	41.2	45.6	70.9	47.4	42.9	44.8	50.7	59.0
Add P+N	35.4	46.3	93.9	52.2	42.8	40.7	53.2	64.9
Response	N	N	N+P	N	N	N	N	N
N Fixers	-	-	++	+	-	-	-	-

Concentrations of total soluble P (TSP) were high throughout the growing season in the upper water column of Cherry Creek Reservoir, and soluble reactive P (SRP) was consistently detectable (>1 µg/L P: Table 3; Fig. 2). Concentrations of nitrate were below the detection limit (3 µg/L) except on one date (4 August, 2003), which appears to have followed a disruption of temporary stratification that allowed accumulation of inorganic N near the bottom of the reservoir. Concentrations of ammonium also were consistently low except on 4 August, but were not below the detection limit (2 µg/L). Although the observed concentrations of ammonium could be considered nutritionally significant to phytoplankton, the total absence of nitrate at the same time suggests that much of the small amount of ammonium consistently measured was not available for uptake (*i.e.*, the measured ammonium was bound: Hamilton and Lewis 1987).

Algal abundance, expressed as chlorophyll *a*, was lowest on the first sampling date (May) but subsequently varied irregularly within a narrow range around a median of approximately 50 µg/L (Fig. 3). Cyanobacteria were dominant numerically except on the first sampling date, but nitrogen fixers (primarily *Anabena*, but also small numbers of *Aphanizomenon*) appeared in abundance on only one date and were undetectable on most dates (Fig. 3). *Aphanothece* and *Oscillatoria* were the dominant genera among the cyanobacteria. Chlorophytes were moderately abundant and were mostly accounted for by *Chlorella*. Diatoms and cryptophytes also were consistently present, but not at high abundances.

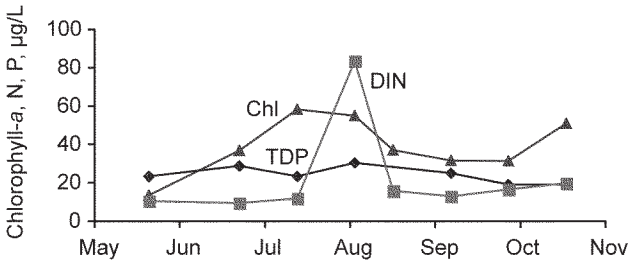

Figure 3.-Concentrations of chlorophyll, TSP, and DIN in the upper water column of Cherry Creek Reservoir during the growing season of 2003.

Nutrient enrichments showed response of phytoplankton biomass to N on all dates (Table 3). In only one case (14 July, 2003) was there also a response to P. This was the single date on which nitrogen-fixing heterocystous cyanobacteria (mainly *Anabena*) were abundant.

Discussion

Cherry Creek Reservoir is a discontinuous polymictic lake (Lewis 1983); it does not sustain density stratification throughout the growing season, but is stratified for periods of several days irregularly during the growing season. Nutrient chemistry suggests that N deficiency established a limit on biomass accumulation, given the absence of N fixation on most dates, and the results of the nutrient-enrichment experiments are consistent with this interpretation. The reservoir was not entirely unsuitable for growth of N fixers, as shown by their brief appearance during July, but weak light avail-

Table 4.-Estimation of excess P available to phytoplankton in Cherry Creek Reservoir, 2003, as explained in the text.

	21 May	23 Jun	14 Jul	4 Aug	18 Aug	8 Sep	29 Sep	20 Oct
Algal Carbon, µg/L	354	986	1563	1474	988	845	837	1366
Particulate P, µg/L	26	44	41	55	48	50	50	44
Mass Ratio, C:P	14	22	38	27	21	17	17	31
Excess P, µg/L	22	34	25	40	38	42	42	30
Total P, µg/L	49	72	64	85	75*	74	69	63
Excess P, %	46	47	40	47	51	56	60	43

* TSP approximated.

ability associated with repeated deep mixing probably prevented significant N fixation, which demands large amounts of energy (Lewis and Levine 1984, Viner 1985) or repressed photosynthesis (Walsby *et al.* 2003).

Suppression of algal abundance in Cherry Creek Reservoir through control of P would require that P concentrations be reduced to the threshold of nutrient saturation for P (Fig. 1). The amount of P reduction required to reach this threshold can be estimated from the stoichiometry of phytoplankton. The Redfield ratio for phytoplankton can be taken as an indication of the P content of healthy cells occupying an environment where P is relatively scarce (Sterner and Elser 2002). Under these conditions, the mass ratio of C to P is close to 41:1. The literature on phytoplankton growth shows that P starvation begins when the C:P ratio increases to about 100 (Nalewajko and Lean 1980, Healey 1982), although the mass ratio of severe P starvation may be accompanied by even higher ratios (*e.g.*, 200:1, Sterner and Elser 2002). Thus, the objective of P management would be to reduce concentrations of P in the water column to a C:P mass ratio of at least 100:1, and possibly higher.

The C content of phytoplankton can be estimated directly by particulate organic carbon (POC) analysis or indirectly by chlorophyll. Both of these measures are imperfect in that POC measurements include non-algal carbon, and the ratio of C to chlorophyll is variable (Falkowski and Raven 2007). For approximation purposes, however, the ratio of C to chlorophyll is used here. Literature complied by Kalff (2002) on the wet mass:chlorophyll ratio, when converted at a ratio of 0.15 for dry mass:wet mass, as suggested by Kalff, yields a median C:chlorophyll ratio of 27 (standard error = 8). Table 4 shows the amount of C in Cherry Creek Reservoir that can be accounted for by phytoplankton biomass as estimated by chlorophyll (Table 4). Particulate P, which is taken as an indication of phytoplankton P, is then used to estimate the C:P mass ratio of phytoplankton. The amount of phosphorus in excess of the 100:1 mass ratio is designated "excess P," which can be compared with total P. In Cherry Creek Reservoir, excess P had a median value close to 30 µg/L, or about 50% of total P.

The total P inventory of the water column for Cherry Creek Reservoir would need to be reduced by about half before suppression of phytoplankton biomass by P limitation could begin (Table 4). No incremental water-quality benefits could be expected between the current concentrations and the onset of P limitation at about 50% of current concentrations.

For some reservoirs, a reduction in P concentration of 50% or more could be considered practical. The circumstances of Cherry Creek Reservoir, which may not be uncommon, would make such a reduction quite difficult insofar as most P originates from dispersed sources. The additional complication of internal loading, which could reduce the effectiveness of external phosphorus control, could make control of algae by P suppression even more difficult (Cooke *et al.* 2005).

An infeasible projected P reduction could be the basis for a switch to N management rather than P management. N management is likely to be much more expensive for point sources because it involves nitrification followed by denitrification, typically with organic carbon supplementation (methanol), whereas P control for point sources is achieved by precipitation (Metcalf and Eddy 2003). Also, watershed management of N may be difficult because of the high mobility of nitrate in groundwater. Even so, expensive N management may be preferable to cheaper but ineffective P management.

One risk of N management could result from an unexpected change in physical conditions that renders N fixation more effective, thus undermining N management. In Cherry Creek Reservoir, for example, greater stability of the water column caused by changes in water management or even climate warming could create more favorable conditions for N fixers.

Cherry Creek Reservoir is an illustration of the importance of nutrient saturation to nutrient management in lakes. Wherever phosphorus saturation is continuous and N fixers are absent, present only sporadically, or of low abundance, suppression

of phytoplankton biomass by P management may be feasible in some cases, but quite impractical in others, and typically will involve an initial interval of P suppression that produces no suppression of phytoplankton biomass.

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