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Relationships between phosphorus loading and trophic state in calcareous lakes of southeast Wisconsin

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Abstract

The relationships among external phosphorus loading, lake phosphorus concentrations, and indices of lake trophic state are investigated for four calcareous and one noncalcareous lake in southeast Wisconsin. The total P and molybdate-reactive P concentrations during winter and spring overturn are significantly higher in the calcareous lakes than predicted by models based on regional studies of Canadian Shield (ELA) lakes and the central New York Finger Lakes. The calcareous Wisconsin lakes have relatively low phosphorus retention coefficients and are eutrophic despite their low or only moderate external P loadings. By contrast, noncalcareous Devils Lake is oligotrophic; it is also adequately represented by the ELA loading vs. response equations.

The calcareous Wisconsin lakes and edaphically similar Lake Minnetonka, Minnesota, have lower epilimnetic chlorophyll concentrations in summer than predicted by the Dillon and Rigler equation (based on lake mean total P at spring overturn). Because these stratified lakes are frequently phosphorus-limited in midsummer, the failure of the Dillon-Rigler model may be related to seasonal cycles of mixed-layer concentrations of total P (and SRP) and also to the seasonal patterns of loading. From other studies I suggest that these observations may be part of a larger edaphic pattern related to low phosphorus binding tendencies of certain calcareous lake sediments.

The cultural eutrophication of lakes has been an important, albeit usually local issue for a long time, but the systematic scientific search for mathematical models of this complicated process is relatively recent. The most important and practical mathematical models that have been developed, starting with Vollenweider's now classic work, are "input-output" models, relating various indices of trophic state to external loading of a limiting nutrient (usually phosphorus). Part of their appeal lies in their simplicity; part, too, lies in their evident success in identifying relationships common to many lakes, rather than focusing only on the seemingly idiosyncratic behavior of individual lake systems. Nevertheless, upon close scrutiny, all of these input-output models have considerable unexplained variation which must be reduced before they can attain wider practical utility.

Input-output models have been both "local" and "encompassing." Each local model defines statistically the external loading vs. lake response relationships for a lake *set* whose members share important edaphic and climatic influences; two of the best examples are Schindler et al.'s (1978) study of the ELA lakes in the Precambrian Shield of NW Ontario, and Oglesby and Schaffner's (1978) study of the lakes in central New York State. The most encompassing models are defined on lakes of the world; Schindler's (1978) study is of this type. Obviously, most loading-response models lie somewhere between these extremes. These include all of the regional studies sponsored by the OECD, including, for example, that for the North American lake set. Reckhow (1979), among others, has examined several different models defined on the North American lake set.

Most modelers have recognized the limitations on extrapolation imposed by the characteristics of the set studied. Thus, Schindler et al. (1978, p. 196) concluded that their regression relationships "should provide a useful initial guide for those who wish to alter the nutrient inputs or flow regimes in Shield lakes." Similarly, Oglesby and Schaffner (1978, p. 143) remarked: "Whether the relations established here for a group of New York lakes can be extrapolated to other situations remains untested." The authors of more encompassing models have often been equally explicit. Reckhow and Simpson (1980, p. 1440) state: "Since the model was constructed only from

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lakes within the north temperate climatic zone, it should be applied only to lakes within this zone."

I examine here relationships between external phosphorus loading and trophic state for four calcareous and one noncalcareous lake in southeast Wisconsin. In the first part I specifically test the regression equations developed by Schindler et al. (1978) and Oglesby and Schaffner (1978) for two other localized North American lake sets and show how my lakes deviate from the model predictions. From a statistical standpoint these *inter*regional comparisons are facilitated because of the very small *intra*regional variation found in both the ELA and New York studies. Moreover, in both of these studies a simple two-parameter (slope and intercept) linear model was fit relating lake P to external loading, based on a fairly large sample size. In each study the model r^2 was 0.83, and no residual (actual minus predicted value) exceeded 10 mg P m^{-3}. The ± 2 SE confidence envelopes were also $<50\%$ of the predicted value throughout the middle and upper portions of the loading range.

The comparisons with the ELA involve mainly cultural and edaphic differences, because climatic and hydraulic features are quite closely comparable between these two areas. Air temperature and precipitation decrease moving 750 km NNW from Madison to Kenora, Ontario, but the amount and seasonal distribution of the precipitation *excess* (precipitation minus evapotranspiration) changes relatively little (12–18 cm yr^{-1}; cf. Linsley et al. 1958; Brunskill and Schindler 1971). Insolation during the ice-free season is almost identical at the two locations (Brunskill and Schindler 1971; NOAA data for Madison). However, the differences in regional soils are profound. Upper soil horizons in the ELA region are thin, carbonate-free, organic-rich, and extremely acid (pH values down to 4; cf. Brunskill and Schindler 1971). Subsurface drainage is shallow because of the outcropping plutonic rocks. Because of the chemically resistant minerals in the bedrock and related glacial drift, and the shallow drainage, drainage is strongly influenced by humic materials. Soils in southeast Wisconsin are thick, fertile, pervious, low in humic substances, and well buffered by carbonates.

The comparisons with the New York lakes involve both climatic and edaphic differences; cultural influences are more nearly similar than in the ELA comparison. Central New York has significantly higher annual precipitation (by 15–25 cm) and much higher winter precipitation (by about 40%) than Madison. Potential evapotranspiration is about 9 cm yr^{-1} lower in central New York than at Madison (Linsley et al. 1958, p. 110); for this reason hydraulic export from the land drainage basin is about 3–4 times that in the Madison region. Edaphic and topographic factors are also different in central New York. Although carbonate rocks influence water chemistry over northern portions of the New York drainage basins (Broughton et al. 1972), the uplands (Allegheny Plateau) are characterized by infertile acidic soils. The clastics eroded from these soils have low exchangeable P (Schaffner and Oglesby 1978). Because of the annual precipitation pattern, and poor infiltration on the steep shaley soil slopes, erosion of clastics can be important in central New York in winter and spring (Stewart and Martin 1982).

After examining how well the calcareous Wisconsin lakes conform to the above two regional models, I examine briefly how well they conform to two more encompassing models. In the first case the phosphorus concentrations are much higher than predicted from a general model for the diverse North American lake set (Reckhow 1979). The residuals appear related to hypolimnetic anoxia, and mirror the results obtained in the two more localized comparisons. Finally, I show that the chlorophyll predictions based on the Dillon and Rigler (1974) model are too high for these stratifying calcareous Wisconsin lakes and for edaphically and morphometrically similar Lake Minnetonka, Minnesota.

In the discussion section I show how these results may be part of a larger edaphic pattern, propose a geochemical interpretation of the pattern, and note the importance of these results to the mathematical models of lake trophic state.

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Methods

The lakes were sampled before 1977 with either a submersible pump or a plastic Van Dorn sampler; samples collected after 1976 were taken with a Masterflex peristaltic pump. The deepest region of each lake was sampled (profile) and, for the three larger lakes, frequently additional stations as well (cf. Stauffer 1974).

Analytical procedures for chlorophyll concentrations and standing crops are given by Stauffer et al. (1979), sampling procedures by Stauffer (1981*a*, 1982). Transparencies (SDT) were measured with a 25-cm Secchi disk with alternating white and black quadrants.

Phosphorus fractions were determined according to the scheme of Strickland and Parsons (1968), and with the persulfate digestion procedure of Menzel and Corwin (1965). Before 1976 phosphorus colorimetry followed Murphy and Riley (1962); after 1976 this procedure was modified slightly (Stauffer 1983*a*). Neither arsenic nor silica is an important analytical interference for P in these lakes and using these procedures. Molybdate-reactive silica was determined with the metol procedure (Strickland and Parsons 1968). Nitrate and ammonia were determined with the brucine and phenol-hypochlorite procedures specifically adapted to a Technicon AutoAnalyzer (Kluesner 1972).

Lake-average concentrations or conditions were computed with the usual areal-weighted summations. Because I concern myself here only with lake-average conditions, I adopt the following simplified notation (omitting overbars). Let SDT_s, Chl_s, and TP_s denote the mean *epilimnetic* transparency, chlorophyll concentration and total P concentration during midsummer (July–August). Let TP_w denote the lake-mean total P concentrations in late winter (just after ice-out), and TP_y the mean-annual concentration in the entire water column. The use of this notation facilitates comparisons between Wisconsin lakes and those of central New York and the ELA.

Drainage basin influences

Geology and hydrology—The calcareous lakes studied are all glacial remnants situated in the "Eastern Ridges and Lowlands," a physiographic province of SE Wisconsin with low to moderate hill slopes and pervious fertile soils derived from loess and calcareous glacial drift (Martin 1965). The two largest, deepest, and most intensively studied of the lakes (Mendota and Green) have nearly identical edaphic settings; both basins were incised into the Cambrian sandstone outcropping at present-day lake levels, while local drainage basin relief is provided by the same NE-trending "Magnesium Limestone" cuesta (Martin 1965). Fish Lake lies close to the NW edge of Lake Mendota's drainage basin and the cuesta scarp. Topographic relief is even gentler in the Lake Delavan drainage basin because of its position on the "Trenton Limestone Lowland" just west of the Niagara dolomitic escarpment in Walworth County (Martin 1965).

Fertile soils are prevalent in the lowlands and everywhere along the gently dipping (toward the SE) backslope of the cuesta which forms most of the Green and Mendota drainage basins. The better soils are intensively but conservatively cultivated. Uplands and stream borders are protected by woods or perennial grasses.

The principal geochemical influence on the lakes is the weathering of the locally abundant dolomitic limestone. The Mg:Ca atomic ratios in the lakes equal or exceed 1.0 because of both this dolomitic influence and the deposition of calcitic marl during summer stratification. Sulfate concentrations in the three drainage lakes are 25–30 g m^{-3} and probably reflect weathering of gypsum. Alkalinities at turnover are 3–4 eq m^{-3} for the drainage lakes, but only 2 eq m^{-3} in Fish Lake.

The climate is continental, with dry cold winters and warm moist summers. The mean annual precipitation is 77 cm in both Dane and Green Lake Counties and about 5 cm higher further south in Walworth County (NOAA climatol. data 1980). In a normal year net exports of water out of the land drainage basin are 12–15 cm throughout the region, much of it in late winter and spring [Rohlich 1963; Dane Co. Regional Planning Comm. (DCRPC) 1978]. Between late June and mid-September potential evapotranspiration exceeds expected precipitation (Linsley et al. 1958, p. 110 and 118; NOAA climatol. data 1980); soil moisture deficits then accumulate in the watersheds.

Because of this antecedent moisture deficit, water exports during fall are small unless late summer or fall has been abnormally wet. Midwinter is a period of stream baseflow recession to annual minima; lake levels typically are minimal before the spring thaw and maximal in mid to late spring.

Erosion rates are low in SE Wisconsin, because of the moderate amounts, moderate intensity, and favorable seasonality of the precipitation, the gentle land slopes, and the high soil infiltration capacities during the frost-free period (ranging up to 12 cm h^{-1} in Dane County soils under prairie perennials: DCRPC 1978). Hindall (1976) reported a mean suspended solids loss rate of 100 kg ha^{-1} yr^{-1} for the area. Erosion rates were an order of magnitude higher in the "Driftless Area" in the SW corner of Wisconsin (Hindall 1976). Relief is higher in that region. Most soil erosion occurs in late winter and early spring. Because of the low erosion rates, chemical weathering predominates over physical weathering. On the basis of the Ca and Mg concentrations in Green Lake, the mean annual chemical weathering rate for the dolomite is $\sim$25 g m^{-2} yr^{-1} (as compared to $\sim$10 g suspended solids). Because of calcareous influence, vegetation characteristics, and good soil drainage, the regional streams and groundwaters have negligible humic coloring, as do the lakes.

Noncalcareous Devils Lake is set between two moraine dams, in a rugged, mostly forested, quartzitic drainage basin only 16 km NW of Fish Lake (Martin 1965). Like the calcareous lakes, it is free of humic coloring (Hutchinson 1957). Climatic influences are closely comparable to those for the neighboring calcareous lakes.

Biologically available phosphorus—Because of the complex biogeochemical relationships of P in lakes and their associated drainage basins, some attempt must be made to define a *potential* "biologically available phosphorus" component (here abbreviated BAP), and its unavailable complement (Schaffner and Oglesby 1978). Difficulties arise in accurately defining BAP because of the underlying question: Available for algal uptake within what period? Perhaps the best reply is: Within the hydraulic residence time of that P component in the system under study (before sedimentation or washout). For some springs or streams this residence time may be only a few minutes. For the lakes studied it represents years for the soluble components of the external P flux and more nearly the length of time required for settling through the water column for certain particulate fractions (cf. Edmondson and Lehman 1981). The potential BAP fractions for these calcareous lakes thus might include the following: 1) soluble inorganic phosphate, or sometimes, more operationally, the soluble molybdate-reactive (SRP) fraction (Strickland and Parsons 1968); 2) soluble inorganic polyphosphates (especially detergents, readily cleaved biologically to form SRP in natural waters); 3) the enzymatically releasable soluble organic P fraction (Rigler 1973; Francko and Heath 1979); 4) nonrefractory particulate organic P; and 5) the particulate inorganic P which is desorbed in the water column before settling and incorporation into the surface sediment. Settling times are relatively short and adsorption-desorption depends on the difference between the inorganic phosphate concentration in the water and the "crossover" or apparent sorption "equilibrium" concentration for the particles (Mayer and

Gloss 1980). Concentrations in lake water and sorption on particles both vary seasonally in Wisconsin.

Soluble inorganic P is relatively enriched in soil slurries of rich fertilized agricultural topsoils (Schroeder 1976), particularly at low temperature and high pH (Mayer and Gloss 1980). The readily mobile P fraction then declines rapidly with soil warming, plant emergence, and development. The calcareous SE Wisconsin topsoils studied by Schroeder (1976) had SRP crossovers in early spring that were very close to concentrations in Lake Mendota between mid-October and mid-May (80–120 mg m^{-3}). Lake Delavan has even higher overwinter concentrations of SRP; hence incoming clastics might actually adsorb and remove some SRP from the water. Because particle settling rates are rapid in these hard waters (Ahern 1976), there is little or no discernible tendency for the inorganic clastics carried in by the spring flush to release soluble P before settling to the lake bottom and being incorporated into the surface sediments. This probably explains why erosion accompanying the very severe wind and rain storms of 27 May 1973 and 13–15 May 1978 had no discernible effect on the major P fractions in Lake Mendota (W. Sonzogni and R. Stauffer unpubl. data).

Green Lake has intermediate concentrations of SRP in early spring (40–55 mg m^{-3}); these are probably below soil adsorption crossovers during part of the spring erosion pulse. However, the important streams entering Green Lake first traverse shallow embayments that act as settling basins. Fish Lake has relatively low SRP concentrations at all seasons, but being a seepage lake, is subject to minimal inputs of erosion products.

Because of the greatly reduced epilimnetic SRP concentrations in all of these lakes after May, the desorption of P associated with the clastics load could be more important in summer. This is particularly true after the onset of hypolimnetic anoxia in Delavan and Mendota in early-midsummer because the reduction of the amorphous Fe(III)-oxide coatings on the clastics will result in the release of adsorbed phosphate. Because of the climatic and vegetation cycles, erosion rates are normally low after late spring.

Detrital apatite is an important component of external P loading that is never available for algal growth in these lakes because the epilimnetic waters are supersaturated with apatite all year (Stauffer unpubl.). Williams et al. (1971*b*) found apatite fractions averaging 23 ± 6% (of total inorganic P) in six SE Wisconsin calcareous lake sediments (including both Mendota and Delavan); the apatite is considered detrital, not endogenic nor authigenic. The same six calcareous lake sediments featured an additional 9 ± 3% of highly refractory inorganic P (released by Na_2CO_3 fusion). Combining these two particulate fractions, I conclude that at least 30% of the inorganic particulate P flux would not have been utilizable by algae even when lake SRP concentrations were low enough to allow complete desorption of the mobile particulate P fraction. Sagher (1976) and Williams et al. (1980) have stressed this nonavailability of certain particulate P fractions.

Because of operational limitations, in few if any stream monitoring projects is the P flux routinely classified as described above. More typically, TP is measured, and either total soluble P or total molybdate-reactive P (TRP). By definition, total soluble P includes components 1–3, but none of 4 and 5. If the particulate P is associated mainly with clastics (certainly true here during the important spring flush), *and* if the crossovers for the suspended sediment are similar to lake water concentrations, then total soluble P ~ equivalent to BAP. By contrast, TRP includes all of component 1, the most labile fractions of 2 and 3 (Rigler 1968; Tarapchak et al. 1982), *and* much of the potentially desorbable P associated with amorphous Fe(III)-oxide coatings on clastics. Because component 2 is unimportant for agricultural runoff, and because P associated with amorphous Fe(III) oxides is quantitatively important accompanying spring erosion, I conclude that TRP *overestimates* potential BAP for the spring lake conditions specified above. Thus, my BAP loadings for these lakes (Stauffer 1983*b*) may be too high.

External phosphorus loadings—Table 1

Table 1. Hydraulic parameters and external phosphorus loadings for four calcareous (C) lakes and one noncalcareous (NC) lake in southeast Wisconsin. Loadings apply to 1960–1972 (mean) and 1978. A_{db} is area of land drainage basin. L—Areal loading; Λ—mixed layer volumetric loading. L_{WTP} is the percentage of L_{BAP} from waste treatment plants.

Lake	A_{db} (km²)	A_o (km²)	$\bar{z}$ (m)	q_s (m yr⁻¹)	τ_ω (yr)	L_{TP} (mg m⁻² yr⁻¹)	L_{BAP} (mg m⁻² yr⁻¹)	Λ'_{BAP} (mg m⁻³ yr⁻¹)	L_{WTP} (%)
Mendota (C)*	581	39.1	12.4	2.0	6.2	1,040±180	670±140	84	38
Delavan (C)	97	7.2	7.5	2.1	3.6	1,590±170	1,240±140	155	65
Green (C)†	242	29.7	31.5	1.2	26	745±95	550±75	69	57
Fish (C)	2.5	0.88	6.0	0.25	25	90±25	60±20	12	0
Devils (NC)	14	1.53	7.9	~1.7	5	95±45	65±25	11	0

* For 1978: L_{TP} = 790±180; L_{BAP} = 420±150; Λ' = 53±19; WTP = 0%.
† For 1978: L_{TP} = 465±95; L_{BAP} = 270±75; Λ' = 34±9; WTP = 13%.

summarizes hydrographic data for the lakes and their watersheds, and includes areal loadings (L) and mixed layer loadings (Λ) for both TP and BAP (taken from Stauffer 1983*b*). My loading calculations differ from those of Schaffner and Oglesby (1978) in several ways. First, my per capita loadings for waste treatment plants are 10% higher than theirs. Second, I have adopted a BAP export coefficient for active agricultural land that is 92% higher than what they used; moreover, except for Fish and Devils Lakes, all lands in the Wisconsin watersheds were classified as either urban or active agricultural. Third, I have discounted nonsewered septic systems as important P sources in all the calcareous Wisconsin watersheds except Delavan (cf. Stauffer 1983*b*). By contrast, Schaffner and Oglesby (1978) assumed that half of the TP from these residential sources ultimately reached the lakes. They considered this likely to result in a positive loading error; it is an exceptionally low retention coefficient for septic systems (Reckhow and Simpson 1980).

For many of the New York lakes the population was 100% unsewered (vs. relatively low percentages in the Wisconsin drainages); the minimum was 53% for Seneca Lake. The calculated input from unsewered septic systems averaged 43 ± 3% (SE of mean) of the aggregate BAP loading from all sources for the 13 New York lakes studied. However, for several lakes of particular importance here the percentage was significantly lower (Canadarago, 26%; Cayuga, 29%; Conesus, 32%; Oneida, 36%).

Model formulations: lake TP vs. external loading—All of the phosphorus "input-output" models evaluated here have the general mathematical form

$$\widehat{\mathrm{TP}}_{\mathrm{lake}} = \hat{a} + \hat{b}\frac{L}{X} \qquad (1)$$

where $\hat{a}$ and $\hat{b}$ are fitted intercept (sometimes constrained to be zero) and slope coefficients, and X represents a variable "divisor" for the areal external loading. The models are linear in L, but not in X. The divisors differ, and include q_s, the annual outflow volume per unit A_o; $q_s(1 + \tau_\omega^{1/2})$, the "Vollenweider divisor"; $(11.6 + 1.2\,q_s)$, cf. Reckhow and Simpson (1980); and h_{mix}, the mixed layer depth in midsummer (Oglesby and Schaffner 1978).

All divisors except h_{mix} include the flushing parameter, q_s. Schindler et al. (1978) reported that q_s (V_o in their notation) was as effective a divisor for ELA lakes as the more complicated Vollenweider expression. The fitted equation for ELA lakes

$$\widehat{\mathrm{TP}}_{\mathrm{y}} = 8.5 + 0.081 L_{\mathrm{TP}} q_s^{-1} \qquad (2)$$

showed that only ~8% of the phosphate P added to these naturally oligotrophic shield lakes was retained in the water over the course of a year. Still, logic implies that the Vollenweider divisor should be more satisfactory than q_s for lake sets offering a wider range in τ_ω. This is true because in the limit $\tau_\omega \rightarrow 0$, $b \rightarrow 1.0$ when q_s is used as a divisor. Conversely, as τ_ω increases, the *fraction* of the external loading concentration (defined by $L_{\mathrm{TP}} q_s^{-1}$) that is retained in the water should decrease. This is obviously true of the oceans and all other closed basins. Reckhow's model addresses this problem by in-

Table 2. Lake phosphorus conditions vs. predictions for 1972. Predicting equations: R&S—Reckhow and Simpson (1980); O&S—Oglesby and Schaffner (1978); ELA_1 from Schindler et al. (1978) for ELA lakes based on $L_{BAP}q_s^{-1}$ and $L_{TP}q_s^{-1}$ (range for these two defined loadings); ELA_2, as above, but based on Vollenweider divisor (*see text*). All concentrations are mg P m^{-3}.

Lake	Measured			Predicted TP_y				Predicted TP_s	
	TP_y	TP_w	TP_s	R&S	O&S*	ELA_1	ELA_2	ELA_1	ELA_2
Mendota	135	144	42	74	29	36–51	27–37	39–56	30–41
Delavan	170	200	87	113	53	56–70	48–59	62–77	53–66
Green	51	52†	15	57	25	46–59	23–28	50–65	25–31
Fish	20	26	16	8	5	28–38	16–20	31–42	17–22
Devils	14	18‡	13	7	5	12–13	10–12	13–14	11–12

* TP_w.
† May be 15% *low*.
‡ 10–12 mg m^{-3} in February 1971 and March 1972.

corporating a fitted "settling parameter" (11.6) into the divisor.

Results

SE Wisconsin lakes vs. ELA lakes—When the ELA-based equations are applied to the Wisconsin lakes the predicted values for TP_y are far too low for both Mendota and Delavan, but highly accurate (given prediction uncertainty) for Devils Lake (Table 2). The prediction for TP_y in Green Lake with q_s as a divisor is quite accurate; however, the comparable prediction using the Vollenweider divisor is too low by a factor of at least 2 (Table 2). The situation is reversed for Fish Lake; here the predicted annual average concentration based on q_s as a divisor is too high.

The two ELA-derived equations relating TP_s to external load give much better results for Mendota and Delavan; however, even here the predictions based on L_{TP} are 12–25% too low for Delavan. Naturally the predictions based on L_{BAP} are even more seriously biased. Conversely, both predicted values (TP_s) for Green Lake are far too high. For both Green and Fish Lakes the Vollenweider expression gives far superior results—although still too high. In light of the above results it is important to stress that observed TP_s (July–August mean) is significantly lower than values in June or September for both Mendota and Delavan. By contrast, the midsummer epilimnetic concentrations in Fish and Green Lakes are highly representative of the broader mid-June–mid-October interval. The ELA-based equations accurately predict TP_s in Devils Lake.

The predicted values for TP_s are higher than for TP_y (ELA equations). This ordering is exactly opposite to the pattern observed in all four calcareous lakes (Table 2).

The predicted values for Chl_s based on external P loading are very accurate for Delavan, slightly high for Mendota, and far too high for Fish and especially Green Lakes (*see Table 4*). Here again, the Vollenweider expression is much more satisfactory than the equation based on $L_{TP}q_s^{-1}$. The ELA-based equation predicting Chl_s from TP_s overestimates actual Chl_s in all the Wisconsin lakes.

It is important to emphasize that the depth and hydraulic parameters for Delavan, Mendota, and Devils Lakes correspond closely to the ELA lake set analyzed by Schindler et al. (1978). Green Lake is much deeper than any of the ELA lakes, and Fish Lake has a q_s value lying far outside of the ELA range. Because of these characteristics, τ_ω for both Fish and Green Lakes lies far outside of the ELA range (0.6–7.4 yr) reported by Schindler et al.

SE Wisconsin lakes vs. New York lakes—The mean TP concentration at ice-out is much higher in each of the four calcareous lakes than predicted by the regression line of Oglesby and Schaffner (1978). Concentrations observed in noncalcareous Devils Lake are also higher than predicted (Table 2); however, here the difference is much smaller than for the calcareous lakes (Table 2; Fig. 1). In Fig. 1 I include the two largest residuals from the New York data; these serve to dramatize the interregional comparison.

The differences between the Wisconsin

Table 3. Nutrient conditions in Wisconsin lakes before and after ice-out in 1972. Data for Conesus Lake, New York, taken from Oglesby and Schaffner (1978). (NA—Not analyzed.)

Sampling date	Depth interval (m)	TP (mg P m^{-3})	TRP (mg P m^{-3})	Atomic ratio* TRSi:DIN:TRP
Mendota				
16 Mar 72†	0–16	97	84	NA:19.5:1
12 Apr 72†	3–15	111	101	1.5:16.0:1
28 Apr 72	0–18	140	107	2.8:16.5:1
Delavan				
12 Mar 72†	0–13	170	144	NA:14.5:1
30 Apr 72	0–16	195	129‡	0.05:11.5:1‡
Green				
11 Mar 72†	0–40	50	40‡	NA:19.0:1‡
13 Apr 72†	10–50	44	27	2.5:NA:1
3 May 72	0–30	52	38	3.5:16.5:1
Fish				
12 Mar 72†	0–12	15	3‡	NA:370:1‡
29 Apr 72	0–8	25	2	27:230:1
Devils				
15 Mar 72†	0–8	12.5	4.5‡	NA:100:1‡
29 Apr 72	0–12	18	2.5	110:180:1
Conesus				
Winter 73	$0–z_{max}$	17.5	12.5‡	59:36:1
Spring 73	$0–z_{max}$	—	2.5‡	250:125:1

* Total reactive silicate—TRSi; dissolved inorganic nitrogen—DIN; total reactive phosphorus—TRP.
† Ice cover.
‡ SRP.

calcareous and New York lakes are even larger if one compares concentrations of TRP or SRP in late winter (Table 3). Thus, although Green Lake is morphometrically comparable to the New York Finger Lakes, its TRP concentration following ice-out in 1978 (59 mg m^{-3}) was an order of magnitude higher than those reported by Oglesby and Schaffner (1978, p. 137) for four of the New York Finger Lakes. The calcareous lakes also have much smaller $SRSi_w$:TRP_w and DIN_w:TRP_w ratios than do the New York lakes; this is not true of Devils Lake (Table 3).

As shown by Table 1, these differences cannot be explained by loading errors. Nor can they be explained by any possible redefinition of the BAP fraction of TP. For all of these calcareous lakes the BAP fraction (of TP) exceeded 64%; for Delavan it was 78%. Even if the entire external P loading is considered biologically available, no change of inference results.

How sensitive are the Wisconsin vs. New York loading vs. response relationships (TP_w) to Schaffner and Oglesby's (1978) different treatment of unsewered residences? If the same assumption were made about septic wastes as adopted by them, the BAP loadings for Delavan and Green Lakes would be increased by 22 and 8% before 1972. Both direct and indirect evidence indicate that such high deliveries do not occur (Stauffer 1983*b*). In any case, such small hypothetical adjustments in loading would have no effect on the interregional inferences described here. Alternatively, if no septic wastes were to reach the New York lakes, the New York regression line (cf. Fig. 1) would have an increased slope (by ~55%). For Canadarago, the New York lake with the highest mixed layer loading (Λ') and a morphometry similar to Lake Delavan, its recalculated position shifts (point C to C′) as shown in Fig. 1. Obviously, these adjustments would also have no influence on my inferences here.

The New-York-based regression equation relating Chl_s to TP_w very seriously overestimates Chl_s in all the Wisconsin lakes.

Among the calcareous lakes the discrepancy is most serious for Green Lake (the deepest), and least serious for Fish and Delavan (two shallowest). The discrepancy between the predicted and actual values exists even though I compare their prediction with observed chlorophyll in the upper euphotic zone. The mean chlorophyll in the upper 10 m of Mendota and Delavan (Oglesby and Schaffner procedure) is lower than in the upper euphotic zone, undoubtedly because of self-shading and blue-green algal buoyancy (Stauffer 1982). Lakes Mendota and Delavan have such high TP_w that one could argue that they lie outside of the relevant domain for the regression equation. The very high predictions for Green Lake cannot be explained in this way. Oglesby and Schaffner (1978) successfully tested their regression equation using Lake Washington data with TP_w ranging from 18 to 67 mg m^{-3} in various years. Green Lake is morphometrically similar to Lake Washington, and its TP_w falls within that range. In light of this discrepancy, it is not surprising that the New York regression equation relating SDT_s to TP_w also seriously underestimates the transparency of Green Lake's epilimnion in both 1971 and 1972 (predicted 1.1 m vs. observed values >5 in both summers).

Despite the above discrepancies, the New York regression equation relating Chl_s to external loading seriously *underestimates* Chl_s in all of the Wisconsin calcareous lakes except Green Lake (Table 4). The use of this equation should probably be restricted to the three calcareous "drainage" lakes because the external loadings for both Fish and Devils Lakes lie far below the range of values for the New York data set.

I can summarize the above results by saying that none of the regression relationships found for the New York lakes has predictive value for the lakes in southeast Wisconsin. All of the Wisconsin lakes studied have significantly higher TP_w than predicted by the New York loading vs. response equation. The difference is smallest for noncalcareous Devils Lake. All of the calcareous lakes have lower Chl_s than would be expected from the TP_w (New York relationship); this discrepancy becomes more serious as mean depth increases. Nevertheless, except for Green

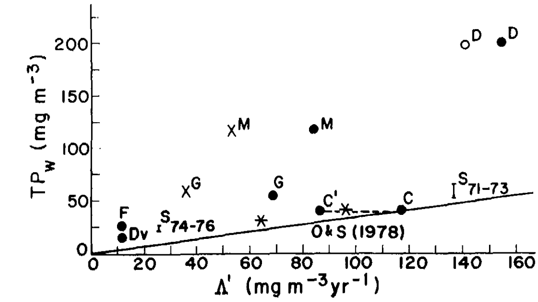

Fig. 1. Mean concentration of total P after ice-out (●—1972) vs. annual mixed layer loadings for BAP (Λ'). Lake symbols: M—Mendota (× in 1978); G—Green (× in 1978); D—Delavan; F—Fish; Dv—Devils; C—Canadarago; C′—Canadarago, assuming no loading from septic tanks; S—Shagawa before and after elimination of wastewater input (bars indicate range of values in various years). O—Delavan (1972) based on independent loading estimate of U.S. EPA National Eutrophication Survey. Asterisks represent two largest residuals (absolute value; Oneida Lake) for the Oglesby and Schaffner (1978) regression line for New York lakes. Hydraulic characteristics of Shagawa Lake are similar to Canadarago and Oneida lakes. (Nutrient conditions in Shagawa Lake from Larsen et al. 1979.)

Lake, these calcareous lakes are more eutrophic (on the basis of Chl_s) than would have been predicted (New York relationship) from external loading. Clearly, these differences are partly related to the marked decline in mixed layer TP concentration between spring overturn and midsummer stratification. Because of the fairly wide range in $\bar{z}$ among these four calcareous lakes, TP_w is thus an inconsistent indicator of Chl_s.

Encompassing model: Reckhow and Simpson—What happens when I compare TP_y with the predictions of

$$TP_y = L_{TP}/(11.6 + 1.2q_s) \qquad (3)$$

derived from the National Eutrophication Survey of 47 north temperate lakes (Reckhow 1979; Reckhow and Simpson 1980)? This equation also seriously underestimates phosphorus concentrations in Mendota, Delavan, and Fish Lakes, but estimates Green Lake quite accurately (Table 2). The first three lakes are relatively shallow and have anoxic hypolimnia after midsummer; Green Lake does not, but has a large areal hypolimnetic oxygen deficit (Hutchinson 1957; Stauffer unpubl.).

Reckhow (1979) was aware of the possi-

Table 4. Lake chlorophyll conditions vs. predictions for 1972. Predicting equations: D&R—Dillon and Rigler (1974) based on TP_w; O&S—Oglesby and Schaffner (1978) based on TP_w and Λ; ELA_1 and ELA_2—*see Table 2 caption*; ELA_3—ELA lakes based on TP_s (Schindler et al. 1978). Concentrations are mg m^{-3}.

	Measured			Predicted Chl_s					
Lake	SDT_s (m)	Chl_s	Chl_s*	D&R (TP_w)	O&S (TP_w)	O&S (Λ')	ELA_1	ELA_2	ELA_3
Mendota	1.8	24	29	95	77	16	37–57	26–40	43
Delavan	1.1	68	71	159	112	31	65–84	55–71	96
Green	6.0	2.7	3.2	23	27	11	51–69	20–28	11
Fish	4.7	3.6	5.1	8	12	−1	27–40	11–16	12
Devils	9.0	1.9	1.6	4	6	−1	4–7	3–5	8

* Based on SDT_s: $\log_{10}Chl_s = 1.92 - 1.81 \log_{10}SDT_s$ (DCRPC 1978; Madison lakes).

ble importance of hypolimnetic anoxia and so developed a separate loading-response equation for this subclass. This anoxic equation predicts mean TP concentrations in Mendota (245 mg m^{-3}) and Delavan (485 mg m^{-3}) that are 3–4 times those predicted by the general equation (*see above, Table 2*) and also higher than observed conditions by 82 and 185%.

If one applies the Reckhow equations to BAP loadings instead, the results are significantly worse for the general purpose model and significantly better for the anoxic model.

Devils Lake—As noted earlier the ELA-based equations provide predictions of TP_y and TP_s for Devils Lake that are highly accurate and also significantly lower than for any of the calcareous lakes. By contrast, neither the Oglesby and Schaffner (1978) model nor the Reckhow and Simpson (1980) model is able to distinguish conditions in Devils Lake from the closely neighboring Fish Lake (Table 2). This is a serious failure because, unlike all of the other lakes, Devils Lake is distinctly oligotrophic, as evidenced by its oxic hypolimnion despite moderate mean and maximum depths (z_{max} = 14 m), and its very high SDT_s (Table 4; most transparent epilimnetic water in southeast Wisconsin).

Nevertheless, because of its larger watershed, Devils Lake probably receives higher external P loading than Fish Lake and is definitely more susceptible to storm runoff than is the seepage lake. Immediately after a killing frost and above normal rainfall in fall 1972, Devils Lake had a mean TP concentration (24 ± 1 mg m^{-3}) 50% higher than Fish Lake (both sampled on 27 October). In response to this runoff, mean Chl increased fivefold to 11 mg m^{-3} in Devils Lake, whereas no change occurred in Fish Lake; however these nutrient inputs are not efficiently retained in the water as evidenced by the fact that TP_w is invariably 40–50% lower than in Fish Lake.

Chl_s vs. TP_w: Dillon and Rigler model—Dillon and Rigler (1974) reported a regression equation relating Chl_s to TP_w for lakes with TN:TP weight ratios >12. The Dillon and Rigler equation predicts Chl_s far higher than the observed values (Table 4); for Lake Mendota the prediction is too high by >200%. In Mendota and Green Lakes during summer TN:TP >12 (R. Stauffer and W. Sonzogni unpubl. data). The predicted value is even too high for the epilimnion of Fish Lake, a seepage lake with a very high N:P ratio.

The Dillon and Rigler (1974) equation also consistently overpredicts Chl_s in Lake Minnetonka, Minnesota (Table 5). This calcareous Minnesota lake is morphometrically and edaphically similar to the calcareous Wisconsin lakes.

Discussion

Critique of Wisconsin data: Figure 1—The high TP_w concentrations for the Wisconsin lakes are not influenced by any important analytical or sampling biases; they are highly accurate (Green Lake estimate is probably ~15% *low*) and reproducible measures of BAP in these lakes. The coefficient of variation (among years) for TP_w is ~10% for the three calcareous drainage lakes (Lee et al. 1977; Stauffer 1974; Stauffer unpubl. data). Erickson (1980) reported TP concentrations in Fish Lake on 25 April 1978 which

Table 5. Chlorophyll conditions and model predictions (equation 2 in Dillon and Rigler 1974) for Lake Minnetonka, Minnesota. Observed values from Megard (1972) as subsequently reported by Dillon and Rigler (1974).

Lake region	Observed		Predicted
	TP_w	Chl_s	Chl_s
Browns Bay	86	33	46
Wayzata Bay	72	35	36
Gale Island	66	35	32
Carman Bay	66	18	32
Crane Island	100	30	58
Crystal Bay	88	22	48
Mean	80	29	42
SD (mean)	6	3	4

Table 6. Hydraulic characteristics of 13 New York lakes (Schaffner and Oglesby 1978), Lake Washington, Shagawa Lake, and five Wisconsin lakes (h_{mix} is mixed layer depth in midsummer).

Lake	$\bar{z}$ (m)	τ_ω (yr)	h_{mix} (m)	q_s (m yr^{-1})	$\frac{h_{mix}}{q_s(1+\tau_\omega^{1/2})}$
New York					
Conesus	11.5	1.4	8.8	8.2	0.40
Hemlock	13.6	2.0	8.5	6.8	0.52
Canadice	16.4	4.5	7.7	3.6	0.69
Honeoye	4.9	0.8	4.9	6.1	0.42
Canandaigua	38.8	7.4	9.6	5.2	0.49
Keuka	30.5	6.3	10.0	4.8	0.59
Seneca	88.6	18.1	11.5	4.9	0.45
Cayuga	54.5	9.5	11.6	5.7	0.50
Owasco	29.3	3.1	11.2	9.5	0.43
Skaneateles	43.5	17.7	10.7	2.5	0.82
Otisco	10.2	1.9	10.0	5.4	0.78
Oneida	6.8	0.6	6.8	11.3	0.34
Canadarago	6.7	0.8	6.7	8.4	0.42
Washington					
Washington	32.9	2.3	11.0	14.2	0.31
Minnesota					
Shagawa	5.9	0.65	5.5	9.1	0.34
Wisconsin					
Mendota	12.4	6.2	8.0	2.0	1.15
Delavan	7.5	3.6	7.5	2.1	1.25
Green	31.5	26	8.0	1.2	1.10
Fish	6.0	25	5.0	0.25	3.3
Devils	7.9	5	6.0	1.7	1.10

were identical to those I found on 20 April 1972. Furthermore, the fraction of TP_w which is molybdate-reactive, and readily available for algal use (Walton 1971) is high (often >80%) for all three calcareous drainage lakes (Table 3; *see also* Lee et al. 1977; Stauffer unpubl. data). Except during unusually wet early springs (especially 1973) clastic turbidity is low in these lakes, and Secchi transparencies can exceed 10 m in May. Nor do the high TP_w concentrations represent a transitory maximum related to the late winter thaw; in Mendota (the most thoroughly studied of the lakes) the mean concentrations at ice-out are frequently ~20% *lower* than in the preceding fall (Lee et al. 1977; Stauffer unpubl. data).

Neither can the anomalous positions of the SE Wisconsin lakes in Fig. 1 be attributed to niggardly loading estimates (Stauffer 1983*b*) nor to above normal runoff from agricultural land in the years immediately preceding the 1972 sampling dates. Instead, the loading estimates are on the high side, and, from the weather record, we know that from 1966 to 1972 over-winter (December–April) and annual means of precipitation were within 1 cm yr^{-1} of standard 1941–1970 norms (NOAA climatol. data) in both the Mendota and Green Lake drainage basins. If anything, one might expect that the lakes would have been out of equilibrium with respect to the increasing loads of BAP from waste treatment plants (before 1972). For Green Lake, especially, with $\tau_\omega = 26$ yr, this disequilibrium would imply that observed TP_w (1972) should have been *low* in comparison to the equilibrium lake concentration (for the loading in Table 1). Ambühl (1981) has described a similar situation for Sempachersee, Switzerland.

Hydraulic influences: Oglesby and Schaffner model for TP_w—Earlier I noted that Oglesby and Schaffner's (1978) fitted regression equation for 13 New York lakes

$$\widehat{TP}_w = 1.0 + 0.34 L_{BAP}/h_{mix} \qquad (4)$$

was unique within a family of prediction models because it was independent of q_s. I now show that this distinction is more apparent than real.

Table 6 lists hydraulic and morphometric parameters for the New York lakes (taken mainly from Schaffner and Oglesby 1978, p. 128). In preparing this list I have adopted $q_s = 8.4$ m yr^{-1} (instead of 11.2 m yr^{-1}) for Canadarago Lake because the most important influent (Herkimer Creek) enters the lake only a few meters away from the outlet (Hetling et al. 1977). This spatial relation-

Table 7. Divisor ratio $R_d = h_{mix}/q_s(1 + \tau_\omega^{1/2})$ for each Wisconsin lake compared to mean ratio for New York lakes (Oglesby and Schaffner 1978). Predicted TP_w then based on Vollenweider-type equation adapted to New York lakes.

Lake	R_d (Wis.) : $\bar{R}_d$ (N.Y.)	Observed TP_w	Predicted $\widehat{TP}_w$
Mendota	2.15	144	62
Delavan	2.35	200	124
Green	2.10	52*	51
Fish	6.25	26	26
Devils	2.10	16	9
Shagawa†	0.64	50–65	30

* May be ~15% *low*.
† 1971–1973.

ship is likely to result in "short circuiting" of creek water directly to the outlet, particularly during the key flushing episodes of winter and early spring (Englert and Stewart 1983).

Although the hydraulic flushing q_s is variable among these 13 lakes, the mean value, $\bar{q}_s = 6.6 \pm 0.8$ (SE of mean), is 73% of $\bar{h}_{mix}$ (9.1 ± 0.6 m). Moreover, the ratio q_s:h_{mix} is smallest for the deepest lakes with the longest τ_ω. This suggested that the divisor ratio $R_d = h_{mix}/q_s(1 + \tau_\omega^{1/2})$ might be more nearly constant. As shown by Table 6 this is in fact true; $\bar{R}_d = 0.53 \pm 0.04$ (SE of mean). If only three lakes are excluded as outliers (Skaneateles, Otisco, Oneida), the mean divisor ratio $\bar{R}_d$ becomes 0.50 ± 0.027. Moreover, the lake whose R_d value is furthest from the mean (Skaneateles) has by far the lowest loading value (L_{BAP}) among these lakes. Thus, this lake is of little importance in fitting the regression equation: $TP_w = f(L_{BAP})$. To a *very* close approximation, then, the "new" divisor (h_{mix}) introduced by Oglesby and Schaffner (1978) is statistically equivalent to the Vollenweider divisor $[q_s(1 + \tau_\omega^{1/2})]$ after it is divided by 2. Considering the appreciable uncertainty in q_s and L_{BAP} for each of these New York lakes, the trend coefficient fit with h_{mix} as a divisor (Eq. 4) is equivalent to $\hat{b} \doteq 0.68$ with the Vollenweider divisor.

Table 6 also contains R_d for Lakes Washington, Shagawa, and my five Wisconsin lakes. The ratio R_d is near the bottom of the New York range for both Washington and Shagawa, but well above the upper limit for every one of the Wisconsin lakes. This upward shift in the ratio occurs because of the weaker flushing of the Wisconsin lakes.

Suppose now that the "correct" input-output model is the Vollenweider formulation applied to L_{BAP}, e.g.

$$\widehat{TP}_w = \hat{a} + \hat{b}\, L_{BAP}/q_s(1 + \tau_\omega^{1/2}) \qquad (5)$$

where, as in the case of Oglesby and Schaffner's model, the intercept $\hat{a}$ is not significantly different from zero. Based on this equation, and on the observations of Oglesby and Schaffner (1978) in central New York, we can make a new set of predictions $\widehat{TP}_w$ for the Wisconsin lakes that adjusts for the systematic differences in regional flushing rates (Table 7).

These revised predictions are much more acceptable for Green and Fish Lakes, but still far too low for Mendota and Delavan (the two drainage lakes that undergo hypolimnetic anoxia). The seeming closeness of the new prediction for Green Lake is also questionable on several grounds. First, my loading estimate for this lake is substantially higher than reported by the National Eutrophication Survey (0.75 vs. 0.25 g m^{-2} yr^{-1}). Second, based on evidence of persistent lateral concentration gradients along the main WSW-ENE transect of Green Lake, my 1972 estimate of TP_w (sampled deep-hole region) is likely to be ~15% low for the whole lake (Stauffer unpubl.). Third, this lake is unlikely to have been at steady state with respect to increasing loading. The new prediction is still slightly low for Devils Lake; however, little should be made of this difference considering its position near the origin (Fig. 1), the nonstationary TP_w (cf. footnote of Table 2), and the high uncertainty in both loading and flushing for this lake.

From the above analysis I conclude that systematic regional differences in basin hydraulics probably account for a significant amount of the prediction bias when the Oglesby and Schaffner (1978) model for TP_w is applied to Wisconsin lakes. Nevertheless, the actual concentrations (TP_w) in these calcareous Wisconsin drainage lakes are still much higher than predicted after adjustment for hydraulic effects. Furthermore, because the independent variable regressed by Oglesby and Schaffner (1978) is very nearly

Table 8. Lake phosphorus conditions vs. predictions for five New York lakes studied by Oglesby and Schaffner (1978). Predicting equations as in Table 2 caption. All concentrations are mg P m^{-3}.

Lake	Observed TP_w	Predicted TP_y O&S*	R&S	ELA_1	ELA_2
Canadarago	40	40	46	14–17	16–19
Oneida†	33	33	35	13–15	14–17
Conesus	18	18	31	13–15	13–15
Owasco	15	20	42	14–17	13–15
Cayuga†	21	21	46	18–21	14–15

* TP_w.
† Predetergent ban.

a linear transformation of the Vollenweider variable, the New York study does not represent an adequate test of the mixed layer loading concept. The model cannot properly be tested by using Lake Washington because its hydraulic characteristics are quite similar to those of several of the New York lakes. Finally, I have shown that a Vollenweider-type model could not fit both the New York and Wisconsin data with a fixed $\hat{b}$ coefficient: the coefficient must be larger for the calcareous drainage lakes in SE Wisconsin. I showed above that the same b coefficient fitted to the ELA lakes leads to even more serious prediction bias when applied to the calcareous Wisconsin lakes (Table 2).

What happens then when the various models are applied to the New York lakes analyzed by Oglesby and Schaffner (1978)? In addressing this question I focus on five lakes (Canadarago, Oneida, Conesus, Owasco, Cayuga) having relatively high areal loading rates, relatively low uncertainties in loading related to septic systems, and relatively high fractions of the drainage basin involved in active agriculture. Moreover, three of these lakes have received especially thorough study (Canadarago, Oneida, Cayuga), and three of them are most nearly comparable to Wisconsin calcareous lakes in mean depth and stratification (Canadarago vs. Delavan; Conesus vs. Mendota; Owasco vs. Green).

Table 8 shows, as expected, that the Oglesby and Schaffner model (for TP_w) fits these lakes very well (the Owasco prediction is ~33% high). However, the predictions based on the two ELA-derived equations are low, especially for the two shallowest

Table 9. Changes in nutrient conditions of mixed layer in Wisconsin lakes between early May and early July 1972. Stratification began about 10 May and was well developed by late May in all five lakes.

Lake	Sampling date	TP (mg m^{-3})	TRP (mg m^{-3})	DIN : TRP
Mendota	12 May	104	85	14.5
	27 May	96	73	14.5
	10 Jun	73	30*	16.5*
	24 Jun†	66	14*	29*
	30 Jun	57	5*	—
	8 Jul	44	3*	~40
Delavan	13 May	171	130	11.5
	25 May	178	128	11.5
	6 Jun	126	68	12.5*
	20 Jun†	158	72	6.0
	5 Jul	100	30*	8.5*
Green	13 May	53	30	15
	25 May	23	10	25
	8 Jun	23	3*	~50*
	23 Jun†	25	6	35
	10 Jul	21	1*	~60*
Fish	12 May	23	1	~240
	26 May	20	2	~130
	7 Jun	19	1	~150
	23 Jun†	19	5	60
	10 Jul	18	2	~65
Devils	12 May	12	<1*	≳100*
	26 May	10	3	~20
	7 Jun	11	1	~100
	23 Jun†	17	4	60
	10 Jul	12	1	~100

* SRP instead of TRP.
† High wind energy during 20–23 June.

lakes. Conversely, the Reckhow and Simpson (1980) equation leads to predictions that are invariably *higher* than observed, in some cases by large percentages (three deepest lakes). This model fits neither the New York lakes nor the Wisconsin calcareous lakes. Instead, it more nearly describes a lake response intermediate in character between these two regional lake sets. The residuals are a function of mean depth.

Seasonal progression: Wisconsin calcareous lakes—It remains to be explained why the TP_w values are high, yet the TP_s and Chl_s values are seemingly low for the calcareous Wisconsin lakes that stratify permanently in summer. These lakes are rich in P in early spring, but most of the nutrient in the surface waters is taken up, converted to algal biomass, and sedimented through the developing thermocline by the middle or end of June (Table 9). Because external loading is low in all of these lakes during

Table 10. Eplimnetic phosphorus fractions in late (26–31) July 1972 (no data for Devils Lake). Because Mendota was sampled frequently its mean (and SE of mean) are also reported separately. SOP—Soluble organic P; PP—particulate P. On 7 June 1972 (last available date) epilimnetic P fractions in Devils Lake were: TP = 11.5; SRP ≤ 1.0; SOP = 8.0; PP = 2.5 mg m^{-3}.

Lake	Phosphorus fractions (mg m^{-3})				PP : Chl*
	TP	SRP	SOP	PP	
Mendota	37	≤0.5	11	26	0.80
Delavan	59	1.0	15	43	0.75
Green	12	≤0.5	9	3	1.1
Fish	11	≤0.5	5	5	1.5
Mendota $\bar{x}$†	39	2.0	16	21	0.78
SE (of $\bar{x}$)	1.5	0.5	2.0	2.0	0.10

* Ratio by weight.
† Eight dates between 8 July and 4 September 1972.

summer stratification, the lakes then depend on internal cycling and transport to maintain high productivity and high standing crops during mid- to late summer (cf. Stauffer and Lee 1973). As would be expected, the latter process is morphometrically controlled (Stauffer 1974).

The Chl_s values are lower than predicted by an ELA-based equation with TP_s as an independent variable. This is understandable because the high TP_s values in the ELA lakes resulted from summer loading with phosphate. Of all the possible chemical forms of P in the environment, this phosphate is the most available to algae and therefore the most likely to be converted directly into new algal biomass. By contrast, the comparable TP_s values for the calcareous Wisconsin lakes represented remnants of much higher concentrations present in the lake at vernal overturn. In some cases these remnants were 75% soluble organic P (Table 10), some portion of which may have been unavailable to algae.

Neither TP_s nor Chl_s is low in the calcareous Wisconsin lakes as compared to external P *loading*. In fact, the opposite is true for both Mendota and Delavan in comparison to the New York lakes (Table 4).

Calcareous lakes outside Wisconsin—The evidence just presented suggests that the P economies of the calcareous Wisconsin lakes are radically different from those of a noncalcareous lake in Wisconsin, lakes in central New York State, and lakes in the Canadian Shield of western Ontario (ELA). The Wisconsin calcareous lakes have anomalously high over-winter P concentrations and are comparatively eutrophic for their external loads. From scattered evidence in the literature I now suggest that this difference is part of a larger edaphic pattern.

First, the calcareous lakes in Minnesota are similar to those in Wisconsin. Lakes Sallie, Lower Minnetonka, and Calhoun have higher TP_y, TP_w, or both than predicted by ELA- or New-York-based regression equations. The concentrations are also higher than predicted by Reckhow and Simpson's (1980) encompassing model (Table 11). This discrepancy applies even to Lower Minnetonka, where, because of the very weak flushing, the basin could not have attained steady state with respect to the peak loading before sewage diversion in 1972. (Two years after an 80% reduction in external load, lake P concentrations had dropped by only 20%: Megard 1977.) The seasonal distribution of P (by depth and chemical form) is also closely comparable in the Minnesota and Wisconsin calcareous lakes. Schindler and Comita (1972) reported similar phosphorus patterns and very high primary productivity in Severson Lake, Minnesota; from the basin description and the authors' discussion, it was apparent that these conditions could not be explained in terms of high external loading.

The situation is similar in Ca-rich lakes set in Northern Ireland, England, southern Sweden, Switzerland (Table 11), and also in Baltic Germany. In every case the observed P concentrations are much higher than predicted by any of the equations, whether regional or encompassing. The comparisons for Lough Neagh, Crose Mere, and Norrviken (1969; prewastewater diversion) involved lakes that were probably close to steady state.

Hutchinson (1957, *citing Ohle 1934*) noted that the calcareous kettle lakes in Baltic Germany had comparatively high P concentrations in the 1930s. Krambeck (1981) reported depth-time diagrams for SRP in eutrophic Plußsee (near Plön) that are strikingly similar to conditions in Lake Mendota (SRP_w ≥ 100 mg m^{-3}; epilimnetic SRP very low in late summer; hypolimnetic SRP ≥ 500 mg m^{-3} in late summer). Although

Table 11. Morphometric, hydraulic, loading, phosphorus conditions, and predictions in 13 hard-water lakes outside Wisconsin. Phosphorus predictions based on L_{TP} (*see Table 2 caption*). References: 1—Neel 1977; 2—Megard 1977; 3—Shapiro 1977; 4—Stevens and Gibson 1977; 5—Reynolds 1979; 6—Ahlgren 1977; 7—Ambühl 1981.

Lake, year	Reference	$\bar{z}$	τ_w	q_s	h_{mix}	$\frac{h_{mix}}{q_s(1+\tau_w^{1/2})}$	L_{TP}	L_{SRP}	Observed TP_w	Predicted O&S*	R&S	ELA_1	ELA_2
Minnesota													
Sallie, 1969–73	1	6.3	1.5	4.2	6.3	0.67	2,750	—	350†	150	165	62	65
Minnetonka, 1969	2	8.3	28	0.3	8.0	4.2	500	—	75	21	42	143	60
Calhoun, 1971	3	10.6	3.6	3.0	6.0	0.69	880	—	106†	51	58	32	28
United Kingdom													
Lough Neagh, 1973–75	4	8.9	1.3	6.9	8.9	0.60	1,400	—	133†	55	71	25	27
Crose Mere, 1971–75	5	4.9	2.3	2.1	4.9	0.93	910	—	196‡	64	64	43	41
Sweden													
Norrviken, 1969	6	5.4	0.85	6.5	5.0	0.40	4,000	—	470	273	206	58	71
Norrviken, 1975–76	6	5.4	0.85	6.5	5.0	0.40	480	—	147	34	25	14	16
Switzerland													
Greifen, 1976	7	17.7	1.4	12.8	6.0	0.21	2,670	1,400	397	151	99	25	27
Baldegg, 1974	7	34.0	6.0	5.7	5.0	0.25	2,160	1,530	484	147	117	39	29
Halwil, 1973	7	28.6	4.1	7.0	5.0	0.24	2,040	1,370	223	139	102	32	27
Sempach, 1975–76	7	46.0	16.5	2.8	6.0	0.42	1,090	600	83§	62	73	40	23
Geneva, 1976	7	153	11.0	13.9	10.0	0.17	1,480	700	100	51	52	17	13
Constance, 1971–72	7	100	4.4	22.7	10.0	0.14	1,880	455	80	65	48	15	13

* TP_w based on L_{TP}.
† TP_y.
‡ SRP only.
§ Not at steady state (TP_w increasing 15% per year).

Krambeck did not report the external loading, from information on the drainage basin it is very difficult to rationalize these high concentrations by external load. First, the lake has no permanent inflow or outflow and has a very small land drainage basin (A_{db}:A_o < 3; H. J. Krambeck pers. comm.), most of which is wooded. Ohle (1964) attributed the eutrophic conditions in the Plußsee (and in the nearby Grosser Plönersee) in part to nutrient release from sediments. Reynolds (1979) commented on the similar climatic and geologic settings of the "meres" in the glaciated Shropshire-Cheshire Plain of England and the lakes of Baltic Germany. He also noted their common tendencies toward eutrophy.

The prealpine region of northern Switzerland also contains calcareous lakes in agricultural drainage basins that are inadequately described by the various regression equations, again because observed TP_w is much higher than predicted (Table 11). Furthermore, although Ambühl (1981) did not report nutrient conditions and loads for the Rotsee, Pfaffikersee, and Lake Morat, it is apparent from other reports (Vollenweider 1976; Larsen and Mercier 1976) that the same conditions apply to these lakes as well. The regression equations best depict the current situation in Sempachersee. However, as noted by Ambühl (1981), this lake is not at P steady state; the concentration is increasing significantly each year. Even Lakes Geneva and Constance are inadequately described by the encompassing Reckhow and Simpson (1980) model.

Table 11 also shows that the TP_w predictions using the Oglesby and Schaffner (1978) model are invariably too low—even if L_{TP} instead of L_{BAP} is used in the regression equation, *and* irrespective of the lake's divisor ratio: $R_d = h_{mix}/q_s(1 + \tau_w^{1/2})$. Thus, I conclude that a Vollenweider model could not fit both these lakes and the New York lakes using a similar $\hat{b}$ coefficient.

The same pattern of high P concentrations and eutrophy has been reported for calcareous pothole lakes in the north-central United States and south-central Canada (Barica 1974; Schwartz and Gallup 1978; Mitchell 1984). Schaffner and Oglesby

(1978) were aware of these findings; they rationalized (p. 124): "... shallow prairie lakes ... *almost certainly receive large inputs* of dissolved P through groundwater inflow." However, the investigators, themselves, did not share this view. Mitchell (1984) proved that external loading could not possibly account for the seasonal patterns. Barica (1974) stated (p. 334), "The cycle of these nutrients appears to be essentially internal."

After a detailed hydrological study of the pothole lakes in adjacent areas of North Dakota, Shjeflo (1968) concluded that seepage inflow was a minor source of water for many of these lakes, particularly those set in poorly sorted glacial till. The most important sources were direct precipitation on the pothole surface and runoff from the adjacent grassland watershed (each with close to 50%). Nevertheless, the annual runoff was *much smaller than for lakes in more humid* climates (3 cm yr^{-1} as compared to 12–15 cm for the combined runoff and percolate in the Mendota drainage basin: cf. Shjeflo 1968). Sixty percent of the runoff was dilute snowmelt. From the prevailing A_{db}:A_o ratios for these pothole watersheds (10:1), the areal hydraulic loading from runoff is only ~0.3 m yr^{-1}. The P concentrations would have to be very high indeed to compensate for these weak inflows and still generate a large external P loading! I suspect, as did Allan and Williams (1978) and the other regional investigators, that sediment-water relations also play an important role in regulating the trophic status of the pothole lakes. I predict that the Oglesby and Schaffner (1978) regression model (for lake P) will fail for those lakes because of *both* hydraulic and edaphic factors.

The doline lakes in central Florida also illustrate that alkalinity (coupled with hardness) is an important correlate of lake P and lake trophic state. Hutchinson (1957) noted that Florida lakes had relatively high P concentrations. From an extensive survey, Canfield (1983*a*) reported (his table 3) that lake TP increased systematically and dramatically with increasing total alkalinity, as did indices of trophic state. Conversely, the TN:TP ratio decreased systematically with increasing alkalinity, finally reaching levels among the calcareous subclass indicative of nitrogen limitation of phytoplankton growth (cf. Smith 1982).

Brezonik and Messer (1977) reported on Lake Weir, a *soft-water* lake occupying fused doline basins near the crest of the Central Florida Ridge, and the only subtropical lake included in the North American data set. Although TP in Lake Weir is much lower than in the more alkaline Florida lakes, it is still anomalously high considering the lake's very small external load (0.07 g P m^{-2} yr^{-1}: cf. Brezonik and Messer 1977), and Rast and Lee (1978) could not account for the high TP concentrations in that lake based on external loading.

From these suggestive but still incomplete studies of the Florida doline lakes I conclude that although P concentrations and trophic state increase with alkalinity in that region, the soft-water lakes in central Florida *are nevertheless more eutrophic than* soft-water lakes with comparable external P loadings in the Canadian Shield. Thus, alkalinity alone cannot be used to define the edaphic influence on the response of a lake to P loading. The evidence from the lakes in central New York State also confirms this point (alkalinities close to 2 eq m^{-3}).

Phosphorus retention coefficients: R_{exp}—One important consequence of the high fall-spring TP concentrations in many calcareous drainage lakes is that they retain relatively smaller fractions of their annual external BAP load than many noncalcareous lakes with similar hydraulic properties. Lake Mendota, with $\tau_\omega = 6$ yr, is currently retaining about 35% of its estimated mean annual BAP input, vs. ~60% in the period of slowly increasing loading before 1972. These recent exports reflect no apparent change in lake phosphorus content (Stauffer unpubl.). With the use of my overly generous estimate of external loading to Delavan, the R_{exp} is 0.70 for BAP. Larsen and Mercier (1976) reported $R_{exp} = 0.55$ for TP in Delavan using a more conservative loading estimate and 0.57 for calcareous Nagawicka Lake west of Milwaukee. The R_{exp} for BAP in Green Lake is significantly higher; it is now close to 0.80 vs. 0.90 before 1976. On the basis of the lower loading estimate of Donohue and Associates, it is 0.73 for

Green Lake (cf. Stauffer 1983*b*). By contrast, Schindler et al. (1978, p. 194) reported a mean retention coefficient of 0.92 for SRP added directly to the mixed layers of ELA lakes in summer, with even higher retention coefficients when the phosphate was added to the hypolimnion instead (Schindler et al. 1980). (Note that changing R_{exp} from 0.90 to 0.80 implies a *doubling* of phosphorus export and a 100% increase in the hydraulically weighted mean annual mixed layer TP concentration.)

The retention coefficient mathematically reflects both flushing and the internal processing of P within the lake water-sediment system. If system hydraulics are held constant, a decrease in R_{exp} reflects more efficient internal recycling of P and a lower capture efficiency of the sediments. Larsen and Mercier (1976) were aware of this; it guided their partition of their lake set and subsequent attempts at regression analysis. In their words (p. 1746)

> Only lower mesotrophic or oligotrophic lakes were examined because increasing levels of productivity might decrease a lake's retention capacity by providing an increasingly larger internal supply of P as anaerobic conditions develop . . . thus obscuring relationships between R_{exp} and other lake properties.

What is perhaps less widely realized is that in performing their statistical analysis (R_{exp} vs. q_s or τ_ω^{-1}), Larsen and Mercier (1976) also partitioned their initial set of 73 lakes in another important but unstated manner. They partitioned the lakes edaphically. The first 37 lakes (their table 1) were immediately excluded from statistical analysis; most of these were calcareous lakes (mainly from Wisconsin, Minnesota, the Okanagan region of British Columbia, and the prealpine region of Switzerland). Several of the 36 lakes that survived the first cut were calcareous lakes set in climates and topographies that promote relatively high erosion rates (Aegerisee, Leman, Turlersee, Zürichsee). Four lakes were from Minnesota; their exact locations and edaphic classifications were unspecified.

In the preliminary statistical analysis of the remaining "Group II" lakes, the two largest residuals were identified with Leman and Pelican Lake, Minnesota. In both cases, R_{exp} (observed) was much *lower* than predicted from the regression relationship. In the final statistical analysis ($n = 20$), not a single calcareous lake remained!

Careful scrutiny of Table 11 shows that Larsen and Mercier (1976) were shrewd in excluding Lake Geneva and many other calcareous lakes from their final statistical analysis relating R_{exp} to τ_ω because in most cases TP_y is a large fraction of $L_{TP}q_s^{-1}$ (steady state concentration for a conservative solute).

Phosphorus geochemistry and internal cycling—From these widespread observations, and from earlier suggestive work by Gorham et al. (1974), can we conclude that *stratified* calcareous lakes have more efficient P recycling from the surface sediments to the overlying water (hence lower R_{exp}) than noncalcareous lakes with comparable morphometric and hydraulic characteristics? If so, does this then imply that calcareous lakes as a class generally have higher trophic efficiencies (here defined as carbon fixation per unit load) than noncalcareous lakes? Perhaps, but I suggest that these features are more nearly identified with subclasses of calcareous lakes that satisfy certain other conditions as well.

Concerning the first question, the P recycling efficiency will be highest for those lakes whose sediments are ineffective at binding P, provided that conditions of stratification and washout are held constant. This binding principle was recognized early (Ohle 1937; Livingstone and Boykin 1962) and has often been emphasized since (cf. Boström et al. 1982). Unfortunately, as I have shown, it is missing structurally from the input-output models that are now in use.

As stressed by Williams et al. (1971*a,b*), Fe is generally the most active agent binding P to soils and sediments. Iron performs this role inorganically for pH $\lesssim 8$ and high redox potential (the classic Mortimer model: cf. review by Boström et al. 1982). Iron also interacts with humic substances to bind P strongly at acid to near-neutral pH, irrespective of Eh, in the surface sediments of some soft-water shield lakes (Jackson and Schindler 1975; Schindler et al. 1977). Therefore, other factors being equal, one would expect weaker sediment binding of P in lakes lacking significant external fluxes of Fe and humic substances, or in lakes where Fe and humic substances are diagenetically transformed making them nonreactive toward P. These considerations apply differentially to stratified lakes, because in deeper lakes the pelagic sediments are invariably the major repository for potentially mobile P (cf. Stauffer 1981*b* for a review). Within these hypolimnetic sediments pH and temperature are generally too low to permit release of inorganic P by simple ligand exchange (cf. Boström et al. 1982).

The external flux of Fe depends on its chemical mobility and on erosion rates in the watershed. The chemical mobility of Fe in soils and stream drainages decreases with increasing pH and with increasing redox potential (Stumm and Morgan 1970) and increases with increasing concentrations of organic ligands (particularly humic substances: cf. Kerndorff and Schnitzer 1980). Thus, one might expect high external fluxes of Fe and associated humic substances in poorly buffered shield regions strongly influenced by acid-bog drainage. Some of the Norwegian Shield lakes described by Kjensmo (1967) are of this type. The lake sediments have a high Fe:P ratio (Stauffer 1981*b*, p. 31). Similar conditions apply over parts of the Canadian Shield; they explain the high Fe and humic contents of sediments in Lake 227 in the ELA (Brunskill et al. 1971).

In the fertilized ELA lakes TP_s was higher than TP_w, both because the lakes were loaded only in summer and because the carryover of previously added phosphate was very low during each succeeding winter. The low winter carryover is best explained by nearly irreversible binding of P by amorphous Fe-rich organic colloids (Jackson and Schindler 1975; Schindler et al. 1977, 1980). The binding was not the result of clastics because erosion rates are low in the shield region (Brunskill et al. 1971). Conversely, the chemical mobility of Fe is naturally low in temperate calcareous watersheds, particularly those in dryer climates or those characterized by good soil structure and drainage. The mobility of Fe is also low in upland sandy soils because of superior (even excessive) drainage and good soil aeration (cf. Holland 1978).

For many lakes, erosion is a more important process for delivering Fe to the sediments. Erosion rates are notably low in many glaciated lowland provinces, particularly in pitted outwash or sandy-gravelly till characterized by high soil infiltration capacities and low topographic relief. These conditions apply to much of southeast Wisconsin, in part because of earlier glacial corrasion of locally outcropping sandstones and dolomite. Erosion rates are also minimal in the sandy soils capping the Central Florida Ridge, and overlying the carbonate platform of central Florida; this may explain the very low Fe contents of Lake Weir's sediment (Brezonik and Messer 1977). It may also help account for the high P contents and eutrophic conditions of many hard-water lakes in Florida.

The situation is less clear for the central New York lakes, but here, as in the ELA, it appears that the winter carryover of SRP is relatively low, thus resulting in relatively high DIN_w:SRP_w and $SRSi_w$:SRP_w ratios (Table 3; compare with calcareous drainage lakes; *see also* Oglesby and Schaffner 1978, p. 137). The explanation may be that clastics eroded from the infertile acidic soils of the Allegheny Plateau adsorb SRP, thus removing it from the influents in transit and even from the water column. This adsorption might also occur at the sediment–water interface (sediment capture) when P is remineralized from sedimented seston. The process would have little or no effect on DIN and SRSi.

The P inputs to noncalcareous Devils Lake are also poorly retained in the water over winter. Colman (1979) found that large amounts of Fe were released into the benthic boundary layer of this lake in mid–late winter. Furthermore, because the Fe:P ratio was unfavorably high, the oxidation of this iron as it diffused upward away from the interface resulted in efficient scavenging of P. This scavenging process was much less effective (low Fe:P release ratios) in all of the calcareous lakes (including Fish) studied in Wisconsin. The sediments of Devils Lake are completely different from those of the local calcareous lakes, in part because of higher concentrations of iron (Bortleson 1970). This iron is also more mobile (Colman 1979; Stauffer 1981*b*, unpubl. data). Devils Lake, too, has high DIN_w:SRP_w and $SRSi_w$:SRP_w ratios (Table 3).

In some regions residual soils have been developed from bedrock after long intensive weathering in a humid subtemperate or tropical climate. The residual clay soils have been severely leached of cations, are poorly buffered, and are strongly enriched in hydrous Fe(III) oxides as residual surface-active coatings on the clay minerals (Holland 1978). Following erosion, the hydrous Fe(III) oxides would be expected to adsorb phosphate P and remove it from the water. Weiss and Moore (1977) showed that TP concentrations were anomalously low in the Kerr Reservoir (Virginia-North Carolina) for the external load and attributed this to adsorption of P by settling hydrous Fe oxides. Reckhow and Clements (in prep.) have shown that this pattern of low water column TP per unit load is generally true of reservoirs in the unglaciated Piedmont Province of the SE United States.

The diagenetic transformation of Fe in lake sediments also has implications for P recycling in lakes. Calcareous lake sediments are buffered at higher pH and generally exposed to higher sulfate fluxes than those of noncalcareous lakes (cf. Holland 1978). Both factors promote the diagenetic transformation of Fe to FeS (Stauffer 1981*b*). This reaction markedly reduces the effective flux of the Fe oxides important in binding P.

Calcium can also remove P from the water and immobilize it in lake sediments (Otsuki and Wetzel 1972; Rossknecht 1980), but these interactions have not received very thorough study. Simple inorganic coprecipitation of P with calcite will not occur if calcite is formed only after epilimnetic SRP concentrations have reached low levels, as is certainly the case for Lake Mendota (based on my SRP data and Hawley's 1967 study of Ca). Magnesium often delays the formation of calcite until after algae have taken up the SRP, and it specifically inhibits the formation of apatite and related calcium phosphate minerals (Tomazic et al. 1975; Nancollas et al. 1979). Because the Mg:Ca ratio is higher for dolomitic lithographies and in climates where the evapotranspiration rate nearly equals or exceeds the precipitation rate (cf. Kelts and Hsü 1978), the lake P cycle may be related to geographic and geochemical factors influencing the Mg:Ca ratio. Because increasing Mg concentrations are also correlated geochemically with increasing sulfate, a high Mg:Ca ratio will imply kinetic inhibition of apatite formation in situations where sulfur is available to immobilize Fe. As salinity increases, ion activity coefficients decrease (Stumm and Morgan 1970), thus further raising the threshold concentrations of phosphate P required to induce chemical precipitation.

I would therefore predict low sediment binding of P for glacial prairie pothole lakes, because of their high magnesium and sulfate concentrations, higher ionic strength, the absence of humic materials, and low regional erosion rates (Sloan 1972; Dendy et al. 1973). The same arguments, slightly moderated, apply to many glacial lakes of southern Wisconsin and Minnesota. Erosion rates are an order of magnitude higher in the nearby Driftless Area (Hindall 1976) because of the greater topographic relief in these unmodified valleys, where many reservoirs have been constructed.

According to the above arguments, P binding should be low by ocean sediments and saline lakes resembling the oceans. Callender's (1982) study of the Potomac River estuary shows this along a geochemical gradient involving Fe, S, and ionic strength. Hutchinson (1957) noted the high concentrations of phosphate in saline lakes in semiarid climates. It would be useful to corroborate these observations and examine their origins and implications for models of lake loading response.

Trophic state—The literature also suggests that calcareous lakes whose sediments have low P binding tendencies are more eutrophic and are particularly likely to have summer blooms of blue-green algae. This is true of the moderately saline hypereutrophic prairie pothole lakes (Hammer 1964, 1969; Barica 1974; Schwartz and Gallup 1978). Reynolds (1979) emphasized that blue-green algal blooms in meres of the Cheshire Plain predate the era of modern agriculture. In calcareous lakes of Wisconsin, Minnesota, the Baltic region, and central Florida, phosphorus potential is sometimes high enough to induce nitrogen limitation of summer algal blooms. Such a shift to nitrogen limitation was noted by Smith (1982) and Canfield (1983*b*); it may help account for the failure of the Dillon and Rigler (1974) chlorophyll model when applied to calcareous lakes of those regions.

From the Wisconsin evidence I suggest that the failure of the Dillon and Rigler chlorophyll model also depends on the different relationships among TP_w, TP_s (mixed layer), and external load for these stratified lakes. Although Smith (1982) never says it, his smaller model residuals (vs. those of Dillon and Rigler) may be related only in part to the TN:TP ratio. The stratified calcareous lakes of Wisconsin and Minnesota have high mixed layer TP_w:TP_s and TP_y:TP_s because of their different internal P economies, coupled with seasonal loading effects. A more valid comparison of model residuals would entail use of the same independent variable (TP_w) in the regression analysis.

Implications for modelers—If it can be shown that in general certain subclasses of the calcareous lakes have demonstrably higher recycling efficiencies for P than lakes set in sterile acidic soils, in shield regions, or upland drainage basins with infertile soils and accelerated erosion, then the input-output models developed for heterogeneous groups of lakes will be severely biased when applied to many individual lakes, because the elements of the set are no longer "independent identically distributed" in the statistical sense. If the lake belongs to some distinguishing subclass, it may no longer behave in the manner attributed to the larger and heterogeneous set. Unfortunately, it can happen that few or even no elements of such a heterogeneous set conform to the statistical norm and that the norm is just an accident of set selection. The loading-response models are so imprecise because we have not sufficiently recognized the factors influencing the results. This was recognized by Rigler (1975) and also by Smith (1982) in his identification of additional patterns in nutrient regulation of lake chlorophyll standing crops. A similar effort will have to be made in relating the efficiency of P recycling in lakes to edaphic, morphometric, and hydraulic influences.

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