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Biogeochemical Control of Phosphorus Cycling and Primary Production in Lake Michigan

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Biogeochemical control of phosphorus cycling and primary production in Lake Michigan

Abstract—A 3-yr study in Lake Michigan has shown a 27 mmol P m^{-2} increase in the mass of total P (TP) in the water during spring when the lake is mixed from surface to sediment. This value is an order of magnitude greater than the annual P input from external sources. TP changed in concert with increases in chlorophyll *a* and organic N and decreases in nitrate and soluble Si. The concentration of soluble reactive PO$_4^{3-}$ (SRP) remained relatively constant throughout the study. We hypothesize that the SRP concentration is maintained by a chemical equilibrium with calcium-phosphate species. The increased mass of TP arises from the sequestering of P by algae which displaces the chemical equilibrium and allows more P to be released to the water from the sediments. Solar irradiance and the duration of mixing determine the magnitude of the spring bloom and the demand for P that must be supplied through the flux of P from the sediments to the overlying water.

Numerous studies have been conducted in the Laurentian Great Lakes and other freshwater bodies which indicate that phosphorus limits the growth of primary producers. There is, however, a growing body of evidence which suggests that internal supplies of P from the sediments can support new primary production (Caraco et al. 1992; Marsden 1989). Our observations in Lake Michigan suggest that the flux of P from the sediments is a significant source of P for the primary producers.

Monthly cruises were run during 1986–1988 to a 100-m-deep station in Lake Michigan, 27 km NE of Milwaukee, Wisconsin (43°11'40"N, 87°40'11"W). This station has been sampled on a regular basis for many years and is representative of the open waters of Lake Michigan during the spring mixing period. This assessment is based on previous sampling experience (Rousar 1973; Bartone and Schelske 1982) and the evaluation of satellite images showing uniform lake surface temperatures ≤4°C during spring at this and other offshore locations (Bolgrien and Brooks 1992).

Samples were collected with Niskin bottles at 10–14 depths (*see Fig. 1*). Temperature profiles were measured with a bathythermograph. Colorometric analyses were run for total P (TP), soluble reactive P (SRP), soluble Si, total or-
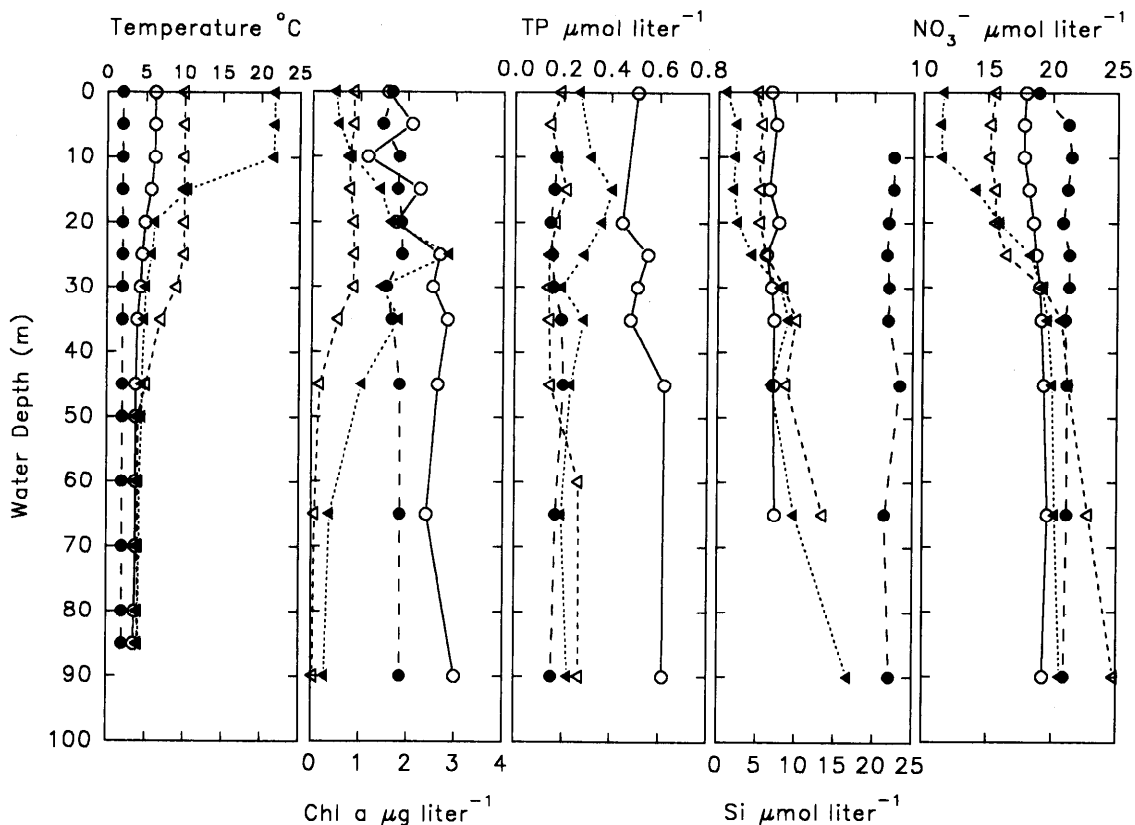
Fig. 1. Representative depth profiles for temperature, Chl a, total P, Si, and nitrate in 1987. Sampling dates: 4 March—●; 18 May—○; 13 July—▲; 19 October—△.

ganic N (org-N), and NO_3^- plus NO_2^- (Am. Public Health Assoc. 1975). Org-N was determined as total Kjeldahl N, which included NH_3. The average concentration of NH_3, determined separately, was <0.7 μM N. Chlorophyll a (Chl a) was determined fluorometrically after extraction with acetone from 0.2-μm pore-size membrane filters (Strickland and Parsons 1972).

During the winter–spring period, the water column was isothermal with temperatures $\leq 4°C$ each year of the study. Dissolved oxygen was near saturation and the concentrations of all the measured chemical variables were essentially uniform from top to bottom from January until the lake became thermally stratified. This uniformity prior to stratification is illustrated in vertical profiles obtained on 4 March 1987 (Fig. 1). Stratification was first observed on 6 June 1986, 18 May 1987, and 1 June 1988 as surface temperatures rose above

4°C and an incipient thermocline was observed. The actual date of stratification in 1988 may have been somewhat earlier because the surface temperature had reached 13°C by 1 June and a strong thermocline was present at ~10 m.

The data presented in Fig. 2 show a significant increase in the concentrations of Chl a and TP between January and May–June during each year of the study as the spring diatom bloom developed. During this same period, the concentration of soluble Si decreased by a factor of 4, while an increase in the concentration of org-N was balanced by an equimolar decline in nitrate. The concentration of SRP did not change significantly during the entire period of the study and was the same as that observed at offshore stations in Lake Michigan during 1970–1971 (Rousar 1973). The concentrations of Si, Chl a, and NO_3^- and the seasonal changes in these variables shown in
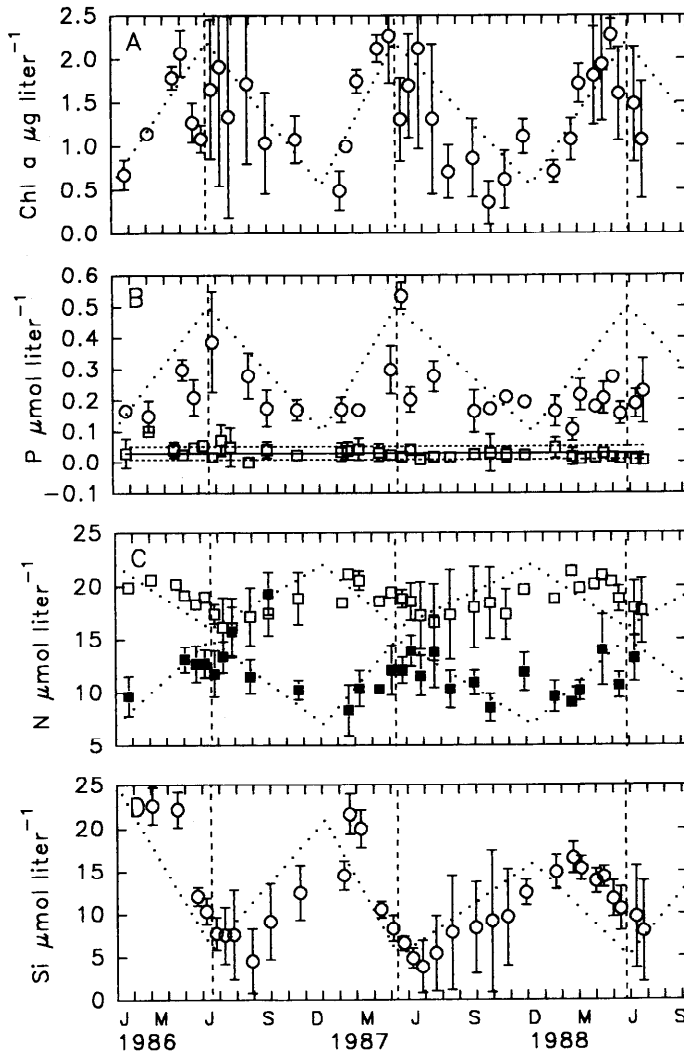
Fig. 2. Mean concentrations of nutrients and Chl a (± 1 SE) for the 100-m water column 1986–1988. A. Chlorophyll a. B. Soluble reactive P (SRP) (□); total P (○). C. NO_3^- (□); organic N (■). D. Soluble silicon. The dotted lines depict general seasonal trends of nutrient utilization and algal growth (Chl a) for the first 180 d of each year and declining algal biomass and nutrient regeneration for the second half of each year after stratification. Vertical dashed lines denote the date each year when thermal stratification was first observed. The lines drawn through the SRP data represent the average value ± 1 SD.

Fig. 2 are also nearly identical to those reported by Rousar (1973). The concentrations of both TP and org-N observed near the end of the spring bloom in 1988 were not as great as in 1986 or 1987, although there was a definite increase over winter minimum values. It is possible that the 1988 sampling times missed the seasonal maximum because thermal stratification occurred between cruise dates.

Once the water column became stratified and complete mixing ceased, losses of Chl a, TP, and org-N by the settling of particles (Eadie et al. 1984) became apparent in the surface waters. After stratification, as illustrated in the profiles for 13 July (Fig. 1), Chl a and TP exhibited a subsurface maxima, and the remineralization of NO^{3-} and Si was evident by the increasing concentrations with depth. The heterogeneity in the vertical profiles after stratification accounts for the greater variability de-

picted on Fig. 2. As stratification began to break down, (19 October, Fig. 1) the thermocline descended and conditions were reset to those observed in the previous winter.

Having set the stage depicting the annual thermal cycle and that of Chl *a*, N, and Si, we now examine the dynamics of P in more detail. Caraco et al. (1992, p.590) repeat the statement, orginally made by Juday et al. (1927)

> Just how ... lakes are able to support a crop of phytoplankton from May to July or August without any appreciable decrease in [the concentration of] soluble phosphorus ... is not known.

This statement is just as appropriate to make for Lake Michigan during the period from March to June when the spring crop of phytoplankton flourishes, the soluble P concentration does not decrease, and the concentration of TP increases dramatically.

A mass balance for P was constructed in a manner similar to that used by Schelske et al. (1986) to estimate areal Si use for the spring mixing period. The mass of TP in Lake Michigan increased from ~13 to 40 mmol P m^{-2} between January and the date when thermal stratification was first observed (Fig. 2). Over the whole lake ($A = 57,800$ km^2; $\bar{z} = 100$ m), the mass of P required to account for the observed increase is ~27 mmol P m^{-2}. The estimated annual external P inputs to the lake from all sources are no more than 2 mmol P m^{-2} (Rockwell et al. 1989); therefore, the difference between the observed increase in P mass and external sources (~25 mmol P m^{-2}) must be accounted for.

Our method for measuring TP includes all forms of P in the water and the estimates for external inputs include all sources of P (including loading from tributaries, other point sources, and atmospheric inputs), so the missing P can only come from sources within the lake itself. The rapid regeneration of P in the water column, as suggested by Conley et al. (1988), cannot account for the missing P because our data show a real increase in the mass of P in the water during spring and not just a recycling of the same P atoms.

Since the water column initially contains nowhere near the mass of P required to support the spring bloom, the sediments must act as the internal source of P required to achieve a mass balance. Such a process also provides an answer to the issue raised by Juday et al. (1927) as it applies to Lake Michigan.

The mass of P in the sediments available for release to the water was estimated from measurements of the average sediment accumulation rate over the whole basin (100 g m^{-2} yr^{-1}), a mixing depth of ~4 cm (20 yr of deposition) (Robbins and Edgington 1975), and a concentration of phosphate in the surface sediment of ~39 μmol P g^{-1} (S. Fitzgerald and V. Klump pers. comm.). By this means, the total mass of P available in the sediment mixed layer was estimated to be 78 mmol P m^{-2}. After allowing for external inputs, calculations of mass balance require that upward of 30% of the P stored in the mixed layer of sediments must be released to support primary production during the spring bloom. This amount is in accord with estimates made by Eadie et al. (1984) of bioavailable, NaOH-extractable P in Lake Michigan sediment.

A mean rate of P release from the sediments of 9.4 μmol P m^{-2} h^{-1} would be required to account for the observed increase in TP over a period of 120 d prior to stratification. Because the waters of Lake Michigan remain at or near oxygen saturation throughout the winter–spring mixing period, P must be released from the sediments under oxidizing conditions.

Release rates based on experimental oxic sediment systems vary between 0.1 and 11 μmol P m^{-2} h^{-1} (Conley et al. 1988; Nürnberg 1991) and appear to be controlled by turbulence and dilution in the overlying waters (Sundby et al. 1992) and uptake by algal cells (DePinto et al. 1981). Twinch and Peters (1984) observed that an equilibrium was maintained for P between aerobic sediments and water. P was released from the sediments when the concentration of SRP in the water was <0.15 μM P and was taken up by the sediments when the SRP concentration was >0.15 μM P. In Lake Michigan, the concentration of SRP was always ≪0.15 μM P. The average release rate we calculated is consistent with those measured in experimental systems where either a biological sink was incorporated in the experiment (DePinto et al. 1981) or the water over the sediments was continually replaced (Twinch and Peters 1984).

During spring mixing, P release is enhanced

by sediment resuspension which provides an "intimate coupling" (Eadie et al. 1984) between recent sediments and the water. Under these conditions, the flux of P to the lake water would be dependent on the geochemical "production" of phosphate in the sediment pore water, as described by Sundby et al. (1992). This, in turn, would be influenced by the degree to which the chemical equilibrium in the overlying water is displaced by the consumption of P by the biota.

Although there is no doubt that a significant proportion of the P in sediments is associated with a reducible Fe/Mn fraction (Eadie et al. 1984; Sundby et al. 1992), the concentration of SRP in Lake Michigan water is lower by two orders of magnitude than that expected to be in equilibrium with ferric phosphate (Stumm and Morgan 1981). The average SRP concentration observed in Lake Michigan, 0.02 μM, is consistent with the sum of the concentrations of soluble phosphate species calculated to be in equilibrium with hydroxyapatite and lake water using an ion-association (solubility) product

$$K_{IAP} = [Ca]^{10}[PO_4{}^{3-}]^6[OH^-]^2 = 10^{-115}.$$

This calculation was made with the geochemical model PHREEQE (Fleming and Plummer 1983) using ambient Lake Michigan water-quality values (pH = 8.2, [Ca] = 870 μM, and [total alkalinity] = 2.2 meq liter^{-1}). The K_{IAP} of 10^{-115} is within the range of values calculated for hydroxyapatite in natural sediments (10^{-100} to 10^{-122}) (Löfgren and Ryding 1985) and is very close to the 10^{-114} value reported for pure apatite by Stumm and Morgan (1981).

The relatively constant concentration of SRP that appears to have existed in Lake Michigan for at least the last 20 yr (Rousar 1973) supports the hypothesis that the concentration of phosphate in the oxidized surficial sediments and overlying water is controlled by a Ca-mediated chemical equilibrium. We further hypothesize that the flux of P from the sediments to the water is mediated by the displacement of this chemical equilibrium through the sequestering of P by the primary producers. This biogeochemical process is reflected in the observed increases in TP, Chl *a*, and org-N and decreases in NO_3^- and soluble Si in the lake during spring mixing.

Confirmation of the magnitude of the P demand by primary producers can be gained by comparing the ratio of org-N to TP in this and other studies. Given an org-N of 13 μM and the TP concentration of 0.27 μM we observed at the end of the spring bloom, the N : P ratio is 49. Estimates of the N : P ratio calculated from the lakewide data of Rockwell et al. (1989) for spring 1983–1985 range between 36 and 53, bracketing the ratio we calculated.

A similar conclusion regarding P demand can be drawn from an examination of Si utilization in Lake Michigan in spring. Schelske et al. (1986) assumed that the P available for uptake by diatoms was 0.25 μmol P liter^{-1} and that this would support the utilization of 18.5 μmol Si liter^{-1}. These values yield a Si : P ratio of 74. In comparison, our data show an increase in mass of TP during spring of 0.27 μmol P liter^{-1} and a measured Si utilization of 18.0 (23.0–5.0) μmol Si liter^{-1}, yielding a Si : P ratio of 67.

The similarity of the N : P and Si : P ratios calculated from data presented here and derived from other studies (Rockwell et al. 1989; Schelske et al. 1986) further substantiates the real increase in the mass of P we observed in spring. These observations, when compared to the springtime decrease in NO_3^- and Si observed by Rousar (1973), suggest that spring primary production and, therefore, the demand for P in Lake Michigan has remained essentially constant over the past 20 yr.

The kinetics for the production of primary biomass, as measured by Chl *a* and the conversion of $PO_4{}^{3-}$ to TP and of NO_3^- to org-N during spring mixing for the 3 yr of this study are illustrated in Fig. 3. The doubling time for each of these processes is ~40 d. It should be noted that the change in concentrations, particularly for TP and org-N, is most pronounced during the 40 d just before stratification. Schelske et al. (1986) concluded from laboratory experiments that Si would be depleted in the waters of Lake Michigan over a period of 39 d during the spring diatom bloom, based on their measured uptake rate of 0.6 μmol Si liter^{-1} d^{-1}, maintaining a soluble P concentration of 0.16 μM. The average rates of Si and P utilization observed in our study, calculated by a method similar to that used by Schelske et al. (1986), are 0.14 μmol Si liter^{-1} d^{-1} and 0.0023 μmol P liter^{-1} d^{-1}. Our value for the Si uptake rate is lower than that calculated by
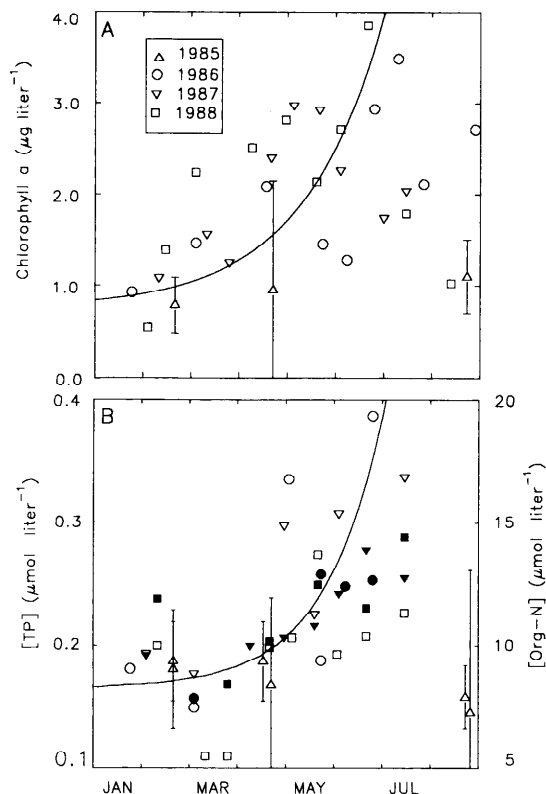
Fig. 3. Kinetics for the production of primary biomass (Chl *a*, A) and the conversion of PO_4^{3-} to TP and of NO_3^- to org-N (B) during spring mixing. For panel B, open symbols represent total P and solid symbols represent org-N. The line drawn through the data is the log-normal best fit for all three variables vs. time [$Y = a + b \exp(0.017t)$, where for Chl *a*, $a = 0.3$, $b = 0.25$; for org-N, $a = 7.5$, $b = 0.15$; and for TP, $a = 0.15$, $b = 0.006$]. The 1985 data are from Rockwell et al. (1989). The bars on the 1985 data indicate the range of concentrations observed throughout the lake. There was no sampling during the period of maximum algal biomass in 1985, which illustrates the importance of frequent sampling to discern important, short-lived seasonal events.

Schelske et al. (1986). This would be expected because the concentration of SRP in lake water is substantially lower (0.02 μM) than the concentration of soluble P (0.16 μM) used in their nutrient enrichment studies.

In discussing the stages of Si limitation in the Great Lakes based on external P loading, Schelske et al. (1986) noted that the most severe stage of Si depletion can occur only when P supplies are great enough to produce water-column Si depletion before the lake is stratified thermally. According to this definition, the Si

utilization observed here, and that reported for 1970 and 1971 by Rousar (1973), could have occurred only if the supply of P was great enough to sustain the observed diatom growth. Because no external sources of P can be identified to achieve a mass balance and there is insufficient P in the water column to account for the deficit, the internal reservoir of P in the sediments must supply the needed P.

In the broad holistic sense, we must now ask if P is "the" factor that limits primary production in Lake Michigan. The addition of P to experimental enclosures of Lake Michigan water, isolated from the sediments, has been shown to stimulate algal growth (Schelske et al. 1986). However, the data presented here suggest that P per se cannot be the overall limiting factor when the lake is unstratified, provided that reservoirs of biologically available P exist within the sediments.

The real limits to spring primary production in Lake Michigan are twofold. First, meteorological variables, which influence wind-driven vertical mixing and solar irradiance, set basic physical limits on the system. Wind mixing is important in that it is the driving force that couples the sediments to the water column and transports nutrients to the euphotic zone. Variable surface irradiance, together with vertical mixing, is also important in determining the light regime to which algal cells are exposed as they mix though the water column. Furthermore, it is these physical variables that determine the onset of stratification, which may isolate deep reservoirs of nutrients from the euphotic zone and result in the termination of the spring bloom. The interannual variability of meteorological conditions over the lake has been shown to influence spring production by 40%, either as a result of reduced mixing under extensive ice cover (Scavia et al. 1986) or changing the onset of summer stratification (Brooks and Torke 1977).

Second, the biogeochemical processes that influence nutrient fluxes between the sediments and water are critical factors regulating the productivity of Lake Michigan. These flux rates would appear to set the upper limits for the rate of new primary production during spring, once light is no longer limiting. The size of the phosphorus pool within the lake itself, coupled with external loading, biogeochemical nutrient fluxes to and from the sed-

iments, and climatic variables will determine the long-term productivity of Lake Michigan.

The ecological resistance to change and the resiliency with which an ecosystem recovers, once displaced, are integrally linked to the basic biogeochemical processes discussed above. Carpenter et al. (1992) noted that ecological theory predicts increased resistance to change with increased internal compartments of nutrients which, in the case of Lake Michigan, would include P in the sediments. The integration of these concepts into management paradigms for the Great Lakes will be critical in determining their ultimate success. Future research and management programs on these lakes and other water bodies must take account of the internal biogeochemical cycling of nutrients and the importance of climate variability in determining overall productivity. Remediation of eutrophication in the Great Lakes by reduction of external P loading will be slow in the near-term, as a result of the mass of P remaining in the sediment mixed layer, but should eventually reduce the inventory of P in the sediments that has been deposited over many years. Long-term research and monitoring programs must be cognizant of the dynamic nature of the lakes in spring and recognize the significance of the climatically coupled biogeochemical processes that determine the overall productivity of aquatic ecosystems.

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Thermal structure of lakes varying in size and water clarity

Abstract — The epilimnion depth of lakes is related both to lake size, which affects wind-induced mixing, and to water clarity, which affects the depth over which solar radiation heats the water. Here we attempt to isolate the relative importance of these two variables by examining lakes that have changed in water clarity with time (between years), by examining nearby lakes of comparable size, and by partitioning a large number of lakes into subsets with a restricted range in size or Secchi depth. Overall, results indicate that both lake size and water clarity are important determinants of epilimnion depth, but the absolute effect (indicated by slope) of Secchi depth is approximately constant in small (<12.5 km^2) as well as large lakes and the Laurentian Great Lakes, while its relative importance (indicated by r^2) appears to be restricted to the small lakes.

Thermal structure affects virtually all biological, chemical, and physical processes in lakes, including primary and secondary production, nutrient regeneration, oxygen depletion, and water movement (e.g. Schindler 1971; Cornett and Rigler 1980; Quay et al. 1980; Gliwicz 1980; Mazumder et al. 1990*a*). It is determined by extrinsic features of the lake, such as inflows and weather, through their effect on the input of heat and physical mixing.

It is also determined by intrinsic factors: basin morphometry and water clarity. Water clarity is particularly interesting from a biological viewpoint, because in most lakes water clarity is largely determined by the number and kinds of planktonic organisms. Hence, plankton communities have the potential to affect their microclimate (Mazumder 1990) as do terrestrial plant communities (Lowry 1969).

Many of the empirical studies dealing with thermal structure of lakes consider mainly the influences of morphometric characteristics such as surface area, mean depth, and volume (Gorham 1964; Schindler 1971; Geller 1992), degree of exposure or shelteredness of lakes (Hutchinson 1957), and fetch—the longest axis of a lake uninterrupted from wind (Shuter et al. 1983; Patalas 1984; Hanna 1990). These studies, therefore, suggest that wind-induced transport of heat to deeper strata determines the depths of the epilimnion and thermocline and retention of heat by the water column (Hutchinson 1957; Wetzel 1975). The influence of water clarity and associated direct solar absorption on the thermal structure has been assumed less important. However, many mechanistic models simulate the thermal structure of lakes and oceans from underwater light penetration and windspeed (e.g. Spigel and Imberger 1980; Imberger and Patterson 1981; Simpson and Dickey 1981), and these models are often very sensitive to the way optical attenuance is modeled (Lewis et al. 1983). Krauss and Turner (1967) observed that the effects of radiation are likely to be important even for models of the oceans.

Although it has always been recognized that water clarity is important in influencing the heating of the water column and associated