# Nutrient internal cycling and the trophic regulation of Green Lake, Wisconsin<sup>1</sup>

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#### Abstract

Algal nutrients (Si, N, P) and dissolved oxygen were studied in Green Lake, Wisconsin, in 1971– 1972, and in 1978–1980 following a reduction of about 35% in total external P loading in December 1976.

Despite oxic conditions, there is more P in the hypolimnion than would be expected from the dissolved oxygen and from classical Redfield stoichiometry. Because of a metalimnetic dissolved oxygen minimum in late summer, the calculation and interpretation of the hypolimnetic oxygen deficit is affected by turbulent transport of dissolved oxygen.

Vertical fluxes of P into the mixed layer are important in late spring and early summer, but, owing to metalimnetic P depletion, negligible between mid-July and mid-October. Vertical transport of Si into the mixed layer is negligible in summer and early fall compared with inputs from the land drainage basin.

Although P is high at spring turnover, epilimnetic concentrations of P are low and Secchi transparency is high by mid-to-late summer. These seasonal changes are caused by sedimentation of P and low seasonal inputs from the drainage basin. This P is recovered in the hypolimnion and recirculated throughout the lake at fall overturn. It causes silica limitation of the diatom bloom each succeeding spring.

The total P content of Green Lake and its seasonal partition among the layers were remarkably stable between 1971 and spring 1980, despite the reduction in external loading in 1976. The hypolimnetic oxygen deficit also showed no significant change between the first and eighth decades of this century.

Stauffer (1985) showed that the calcareous lakes of southeast Wisconsin have anomalously high phosphorus concentrations during winter and at spring turnover, as compared with those expected on the basis of external loads. I examine here one of these lakes, Green Lake, in considerable detail, showing how morphometry and transport phenomena interact to influence nutrient internal cycling in a large, deep calcareous lake and ultimately govern water quality and trophic state of the epilimnion. Imboden's (1974) one-dimensional "twobox" model for the phosphorus economy of the mixed layer explicitly included the effects of vertical transport. This model was

subsequently improved by Imboden and Gächter (1978) to allow for a nonhomogeneous hypolimnetic reservoir. My results from Green Lake illustrate the conceptual power of their model for trophic state prediction and certain shortcomings as well. Differences between Green Lake and several other lakes of similar depth also illustrate why an improved understanding of the factors regulating phosphorus release from pelagic sediments is necessary.

#### Study site

The geologic history and climatic setting of Green Lake were summarized by Stauffer (1985). Juday (1914) described its hydrography and morphometry.

Green Lake proper (minus shallow tributary embayments) has a surface area ( $A_0$ ) of 29.7 km<sup>2</sup>, and mean and maximum depths of 31.0 and 72 m. The maximum wind fetch is 12 km along the WSW-ENE transect (Fig. 1). The main thermocline normally begins at 8–10 m in midsummer and deepens to ~12 m by mid-September.

The main influent, Silver Creek, carrying wastewater from the city of Ripon, enters

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Fig. 1. Bathymetric map of Green Lake, Wisconsin. Sampling stations ( $\times$ ). Station 6' (not shown) midway between 6 and 7.

the comparatively shallow eastern corner. With the exception of spring-fed White and Dakin Creeks, and the small intermittent Hill Creek, all of the tributaries first transit shallow embayments. The mean hydraulic residence time of these embayments is about 1 month (east) and 3 months (west), but longer during winter and summer base-flow periods. Discharge is to the Puchyan River, only 3.5 km WNW of the east end. The hydraulic residence time for the main lake basin is 26 years.

The main depths of sediment influence are in the upper 9 m (30% of total) and in the deeper waters. The sediment influence curve (dA/dV) is 0.04 m<sup>-1</sup> at 6-m depth, falls monotonically to a minimum 0.015 at 21 m, and then commences a quasi-exponential increase to 0.022 at 38 m, 0.030 at 45 m, 0.048 at 53 m, and 0.082 at 60 m, before increasing dramatically in the layer overlying the nearly flat profundal floor of the western basin ( $z_b = 67.5 \pm 1$  m over 2.75 km<sup>2</sup>). The mean height of the water column for the volume below 9 m is 34 m.

### Methods

Sampling—Lake surveys were conducted on 23 July and 18 August 1971, on 12 dates between 11 March and 15 October 1972, on 11 dates between 7 March and 21 October 1978, and on 27 June and 15 September 1979 and 11 April 1980. Stream samples were collected on 12 dates in 1972 and two dates in late June 1979.

Before mid-May 1978 temperature measurements were made at 1-m intervals above 32 m at stations 2 and 6' or 4 and 6' with a Whitney TC-5C (accuracy within 0.1°C; precision = 0.05°C). Dissolved oxygen was measured (above 30 m) with a Yellow Springs meter (model 54). Nutrient samples (250 ml) were collected in acid-rinsed polyethylene bottles by either a submersible pump or a plastic Van Dorn sampler, returned to the laboratory, and stored at 4°C in the dark until analyzed (1–4 days).

Sampling procedures were changed in 1978 after the acquisition of improved equipment. Thereafter, temperature was measured at seven stations (Fig. 1) with a Montedoro-Whitney thermometer (model TCD-100B, accuracy and precision: 0.01°C) at 1-m intervals above 32 m and within 5 m of the bottom, and at 2-m spacing otherwise. Sampling dates were selected with low antecedent wind energy (Stauffer 1980) to minimize sampling errors associated with energetic internal waves (Stauffer 1983a). On four occasions between late June and early September the lake was resampled at all seven stations on the following day, to obtain estimates of sampling error during the period of maximum thermal stratification (Stauffer 1983a).

Oxygen was determined on 7 March 1978 by the azide modification of the Winkler procedure (Am. Publ. Health Assoc. 1971), and with a Montedoro-Whitney model DOR-2A during August–October 1978 and in September 1979. Oxygen profiles were obtained at station 2, and sometimes at 4 and 7 as well.

Nutrient samples (100 ml) were collected (station 2 and stream stations) in acid-rinsed polyethylene bottles with a peristaltic pump (Masterflex). The inlet tube of the pump was connected to a stainless steel flow-through weight, itself taped to the sensor housing of the Whitney thermometer. Filtered hypolimnetic and stream samples were collected (0.4- $\mu$ m pore size; Nuclepore) with a pressure filter apparatus (Nuclepore) connected to the outflow tube of the pump. Beginning in March 1978 all samples were acidified after collection to pH = 1.0 with analytical grade HCl.

Secchi transparency depths were measured in all years using a 25-cm disk with alternating white and black quadrants.

Analytical—Chlorophyll was sampled and analyzed in 1971–1972 following Stauffer et al. (1979).

Dissolved inorganic nitrogen (DIN) was analyzed in 1971–1972, nitrate by the brucine procedure (Kahn and Brezenski 1967) and ammonia by the alkaline-phenolhypochlorite method, both as adapted for a Technicon AutoAnalyzer by Kluesner (1972). Organic-N was determined in midsummer 1971 by autoanalyzer following Kieldahl digestion (Am. Publ. Health Assoc. 1971). Total and soluble molvbdatereactive silica (TRSi and SRSi) were determined in spring 1972 (Strickland and Parsons 1968), and in 1978-1979 with Fanning and Pilson's (1973) modification of this procedure. Phosphorus fractions (cf. Strickland and Parsons 1968) were determined with the Menzel and Corwin (1965) digestion and the ascorbic acid colorimetric procedures (Murphy and Riley 1962: Stauffer 1983b). Arsenic is not an important analytical interference for P in Green Lake.

Fluxes-Atmospheric DIN deposition was based on local precipitation norms and regional concentrations of nitrate and ammonia reported both by Munger and Eisenreich (1983) and Wis. Dep. Nat. Resour. (1982). Deposition rates for TRSi and TP were based on several sources (Reckhow et al. 1980; Eisenreich et al. 1980; Kennedy 1971; Wis. Dep. Nat. Resour. 1982).

Stream-based fluxes (summer) were computed for rural areas from measured concentrations and estimates of mean inflow from the watershed in summer (extrapolations from the closely comparable Mendota watershed).

The TP exports from the Ripon Waste Treatment Plant are based on Stauffer (1985). The DIN output from the same treatment plant is based on per capita releases from similar communities in Dane County, Wisconsin (Sonzogni and Lee 1974). The major reduction in TP loading by the city of Ripon reflects the start-up of an advanced treatment plant (with P removal by iron salts) in December 1976.

Vertical solute fluxes in the lake were computed from concentration gradients (station 2) and estimates of the vertical eddy conductivity ( $K_z$ ). The latter were determined according to Jassby and Powell (1975), as modified by Stauffer (1983*a*) to account for the differential effects of heat penetration into sediments as a function of overlying water depth (cf. Birge et al. 1928;



Fig. 2. Temperature profiles from late winter and spring 1972.

Likens and Johnson 1969). Propagated sampling error  $(K_z)$  is based on the "revisit technique" (Stauffer 1983*a*). The error in  $K_z$ contributed by error in the sediment heat exchange model was not evaluated for Green Lake. However, based on a comparison with the Birge et al. (1928) study of Lake Mendota, the probable model error is  $\leq 20\%$ . This error affects total  $K_z$  error only below 30 m in summer and early fall.

All elemental ratios are reported by atoms.

#### Results

Spring developments—Following a normal ice-out in the second week of April, Green Lake absorbs insolation and circulates convectively for about 3 weeks until it attains 4°C. The long duration of this unforced convective circulation is a consequence of the low water temperature at ice-out (1°–2°C) and the substantial heat capacity of a dccp water column. The low initial temperatures are related to conditions at freeze-up and result from the long fetch and exposed continental location of the lake (cf. Ragotzkie 1978).

One consequence of the long vernal convective circulation is that the lake may stratify permanently soon after it reaches 4°C if ice-out is late (1972, 1978, 1979) or May wind energy is below normal (especially 9– 28 May 1972: cf. Stauffer 1980). Thus, temperature profiles indicate a near cessation of vertical mixing below 5 m during mid-May 1972 (Fig. 2). In other springs, windforced mixing raises the bottom temperature above 5°C.

Because of the prolonged forced circulation in fall and early winter, Green Lake is close to saturation with dissolved oxygen at the time of freeze-up. Most of this is retained until ice-out except in the profundal benthic boundary layer. Thus, on 11 March 1972 the upper 30 m of the water column had 13.1 g dissolved oxygen m<sup>-3</sup>, 0.5 g m<sup>-3</sup> below saturation at 1.5°C (from Benson and Krause 1980). Birge and Juday (1911) reported identical concentrations between 10 and 30 m on 15 February 1906, for water temperatures ranging from 0.9° to 1.1°C. On 7 March 1978, 10 g dissolved oxygen  $m^{-3}$ remained even at 60 m, only 7.6 m above the floor of the western basin (Colman 1979).

Because of the high oxygen content throughout winter, and the relatively long wind-assisted convective circulation period. Green Lake is also close to saturation with dissolved oxygen at the first onset of stratification. Birge and Juday (1911) reported 11.5 g m<sup>-3</sup> at 20–30 m on 15 May 1906 and a slightly lower concentration at 70 m (10.9 g m<sup>-3</sup>). Saturation = 12.2 g m<sup>-3</sup> at the bulk hypolimnetic temperature (5.6°C). The lake was already stratified in mid-May 1906 (8.0°C at the top; 4.75°C at the bottom). For 1978 I assume that the water was saturated with oxygen at 5.5°C after the historic 13-15 May wind storm (energy input of 88  $\times$  10<sup>5</sup> ergs cm<sup>-2</sup>). This assumption could introduce a positive bias of  $\sim 0.5$  g m<sup>-3</sup> in "initial conditions" for stratification in that year.

The spring diatom bloom is influenced by mixing, insolation, and available nutrients. Below-normal insolation (average 310 cal cm<sup>-2</sup> d<sup>-1</sup> or 65% of normal during 11 days preceding 9 May 1972) and deep

	Sampling	TP	TRP	TRSi : DIN : TRP	
	depth (m)	(mg m <sup>-3</sup> )		(atoms)	
11 Mar 72*	10-40	50	40†	NA:19.0:1	
3 May 72	0-30	52	38	3.6:16.5:1	
13 May 72	0-10	53	30	2.4:15.0:1	
7 Mar 78*	10-40	54	51	5.0:NA:1	
27 Apr 78	0-30	59	59	4.4:NA:1	
17 May 78	0-10	45	30	0.2:NA:1	

Table 1. Nutrient ratios in Green Lake: late winter and vernal circulation (NA-not available).

† SRP.

convective circulation probably retarded the vernal diatom bloom in 1972. Very low wind energy, rapid shallow epilimnion formation, weak turbulence, and low silica concentrations (see below) inhibited diatom development after 9 May. The pelagic chlorophyll standing crop increased from 59 to  $94 \text{ mg m}^{-2}$  between 3 and 13 May, but then declined to 74 mg m<sup>-2</sup> by 25 May. The percentage of the standing crop in the upper 9 m declined from 40 to 22% during the long interval of low wind power and premature onset of stratification.

Conditions were more favorable for diatom growth in 1978 because insolation was 130% of normal during the 2 weeks following ice-out.

During the late winter and early spring turnover the concentrations of DIN and total reactive phosphorus (TRP) are well balanced as compared to the often-cited stoichiometric requirements of algae (Table 1: cf. Redfield et al. 1963). A slight downward shift in the DIN:TRP ratio during vernal circulation accompanies the development of the diatoms. This shift may be caused by spring inputs of agricultural runoff (comparatively rich in P over nitrate-N), or to a higher N:P ratio preferred for plankton development, or to a slower turnover rate for N after uptake (Smith 1979; Burns and Ross 1972). There is no evidence that the spring diatom bloom was P-limited.

The vernal diatom bloom is limited by silica in this lake. The TRSi:TRP ratio is initially too low for many diatoms (Table 1; Kilham 1971; Lehman 1979; Tilman and Kilham 1976; Paasche 1980), and uptake causes further skewing of the ratio. By 25



Fig. 3. Secchi disk transparency (SDT) in Green Lake; SDT = 5.5 m on 15 October 1972 (not shown).

May 1972, TRSi had been reduced below  $25 \text{ mg m}^{-3}$  everywhere in the top 10 m of the lake and may have been lower before the bloom declined. This quick exhaustion of silica probably contributed to the low standing crop and early decline of the bloom, hence to the mid-May increase in Secchi transparency (Fig. 3). Between 27 April and 17 May 1978 TRSi declined by 98% (from 235 to  $<5 \text{ mg m}^{-3}$ ) in the top 10 m, by 80% at 30 m, and by 60% even at 60 m. During this same period TP and TRP declined to 47 and 33 mg m<sup>-3</sup> in the top 10 m, with smaller declines in the deeper waters.

One important consequence of silica limitation is that ample DIN and TRP remain unutilized following the decline of the vernal diatom bloom. The greater depletion of nutrients in the upper 5-10 m also ensures positive concentration gradients for both DIN and TRP between 5 and 20 m in late May.

Hypolimnetic oxygen deficit (HOD)-Green Lake's large HOD has been a topic of discussion since it was first systematically measured in 1906 (Birge and Juday 1911; cf. Hutchinson 1957). Because of the lake's long hydraulic residence time, and the absence of humic coloring in both the lake and its influents, the HOD is mainly related to the endogenous production of organic matter.

The shapes of the oxygen profiles in late summer and the magnitude of the HOD were very similar in 1978, 1979, 1905, and 1906 (Figs. 4 and 5). In all 4 years a sharp



Fig. 4. Dissolved oxygen at station 2 in late summer and early fall: 1905, 1906, 1978. Concentrations at 20 and 30 m not significantly different on 20 August 1905 and 14 August 1906. Points from 1905 not connected. h-Lower boundary of epilimnion on 4 October 1906 (otherwise at 8-9 m).

minimum formed by late summer in the metalimnion. Concentrations also fell rapidly below 55 m. The decreases in the bottom waters were evidently the result of oxygen consumption at the sediment-water interface, because dA/dV increases exponentially with depth below 50 m. Conversely, the metalimnetic minima were probably caused mainly by temperature effects on the oxidation of falling seston and other respiratory demands in the water column, because the lake has minimal sediment influence throughout the metalimnion and upper hypolimnion. Zooplankton is often abundant in the upper metalimnion in summer (Birge and Juday 1911).

The metalimnetic oxygen minimum does not develop in every summer. It was not present in July-August 1971 or 1972 (data only to 30 m) nor in late summer 1907 or 1909 (Birge and Juday 1911). The reasons for these year-to-year variations are unknown, but are probably related to the transparency of the mixed layer and thus to



Fig. 5 Dissolved oxygen at station 2 in mid-September 1978, 1979. Thermocline migration retarded in early September 1978.

the potential for photosynthesis in the upper metalimnion. During summers 1971 and 1972, Secchi transparency exceeded 5.5 m (10 m in early June 1972, cf. Fig. 3), and higher chlorophyll concentrations were sometimes found in the metalimnion than in the epilimnion (Stauffer 1974). The Secchi transparency was much lower between mid-May and late summer 1978 and on the one date measured in 1979 (Fig. 3).

On the basis of the early measurements (1905-1909) of Birge and Juday (1911), and my recent (1978-1979) ones, I conclude that there has been no significant change in the

Table 2. Oxygen consumption rates in the hypolimnion of Green Lake (NA-not available).

	Consumption rate for summer*								
interval (m)	20 Aug 1905	14 Aug 1906	14 Sep 1907	3 Sep 1908	20 Aug 1909	10 Sep 1978	15 Sep 1979		
30-50	29	32	30	34	27	22	30		
60	58	75	54	79	52	61	54		
65	100	110	NA	NA	NA	98†	87		

\* Units: mg m<sup>-3</sup> d<sup>-1</sup>, based on measured concentrations and assuming water column had 12.2 g dissolved oxygen m<sup>-3</sup> on 10 May.

† 107 mg m<sup>-3</sup> d<sup>-1</sup>, based on 13 August 1978 sampling.



Fig. 6. Concentrations of TP vs. depth at station 2  $(TP = 280 \text{ mg m}^{-3} \text{ at } 66 \text{ m on } 10 \text{ September, off scale}).$ 

HOD of Green Lake in this century (Figs. 4 and 5; Table 2). With more data, Stewart (1976) reached the same conclusion for Lake Mendota. The two lakes have closely comparable climatic, edaphic, and cultural settings (Stauffer 1985). From the oxygen regime I infer that the major carbon metabolism of Green Lake is essentially unchanged in this century as well.

Nutrient remineralization in the hypolimnion—I now show how the remineralization of Si and P is related to the development of the HOD. The analysis is similar to the study of the Lake Erie central basin in summer by Burns and Ross (1972).

Both P and Si accumulate in the hypolimnion of Green Lake during stratification. For P the time sequence of accumulation is highly reproducible from year to year, as revealed by two profiles from 10 July taken 6 years apart (Fig. 6). Virtually all of the summer increase in TP concentration is soluble reactive phosphorus (SRP) because the sum of the other P fractions (excluding SRP) has a narrow range in space and time below 15 m ( $12 \pm 3 \text{ mg m}^{-3}$ ). For both Si (Fig. 7) and P the concentrations below 20 m in-



Fig. 7. Concentrations of TRSi vs. depth at station 2 in 1978 (TRSi = 1,520 mg m<sup>-3</sup> at 66 m on 10 September, off scale).

crease monotonically with time beginning with the first onset of stratification. The rate of increase increases approximately exponentially with depth. The shapes of the curves below 20 m are nearly mirror images of the HOD and also closely related to dA/dV for the hypolimnion.

From the classic stoichiometry of Redfield et al. (1963) for the aerobic oxidation of average marine phytoplankton,

$$C_{106}H_{263}O_{110}N_{16}P_1 + 138O_2 = 106CO_2 + 122H_2O + 16HNO_3 + H_3PO_4,$$

the loss of 276 oxygen atoms is expected for each atom of remineralized phosphate-P. This ratio is similar to the 300:1 proposed by Tenney et al. (1973) for freshwater plankton assemblages. The expected  $-\Delta O:\Delta P$  ratio is closer to 212 if ammonia accumulates instead of nitrate in the hypolimnion.

The observed  $-\Delta O:\Delta P$  ratios are generally lower than predicted by the above stoichiometry below 30 m in Green Lake throughout summer (Table 3). Moreover, the ratios are lower in the deeper waters in late summer than in early summer (Table

Depth _	· · · · · · · · · · · · · · · · · · ·	15 N	May-13 Augus	ι*			13 Aug	gust-21 Octo	ober*	
(m)	ΔTRSi	ΔΤΡ	$\Delta O_2$	ΔSi:ΔP†	$-\Delta O:\Delta P^{\dagger}$	ΔTRSi	ΔΤΡ	ΔΟ2	ΔSi:ΔP†	-ΔO:ΔP†
12	+87	-40.5	-9.2	-2.4	-440	NA	NA	NA	NA	NA
15	+62	-41.0	-4.5	-1.7	-213	+125	+21.0	+1.8	6.6	-165
18	+20	-42.5	-3.0	-0.5	-137	+155	+41.5	+0.0	4.1	0
20	+33	-21.0	-2.6	-1.7	-240	+130	+32.5	+0.1	4.4	6
25	+40	+2.0	-1.9	22.0	1,840	+145	+14.5	-0.6	11.0	80
.30	+65	+6.0	-2.1	11.9	680	+155	+17.0	-0.6	10.0	70
40	+170	+21.0	-2.6	8.9	240	+115	+8.0	-0.1	16.0	25
50	+130	+21.0	-1.9	6.8	175	+305	+20.5	-2.7	16.5	255
55	+155	+24.0	-2.5	7.1	200	+420	+38.0	-4.3	12.0	220
60	+405	+55.0	-5.4	.8.1	190	+460	+53.0	-4.6	9.5	170
63	+570	+88.0	-8.5	7.1	185	+610	+81.0	-3.4	8.3	80
65	+670	+112.0	-11.3	6.6	195	+575	+67.0	-0.7	9.5	20
66	+790	+141.0	-11.9	6.2	165	—	—	-0.2	_	_

Table 3. Changes in oxygen, silica, and phosphorus below the epilimnion boundary, 1978 (NA-not applicable).

\* Station 2: concentrations—TRSi and TP, mg m<sup>-3</sup>; dissolved oxygen, g m<sup>-3</sup>. † Atomic ratios.

3). However, within the metalimnion (12–18-m zone in Table 3), the loss of dissolved oxygen is not accompanied by the accumulation of excess phosphate-P. The upper hypolimnion (20–30 m) is a transitional zone where the accumulation of P is relatively slow during the first part of stratification and then more rapid between mid-August and late October.

The downward shift in  $-\Delta O:\Delta P$  in the deeper waters with increased duration of stratification is probably a response to the much lower dissolved oxygen concentrations in late summer and thus the enhanced importance of anaerobic decomposition in the upper sediments. The shift in the ratio may also reflect a net release of P from older sediments (in contrast to remineralization of a recently sedimented algal biomass). The ret decreases in P in the metalimnion during the first 3 months of stratification are best explained by biological uptake of SRP (remaining at the end of vernal circulation) by some component of the falling seston, even while some net oxidation of organic matter is taking place. Net uptake of P would be expected if the seston settling out of the epilimnion were acutely P-limited (see below). The upper hypolimnion appears to be a transitional zone.

The hypolimnetic accumulation of P averaged 6.4 mg m<sup>-2</sup> d<sup>-1</sup> (area at the 18.5-m plane) during summer stratification in 1978 and was smaller (4.4 mg m<sup>-2</sup> d<sup>-1</sup>) during

an 80-day period in midsummer 1979 (Table 4). The hypolimnetic  $\Delta Si:\Delta P$  ratio averaged  $11.3 \pm 0.8$  in these two summers and was significantly higher (32) during the one winter studied. The lower rate of P remineralization and accumulation under ice is related to the very high dissolved oxygen concentrations in winter, the low water temperatures in the hypolimnetic region (~4°C less than in summer), and especially the decreased sedimentation of both P and oxidizable carbon from the upper waters after complete turnover in mid to late November. The higher  $\Delta Si:\Delta P$  ratio for winter is best explained by differential sediment capture of P following aerobic decomposition (cf. Burns and Ross 1972; Colman 1979; Mortimer 1969) and by the larger stoichiometric demands for silica of the fall diatom bloom than of the summer phytoplankton assemblages.

Phosphorus and silica concentration gradients in the metalimnion— The TP concentration gradient averaged 3–5 mg m<sup>-4</sup> between 9 and 18 m during late May to mid-July of the 2 years repeatedly sampled (1972, 1978). The metalimnetic gradient was the same on 23 July 1971. (Because of the prolonged spring mixing in 1971, 23 July corresponded to late June and early July 1972 and 1978 in stratification chronology.) The metalimnetic gradients were smaller during late June 1979 than in any previous year studied. By late summer the minimum TP concentrations in the water column are in the main thermocline (9–15 m), while the positive P gradients that had previously extended to 9 m have shifted downward to the lower metalimnion and upper hypolimnion (15–21 m) and increased to 5–8 mg m<sup>-4</sup>.

The metalimnetic TRSi gradients are much more irregular in different years than those for P because of a variable initial condition following the vernal diatom bloom. During 1978, a year characterized by abovenormal early spring insolation and a robust diatom crop, the water column was initially so depleted in Si that the upper metalimnetic TRSi gradient was either zero or negative throughout the summer (Fig. 7). Conversely, metalimnetic TRSi gradients averaged 22 mg m<sup>-4</sup> in late June 1979, following a winter with abnormally deep and persistent snow cover, a spring with a very late ice-out ( $\sim 25$  April), and below normal insolation between mid-April and mid-May.

Vertical transport of heat by eddy diffusion-The measured vertical eddy conductivities  $(K_z)$  exhibited similar depth and seasonal relationships to those in other temperate lakes of Green Lake's size (e.g. Lakes Washington and Zürich). After the onset of stratification, the minimum  $K_{z}$  values were always in the main thermocline, usually at a point 2-4 m below the depth of maximum local stability (parameterized as  $N_z^2$  and called the squared Brunt-Väisälä frequency). Below this minimum, the  $K_z$ values then increased with depth to a hypolimnetic maximum value near 50 m; this maximum corresponded to a minimum  $N_z^2 \sim 2 \times 10^{-6}$  s<sup>-2</sup> (corresponding to a minimum temperature gradient of 0.01°C  $m^{-1}$ ).

The  $K_z$  values in the metalimnion and upper hypolimnion were an order of magnitude higher in late spring than in midsummer in 1978 (Table 5). The lower eddy conductivities in the thermocline in July-August resulted from maximum total water column stability, maximum local stability  $(N_z^2)$ caused by deepening and consolidation of the main thermocline, and a pronounced seasonal minimum in windpower, particularly in mid-to-late summer 1978 (cf. StaufTable 4. Rate of hypolimnetic accumulation of silica and phosphorus in Green Lake.

	No. of	Ra accum	Si-P	
Interval	days	TRSi	TP	(atoms)
1 Jan-7 Mar 78†	66	53	1.90	32
17 May-21 Oct 78	157	62	6.35	10.5
27 Jun-15 Sep 79	80	48	4.35	12.0

\* Below 18.5-m plane: units-mg m<sup>-2</sup> d<sup>-1</sup> ( $A_{18.5} = 17.5$  km<sup>2</sup>); to get rate per unit  $A_0$  multiply by 0.59.

† Ice cover.

fer 1980). The depth and seasonal minimum in  $K_z$  is  $\gtrsim 0.01$  cm<sup>2</sup> s<sup>-1</sup>, one order of magnitude higher than the molecular conductivity (cf. Quay et al. 1980); the metalimnion and hypolimnion of Green Lake are obviously much more turbulent than in small, highly sheltered Lake 227 in the Experimental Lakes Area of Ontario.

Vertical transport of nutrients-Because the  $K_z$  values in Green Lake greatly exceed the molecular conductivity, one would expect some convergence between the turbulent exchange of heat and solutes (cf. Quay et al. 1980; Turner 1968). This convergence in effective transport rate is likely to hold most nearly for the lower metalimnion and hypolimnion, because of the rapid decrease in  $N_z^2$  with increasing depth. As an approximation, then, I will equate the measured eddy diffusivity for heat to the unknown value for solutes in this lake, for the purpose of computing vertical transport of nutrients and dissolved oxygen by the familiar "fluxgradient" algorithm.

The vertical flux of P by eddy diffusion averaged 1.0 mg m<sup>-2</sup> d<sup>-1</sup> at the 9-m plane (but expressed per unit  $A_0$  to make all fluxes directly comparable) during mid-May through early July 1978 (Table 6). The upper metalimnetic flux was likely to have been similar in June 1972, on the basis of closely comparable vertical P gradients and weather. Table 6 also shows that the vertical flux was higher at 12-15 m in late spring and early summer 1978, both because of the increased concentration gradients, and because of increased  $K_z$  (the main thermocline was still shallower in the early summer). Minimum vertical fluxes were in the upper hypolimnion in early summer, because of the very small middepth concentration gra-

Denth		$K_z$ during interval* (1978)								
(m)	19 May-9 Jun	9 Jun-10 Jul	10 Jul-13 Aug	13 Aug-10 Sep	10 Sep-21 Oct	27 Jun-15 Sep				
9	230±25	78±6	24±4	88±10	NA	NA				
12	$400 \pm 65$	$83 \pm 10$	9±4	$18 \pm 3$	NA	$27 \pm 3$				
15	$270 \pm 60$	$95 \pm 15$	$13 \pm 8$	$26 \pm 8$	NA	$11 \pm 2$				
18	$320 \pm 75$	$135 \pm 15$	$17 \pm 8$	$34\pm8$	$50\pm5$	$21 \pm 3$				
21	$300 \pm 75$	$140 \pm 15$	$29 \pm 8$	$57 \pm 10$	45±5	$27 \pm 3$				
25	$260 \pm 65$	$205 \pm 15$	56±9	$85 \pm 11$	$110 \pm 10$	$55\pm4$				
30	$205 \pm 40$	$250 \pm 15$	$110 \pm 10$	$145 \pm 12$	$220\pm12$	80±3				
40	$440 \pm 50$	$520 \pm 30$	$250 \pm 15$	$210 \pm 15$	$120 \pm 10$	$185 \pm 4$				
50	$720 \pm 75$	$550 \pm 40$	$415 \pm 30$	$490 \pm 40$	$250 \pm 25$	$240 \pm 6$				
55	$850 \pm 90$	$640 \pm 50$	$500 \pm 35$	$390 \pm 35$	$260 \pm 30$	$260 \pm 7$				
60	$430 \pm 45$	$340 \pm 35$	$260 \pm 20$	$340 \pm 30$	$145 \pm 20$	$230 \pm 7$				

Table 5.  $K_z$  values in the metalimnion and hypolimnion of Green Lake (NA-not applicable).

\* Units: cm<sup>2</sup> s<sup>-1</sup>×10<sup>3</sup>.

dients. The fluxes then increased with depth below 40 m and were already large by late June 1978 below 55 m (Table 6). From closely comparable concentration profiles in 1972, I would expect a similar depth dependency in that year.

By midsummer the flux of P through the 9- and 12-m planes becomes negligible; by late summer the flux is distinctly negative, because minimum profile concentrations are then found in the upper metalimnion instead of the epilimnion. These calculations prove that the vertical transport of P by eddy diffusion cannot be an important source of P for the epilimnion of this lake during the middle and late summer!

Conversely, Table 6 shows that vertical transport of P through the 18-m plane, and into the *bottom* of the metalimnion, is important in the mid-to-late summer! These

positive (upward) fluxes are a consequence of the comparatively steep P gradients between 15 and 21 m at that time of year and a general increase in  $K_z$  with depth accompanying the rapid decrease in  $N_z^2$ .

Because of the relatively small, local P concentration gradients, the mid-to-upper hypolimnion is a depth zone of only modest vertical fluxes in mid-to-late summer. However, large vertical fluxes are predicted below 50 m because of the rapidly increasing concentration gradients.

The computed vertical fluxes of TRSi are comparable with those for P in that they increase sharply with depth below 45 m (Table 7). Moreover, as for P, the deep water fluxes were higher in midsummer 1978 than in spring, following the accumulation of dissolved silica in the bottom water and thus the intensification of the vertical gradients.

D. 4	44->		Flux (J	) during interval*	(1978)		(1979)
(m)	(km <sup>2</sup> )	19 May–9 Jun	9 Jun-10 Jul	10 Jul-13 Aug	13 Aug-10 Sep	10 Sep-21 Oct	27 Jun-15 Sep
9	20.6	1.0	1.1	0.10	-0.5	NA	ŃA
12	19.4	3.2	1.7	0.10	< 0.05	NA	-0.5
15	18.5	2.7	1.7	0.10	0.3	NA	0.05
18	17.6	1.5	1.1	0.3	1.3	1.7	0.3
			<u> </u>	<u>^ </u>	14	0.6	0.7

Table 6. Phosphorus transport upward by vertical eddy diffusion in Green Lake (NA-not applicable).

		(1979)				
Depth (m)	19 May– 9 Jun	9 Jun 10 Jul	10 Jul- 13 Aug	13 Aug- 10 Sep	10 Sep- 21 Oct	27 Jun- 15 Sep
9	0.2	-1.7	-0.6	-1.7	NA	NA
12	4.8	-1.9	-0.3	-0.9	NA	1.2
15	4.0	1.3	-0.2	-1.2	NA	1.1
18	3.7	1.7	0.1	-0.2	-0.6	1.9
21	3.1	0.7	0.5	1.9	1.6	2.2
25	2.8	1.1	0.7	2.6	3.7	3.8
30	1.7	2.8	3.1	4.4	6.5	4.1
40	4.3	7.5	7.5	3.7	3.2	3.1
50	9.5	10.5	5.0	22.0	18.0	5.9
55	7.5	20.0	25.5	31.5	27.0	8.9
60	2.5	15.5	21.0	25.0	15.0	16.5

Table 7. Silica transport upward by vertical eddy diffusion in Green Lake (NA-not applicable).

\* Units (J): mg SiO<sub>2</sub>-Si m<sup>-2</sup> (A<sub>0</sub>) d<sup>-1</sup>; positive values denote upward flux. Uncertaintics: C.V. (J)  $\approx 25\%$  for |J| > 1.0 and  $Z \le 25$  m; C.V. (J)  $\approx 50\%$  for Z > 25 m; C.V. (J)  $\approx 100\%$  for |J| < 0.5.

Also, as for P, the deep water fluxes of Si were significantly higher in summer 1978 than in 1979. The higher concentrations and fluxes of both elements may have resulted from the more favorable conditions for the vernal diatom bloom in 1978.

Table 7 shows that the turbulent fluxes of TRSi were consistently *negative* throughout the entire metalimnion during summer and early fall 1978. These calculations prove that the measured increase in epilimnetic TRSi during summer 1978 (cf. Fig. 7 and also below) could not possibly have resulted from vertical transport upward through the main thermocline! Small, positive upper metalimnetic Si fluxes were apparent in summer 1979, in response to changed initial conditions following the vernal diatom bloom in that year. Nevertheless, the vertical flux through the 12-m plane can only account for  $\sim 7\%$  of the net measured increase in epilimnetic TRSi between 27 June and 15 September 1979.

Vertical transport of oxygen and the calculation of the areal HOD (AHOD)—According to the concentration gradients shown (Figs. 4 and 5), the potential exists for largescale turbulent transport of oxygen within the metalimnion, upper hypolimnion, and lower hypolimnion of Green Lake by midto-late summer of many years. Below 45 m and above the depth of the metalimnetic oxygen minimum (when present), the di-

Table 8. AHOD for Green Lake in summer 1978.

	AHOD fo	r interval*	
	9 Jun-13 Aug	13 Aug-10 Ser	
A. 10-m plane			
Net deficit	1.28	0.88	
Transport	$+0.28^{+}$	+0.66	
Total deficit	1.56	1.54	
B. 15-m plane			
Net deficit	0.96	0.88	
Transport	$-0.22^{+}$	-0.27	
Total deficit	0.74	0.61	

\* All units = g  $O_2 m^{-2} d^{-1}$  for the designated planes.

† Assumes mean concentration gradient for this time interval is half the measured gradients on 13 August.

rection of net turbulent transport is downward. Between 12 and 25 m the net turbulent transport of dissolved oxygen is upward, out of the lower metalimnion and upper hypolimnion, and into the metalimnetic zone of minimum dissolved oxygen.

These sharp oxygen gradients affect the computation and interpretation of the AHOD for late summer and fall in Green Lake, depending on the year and also on the reference plane identified with the upper boundary of the hypolimnion and used for computing the AHOD. Stewart (1976) adopted a fixed plane (9 m) for computing the AHOD of Lake Mendota. Cornett and Rigler (1980) adopted a different convention, which, if applied to Green Lake, results in a boundary at ~15 m in mid-to-late summer 1978.

From measured oxygen profiles at station 2, and estimates of the depth-dependent, time-averaged eddy diffusivities between 13 August and 10 September 1978, I have computed the AHOD for both the 10- and 15-m planes in Green Lake, with and without the potential effects of eddy transport of dissolved oxygen (Table 8). If transport is ignored the  $AHOD_{10}$  significantly underestimates the total uptake and consumption of dissolved oxygen during that period. Conversely,  $AHOD_{15}$  overestimates the net consumption by  $\sim 40\%$ . The estimated transport across the 15-m plane is larger than the AHOD of many lakes studied by Lasenby (1975) and by Cornett and Rigler (1980) and approximates the difference between the central and eastern basins of Lake

	0.	Nutrient flux (mg m <sup>-2</sup> d <sup>-1</sup> )*			Atomic ratios*	
Source	(cm d <sup>-1</sup> )	DIN	TRSi	TP	N:P	Si:P
Direct precipitation (normal year)	0.30	3.3	0.15	0.08	91	2
Inflow (normal year)	0.25	8	15	0.20	90	83
Ripon Waste Treatment Plant*	NA	1.8	0	0.10 (1.2)	40 (3)	NA
Totals*	0.55	13	15	0.38 (1.5)	75 (20)	45 (12)

Table 9. External fluxes of nutrients to Green Lake: mid-May-mid-September (NA-not available).

\* Values in parentheses are for 1971-1972.

Erie listed in table 4 of Cornett and Rigler (1980). Transport phenomena would have had comparable effects in late summer 1979, but were smaller in magnitude in summers 1905 and 1906.

Lake Mendota does not normally exhibit metalimnetic oxygen minima (Birge and Juday 1911; Stewart 1976; R. Stauffer unpubl. data); hence the unadjusted AHOD underestimates the total consumption of dissolved oxygen below the bottom boundary of the epilimnion and below the upper boundary of the hypolimnion, no matter how defined. In light of this significant difference, it is important to emphasize that Lake Mendota and Green Lake have frequently been compared in assessing the role of hypolimnetic depth development on the AHOD (Hutchinson 1957; Cornett and Rigler 1980).

External fluxes: summer—The large influx of DIN (Table 9) results from precipitation and from the very high nitrate-N concentrations in the three most important tributaries draining this agricultural basin (sometimes >10 g m<sup>-3</sup> as N). Closely comparable DIN exports have also been reported for other fertile agricultural drainage basins in SE Wisconsin (Sonzogni and Lee 1974; Wis. Dep. Nat. Resour. 1978).

The concentrations of TRSi and SRSi in the tributaries are also high, but unlike DIN, narrowly ranging among tributaries and over time (mean =  $6.0 \pm 0.5$  g Si m<sup>-3</sup>). The concentrations are highly representative of stream and groundwaters throughout Wisconsin (R. Stauffer unpubl.) and in temperate localities generally (Edwards and Liss 1973).

Seventy percent of the total phosphorus influx from nonpoint sources represents export from rural drainages (mean TP = 45  $\pm$ 

5 mg m<sup>-3</sup>, but some peak flows of short duration may have been missed). The remaining 30% is a liberally prorated estimate of seasonal TP contributions from the unsampled but small urbanized portion of the watershed (from regional studies including that of Kluesner 1972).

Because of probable errors in both inflow  $(Q_i)$  and mean concentrations, the uncertainty (C.V.) in each of these estimated total external fluxes is  $\sim$ 35%, except for TRSi (C.V.  $\sim$ 25%). Furthermore, the fluxes are all based on the assumption of complete delivery to the main lake. Because of hydraulic detainment in the important tributary marshes, this assumption is likely to result in overestimates of summer nutrient inputs (Bentley 1969), particularly for P released by the Ripon urbanized area and waste treatment plant into the Silver Creek drainage. White and Dakin Creeks, which have high summer flows stabilized by perennial springs along the cuesta scarp, are seriously contaminated by nitrate and have DIN: TP atomic ratios > 500. These streams enter the lake directly.

Despite the uncertainties in the data and the largely unknown seasonal effects of the marshes, Table 9 shows conclusively that the external fluxes of DIN and TRSi are stoichiometrically out of balance with respect to P. Furthermore, if the fluxes of inorganic N and Si were compared instead with the flux of SRP, the "available" nutrient ratios would be inflated by a factor >2. Phosphorus is clearly the limiting nutrient in water entering the lake during the period of stratification.

Comparing Tables 9 and 7, we find that the external flux of Si is at least an order of magnitude larger than the vertical fluxes by eddy diffusion within the metalimnion of Green Lake. The large tributary-based influx of Si can account for the measured net increases in TRSi in the mixed layer between June and September 1978 and 1979 (+15 and +13 mg m<sup>-2</sup> d<sup>-1</sup> in the two summers).

The external fluxes of TP are much smaller (after 1976) than the vertical fluxes through the 9-m plane in late spring and early summer (cf. Tables 9 and 6). However, in mid-to-late summer the external TP flux is invariably larger than the vertical eddy flux (often negative), but still small in comparison with probable releases of P from littoral sediments (30% of total) in this calcareous lake (cf. Holdren and Armstrong 1980; Gallepp 1979). The littoral sediments are also likely to be a net summer source of Si released from dissolving diatom frustules.

Nutrient limitation of the epilimnion— The mean epilimnetic TP concentration declined in early summer until it reached a minimum of  $12-16 \text{ mg m}^{-3}$  by early August in each of the four summers, spanning a decade, when the lake was studied (Fig. 8). There was then little change in epilimnetic TP before the *deep* penetration of the main thermocline in late October.

Several lines of evidence indicate that the Green Lake epilimnion was already severely limited by P in late summer in 1971-1972 and that this limitation intensified after 1976. First, the epilimnetic TN:TP ratio was 62 (28 by mass) following the decline in epilimnetic TP in early summer 1971. The large ratio suggests P limitation of chlorophyll standing crop (Sakamoto 1966; Smith 1982). The high DIN:SRP ratios in July 1972 ( $\gtrsim$  100) also support this hypothesis, as do the large TRSi:TP ratios ( $\geq 25$ ) in mid-to-late summer 1978-1979. The soluble organic P fraction (nonmolybdate-reactive) declined between early June and mid-July, during a period when SRP was reduced below the detection limit (1 mg  $m^{-3}$ ). Despite this reduction (in response to alkaline phosphatase?), the soluble nonmolybdatereactive fraction increased to 75% of the total in midsummer, vs. <10% in early spring and 50% in early June.

Anabaena is also a prominent bloom former in June, before the disappearance of



Fig. 8. Total-P  $A_0^{-1}$  for depth intervals: z < 9.5 m;  $9.5 \le z < 18.5$  m. [To convert the ordinal statistics to mean layer concentrations multiply by 0.131 (z < 9.5 m) and 0.175, respectively. ]

SRP from the epilimnion. Nitrogen fixation by this species may help to shift the epilimnetic DIN:SRP ratio (upward) in early summer, thus helping to ensure P limitation later on (cf. arguments of Lehman 1979).

Furthermore, the external inputs were already deficient in P relative to N in the early 1970s. This imbalance certainly worsened after 1976, because of reductions in external P loading from the Ripon Waste Treatment Plant, coupled with increases in base-flow nitrate-N concentrations (Stauffer unpubl. data from June 1983).

The epilimnetic algal standing crop is not light-limited because Secchi transparency has frequently exceeded 5 m (Fig. 3), even in the early 1970s. Summer chlorophyll concentrations are much lower than in shallower, more nutrient-rich calcareous lakes in SE Wisconsin (Stauffer 1985). This analysis shows why the failure of the Dillon and Rigler (1974) chlorophyll model for this lake (Stauffer 1985) is unlikely to be a consequence of N limitation.

The fall diatom crop in Green Lake develops in the presence of a high TRSi:TRP ratio because the early fall migration of the main thermocline results in the entrainment of metalimnetic water that was left deficient in P at the end of the summer. Partly be-



Fig. 9. Total -P in Green Lake in 1971, 1972, 1978, 1979. Total-P below 18.5-m plane also shown for 1978, 1979.

cause of this nutrient imbalance, 65% of the silica present in the epilimnion on 10 September 1978 remained unutilized on 21 October. By the time deep penetration of the fall thermocline has occurred and entrained significant amounts of nutrient-rich hypolimnetic waters, insolation has undergone its marked seasonal decline at this latitude, leaving the deeply circulating mixed layer subject to light limitation of algal productivity (Lorenzen and Mitchel 1973). The changed conditions in the fall from those in spring partly account for the nutrient carryover to the late winter in the upper waters of the lake and also the higher  $\Delta Si:\Delta P$  ratio in the bottom waters during winter under ice.

Steady state nutrient economy—Because of recycling in the water column and at the sediment-water interface, little P is permanently lost from the lake as a consequence of algal uptake and sedimentation, except as balanced by continuing inputs from external sources. Thus, the TP content of the water was the same on 21 October 1978 as in the previous March, the same in 1978 as in 1972, and, despite seemingly lower concentrations in summer 1979, as high on the day of ice-out 1980 (11 April) as in early spring 1972 (Fig. 9). Comparative studies of the HOD suggest that the lake's nutrient economy must have been similar in the first decade of this century. This seeming steady state in lake P content is interesting, particularly in view of the increasing external P loading from the Ripon Waste Treatment Plant before 1972, followed by a reduction in TP loading of  $\sim 35\%$  by December 1976. Because of the lake's long hydraulic residence time, concentrations may have been increasing slowly in the early 1970s. The same factor, plus variable winter-early spring P-loading from nonpoint sources, may have masked longer term trends in lake P content after 1976. Thus, the recent evidence for steady state may be fortuitous.

## Discussion

Implications for modelers and lake managers-It would be useful to have accurate, generalizable, time-dependent models of primary productivity and algal standing crops in lakes featuring diverse morphometries, edaphic and climatic settings. Ideally, the models should evolve toward mechanistic conceptions so that the relationships among the state variables are realistically represented and understood. A mechanistic model is also less subject to surprises than a black-box statistical model that is defined for one data set and then inadvertently applied for predictive purposes "across unknown differential structures" (as economists say). Oceanographers showed how the development and migration of the seasonal thermocline acts to regulate nutrient and light exposures in the oceanic mixed layer and indirectly controls algal standing crops and primary productivity in the sea (Sverdrup 1953; Menzel and Ryther 1960; Riley 1942, 1965). Imboden's (1974) "steady state model" and the second generation "dynamic model" (Imboden and Gächter 1978) extend Riley's (1965) 1-dimensional ocean mixing model to lakes with variable morphometric configurations, thermocline depths, vertical mixing rates, flushing rates, and external (P) loading rates. Hypolimnetic remineralization and exchange of nutrients at the sediment-water interface are also factored into the model, the latter process without an adequate theoretical framework (cf. Imboden and Gächter 1978).

My studies of Green Lake confirm the general theoretical soundness of the Imboden and Gächter model and also reveal several areas where greater model sophistication is required. Green Lake, with its significant depth development, remineralizes nutrients primarily far below the epilimnetic lower boundary (h).  $K_z$  increases with z for z > h + 3 m, but at a rate which is roughly proportional to  $N_z$  (Quay et al. 1980; Jassby and Powell 1975; Stauffer unpubl.). Because the expected time for diffusion along a path length ( $\Delta z$ ) increases as  $(\Delta z)^2$  (cf. Fischer et al. 1979), an increase in hypolimnetic mean depth is not effectively compensated by increases in  $K_z$ . This theoretical result, based on diffusion theory, is corroborated by the time series for nutrient profiles in Green Lake. An increase in hypolimnetic depth development also retards remineralization because of the lower expected bottom temperatures in deep water in the temperate zone.

Because of the delays in remineralization and vertical transport, Green Lake does not recycle significant amounts of algal nutrients from the deep hypolimnion back into the epilimnion during a single stratification season. Instead of attaining full-lake steady state, the mixed layer is progressively depleted of the limiting nutrient (P) during stratification. In some summers this nutrient depletion results in an increase in Secchi transparency, which in turn permits the development of a metalimnetic algal layer. The deep chlorophyll maximum intercepts nutrients being transported from below 20 m, and thus helps ensure the nutrient impoverishment of the mixed layer. This development of a metalimnetic standing crop profoundly alters the trophic structure of the lake, but is one feature missed by Imboden and Gächter's 1-dimensional model.

During spring and late fall Green Lake conforms more nearly to the light-sensitive model of Lorenzen and Mitchel (1973). This transition is missed by the Imboden models because of the assumption of a static thermocline depth.

Biological consequences of nutrient recycling at the sediment-water interface— Another area where model formulations can be misleading involves generalizations about sediment-water exchange of nutrients. An improved understanding of this process could be readily applied to Imboden's dynamic model, when it becomes available.

In their study of the central basin of Lake Erie, Burns and Ross (1972) found that only 25% of the P in a sedimenting algal bloom was recycled into the overlying hypolimnetic waters accompanying the oxic decomposition of the organic matter. However, under anoxic conditions in the hypolimnion, excess P accumulated in the hypolimnion. Other studies have also shown that anoxia was a necessary precondition for the significant accumulation of SRP in the hypolimnion (Larsen et al. 1979, 1981; Lund et al. 1963; Imboden and Gächter 1978). Green Lake differs from these other lakes (Shagawa, Windermere, Washington, Alpnachersee) in that SRP appears in the hypolimnion in stoichiometric excess long before the onset of hypolimnetic anoxia. This recycled P is redistributed throughout the lake at overturn and ensures that the vernal diatom bloom will be stoichiometrically limited by silica in each succeeding spring. Unlike the Alphachersee (Imboden and Gächter 1978), this recirculated SRP is not flushed out of the lake in large amounts each winter because of the very long hydraulic residence time of Green Lake in the continental climate of Wisconsin (Alpnachersee flushes in 100 days in winter).

Silica limitation in Green Lake is a consequence of the phosphorus loading and the efficiency of the phosphorus cycle within the lake. It is *not* caused by low concentrations of silica in tributary inflow. Green Lake, lying within the Fox River drainage basin of Lake Michigan, represents a scale model of Lake Michigan in many hydraulic, morphological, chemical, and biological aspects. It also conforms to Schelske and Stoermer's (1972) hypothesis concerning silica, phosphorus, and the trophic regulation of Lake Michigan.

As noted by Juday (1924) and Birge and Juday (1911), and emphasized by Hutchinson (1957, 1969), Green Lake is a highly productive lake. Nevertheless, it is not a highly degraded ecosystem; in fact, just the opposite. Hutchinson (1969, p. 20) wrote "A deep lake may be very productive, but if the hypolimnion is large enough, it may show until late summer a fairly orthograde oxygen curve and support *Mysis relicta* at intermediate depths; an example is Green Lake in Wisconsin" (see also Juday and Birge 1927). Because of its hypolimnetic depth development, and the low rate of external P-loading during summer, Green Lake is acutely nutrient-limited by mid-to-late summer. As a result of this limitation, Secchi transparency is often high and the lake maintains its recreational potential at the same time that its annual fishery potential is preserved.

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