

Dynamics of Lake Michigan Phytoplankton: Recent Changes in Surface and Deep Communities¹

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Lake Michigan phytoplankton dynamics were studied from the end of spring isothermal mixing (May) through midstratification (July–August) in 1982–84. Phytoplankton composition shifted from a diatom-dominated community (75% of phytoplankton carbon) during May to a phytoflagellate-dominated community (71% of phytoplankton carbon) during July–August. This summer phytoflagellate dominance in the 1980s is distinctly different from the summer blue-green and green algae dominance in the 1970s. Foodweb interactions caused by a changing zooplankton composition and nutrient supply changes were two possible causes. A deep chlorophyll layer (DCL) developed after the onset of thermal stratification. The DCL initially developed in the 15–30 m region and deepened to 25–50 m in July and the 40–70 m region in August. The DCL in 1982–84 was larger in size and located deeper in the water column than those reported from the 1970s. This difference was related to increases in light transparency found in the 1980s that were a result of increased zooplankton grazing pressure.

La dynamique du phytoplancton du lac Michigan a été étudiée de la fin de la période de mélange isotherme de printemps (mai) à celle de la mi-stratification (juillet–août), ceci de 1982 à 1984. La composition du phytoplancton est passée d'une communauté dominée par les diatomées (75 % du carbone phytoplanctonique), en mai, à une communauté dominée par les phytoflagellés (71 % du carbone phytoplanctonique), en juillet–août. Cette dominance d'été des phytoflagellés notée au cours des années 1980 diffère de façon marquée de la dominance des algues bleu-vert et vertes notée au cours des années 1970. Ce phénomène pourrait s'expliquer par des interactions au sein du réseau alimentaire ayant pour cause une modification de la composition zooplanctonique et par une modification de l'apport en matières nutritives. Une strate chlorophyllienne profonde apparaissait après le début de la stratification thermique. Cette strate, tout d'abord apparue dans la zone des 15–30 m, s'est déplacée vers celle des 25–50 m en juillet et celle des 40–70 m en août. La strate notée en 1982–1984 était plus importante et située plus profondément que celle signalée au cours des années 1970. Cet écart est lié à l'augmentation de la transparence notée au cours des années 1980 suite à une augmentation du broutage zooplanctonique.

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With the establishment of the seasonal thermocline each year, two phytoplankton communities are established in Lake Michigan. The surface, or epilimnetic, community exhibits qualitative and quantitative changes during the transition from spring mixing period through midstratification (Parker et al. 1977; Bartone and Scheelske 1982; Stoermer 1983). In the past, phytoplankton composition has changed seasonally from spring diatom dominance to summer blue-green and green algae dominance. During midsummer, blue-green and green algae constituted approximately 50% of total phytoplankton biomass. The second community that develops during thermal stratification is the subthermocline community or the deep chlorophyll layer (DCL). The DCL is a broad band of relatively high chlorophyll concentrations that contains most of the water column chloro-

phyll (Brooks and Torke 1977) and is responsible for a large portion of primary production (Moll et al. 1984; Fahnenstiel and Scavia 1987). In the past, the DCL typically was located between 15 and 30 m (Brooks and Torke 1977; Moll et al. 1984).

Lake Michigan has undergone both gradual and abrupt changes since the 1970s. Since 1975, total phosphorus concentration during winter–spring isothermy has decreased and the depth of summer light penetration (Secchi depth, transmissivity, PAR extinction) has increased. Abrupt increases in summer transparency have been noted after 1982 (Scavia et al. 1986). Alewife, the previously dominant planktivorous fish, has decreased since the early 1970s and, in 1983–84, were present in the lowest levels observed since their rise to dominance (Wells 1985). Zooplankton total biomass in offshore waters has not changed dramatically during the period 1975–84; however, an abrupt change in summer species composition

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occurred between 1982 and 1983 (Scavia et al. 1986). The previously dominant calanoid copepods were replaced first by *Daphnia pulicaria* (1983) and then by a complex of three daphnid species (1984, 1985) (Scavia et al. 1986; Evans and Jude 1986; D. Scavia, unpubl. data). Phytoplankton photosynthetic parameters (P_{max} and assimilation number) have not changed since the 1970s, but water column production was difficult to compare (Fahnenstiel and Scavia 1987). It has been suggested that abrupt changes in summer zooplankton species composition and water clarity after 1982 are a result of relaxed zooplanktivory due to decreased alewife abundance (Scavia et al. 1986). In this paper we examine Lake Michigan's 1982–84 surface and deep phytoplankton communities and compare them with those reported from the 1970s, with special reference to the potential cascade of ecosystem changes from fish dynamics to phytoplankton species composition and vertical structure.

Methods

An offshore station was sampled 20 times between late spring (May) and the period of stratification (July–August) in 1982–84 (Fahnenstiel and Scavia 1987). Temperature, incident and underwater irradiation, chlorophyll, phytoplankton carbon concentrations, and primary production were determined as described in Fahnenstiel and Scavia (1987).

Sediment traps similar to those described by Eadie et al. (1984) were placed at the base of the epilimnion in 1983 and also at three deeper depths in 1984. The depths of deployment in 1984 varied from 10 to 50 m in relationship to the depth of the DCL. The 1983 traps were free-floating, while 1984 traps were moored. One set of four free-floating traps was suspended in a 1-m² array below a window-shade drogue which was attached at its top to a satellite-tracked buoy (Pickett et al. 1983). All traps were 20 cm in diameter with a height to diameter ratio of 5:1 and had Lugol's poisoned collection bottles. Phytoplankton sedimentation flux rates were determined from microscopic counts of subsamples from the collection bottles and conversion to phytoplankton carbon. Phytoplankton sinking rates were estimated by dividing the flux rate of carbon into the trap (F , milligrams per square metre per day) by phytoplankton concentration in the water above the trap (C , milligrams carbon per cubic metre). Sedimentation exponential loss rates (per day) were calculated with the following equation:

$$L = \ln \left(1 + \frac{F}{C \cdot Z} \right)$$

where Z = thickness of the layer (metres).

Results

Surface Phytoplankton Dynamics

The period of spring isothermal mixing was sampled in May of all three years. Isothermal temperatures ranged between 3.3°C on 21 May 1984 and 4.5°C on 20 May 1983. During this mixing period, phytoplankton carbon and chlorophyll were uniform vertically (see fig. 1 in Fahnenstiel and Scavia 1987). Diatoms dominated during this period comprising, on average, 75% of total phytoplankton carbon (Fig. 1). The dominant diatoms included *Melosira islandica*, *Tabellaria flocculosa* v. *linearis*, and *Melosira italica* ssp. *subarctica* with lesser amounts of *Asterionella formosa* and *Fragilaria crotonensis*.

Thermal stratification was established in June of all three years. As epilimnetic temperatures and water column stability increased during thermal stratification, epilimnetic chlorophyll and phytoplankton carbon concentrations decreased (Fig. 2). The period of thermal stratification was divided into two periods, based on epilimnetic temperatures (Fahnenstiel and Scavia 1987).

The decrease in epilimnetic phytoplankton carbon and chlorophyll during thermal stratification was primarily the result of decreased diatom abundance (Fig. 1). From the onset of thermal stratification to midthermal stratification, epilimnetic diatom carbon exhibited a dramatic decrease. During this same period there was also a shift in dominance within the diatom community. During early stratification, *Tabellaria* spp. and *Melosira islandica* usually co-dominated, and as thermal stratification progressed, *Fragilaria crotonensis* became the main diatom.

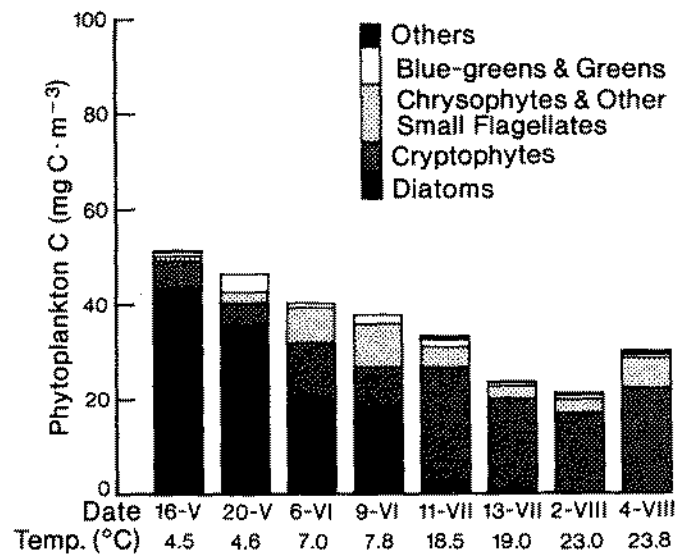
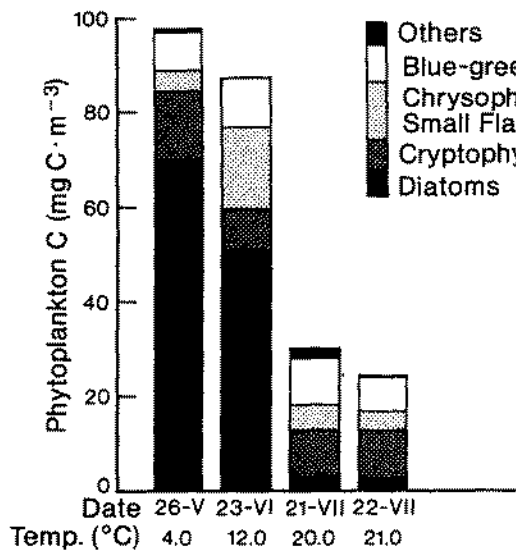
Phytoflagellates dominated the nondiatom fraction and generally exhibited maximum abundance during thermal stratification (Fig. 1). The dominant phytoflagellates during midstratification were *Cryptomonas* spp. and *Rhodomonas minuta*. Blue-green and green algae were significant contributors to midstratification phytoplankton carbon only during 1982 when they comprised approximately 32% of the total. During midstratification in 1983 and 1984, blue-greens and greens comprised, on average, 3–4% of phytoplankton carbon. The dominant contributor of blue-green and green algae biomass was *Anabaena flos-aquae*.

The large decrease in epilimnetic diatom abundance during early thermal stratification was due to sedimentation losses. Diatoms accounted for 90–100% of phytoplankton carbon found in sediment traps placed at the bottom of the mixed layer in June of 1983 and 1984. Diatom loss rates from the epilimnion for the periods 6–10 June 1983 and 4–18 June 1984 were 0.17 and 0.07 · d⁻¹, respectively. These same sedimentation losses, calculated for the entire phytoplankton assemblage, were 0.12 · d⁻¹ for 1983 and 0.04 · d⁻¹ for 1984.

During the midstratification period the importance of sedimentation as a loss for epilimnetic phytoplankton populations decreased, paralleling the decrease in diatom abundance. Diatoms accounted for 23–62% of phytoplankton carbon found in the sediment traps yet only 0.03–28.00% of the phytoplankton carbon in the epilimnion. Epilimnetic sedimentation loss rates for the periods 11–14 July 1983 and 6–10 August 1983 were 0.0015 and 0.0007 · d⁻¹, respectively. In 1984, a similar low sedimentation loss rate, 0.0013 · d⁻¹, was found for 24 July to 22 August.

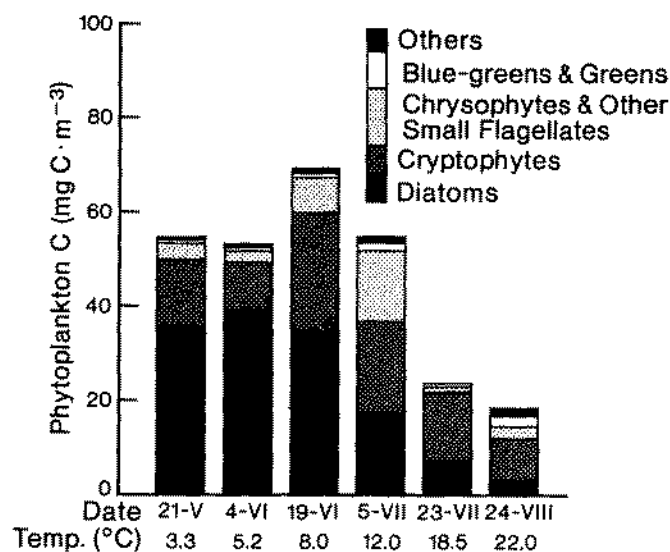
Deep Phytoplankton Dynamics

Pronounced deep chlorophyll and phytoplankton carbon maxima were found throughout the period of thermal stratification (See fig. 1 in Fahnenstiel and Scavia 1987). These deep chlorophyll and carbon maxima were found between 15 and 30 m during early stratification and deepened to 25–70 m in midstratification. Chlorophyll concentrations in this DCL were from 1.2 to 2.7 times (mean = 1.8 times) the epilimnetic concentrations during early stratification and from 2.9 to 10.3 times (mean = 5.7 times) the epilimnetic concentrations during midstratification. Average deep carbon concentrations never exceeded 4 times the epilimnetic concentrations and averaged 1.3 times in early stratification and 2.6 times in midstratification.



a

b



c

FIG. 1. Phytoplankton composition of surface mixing layer (epilimnion) for various dates and surface mixing layer temperatures in (a) 1982, (b) 1983, and (c) 1984.

Discussion

Surface Dynamics

Historically, surface phytoplankton populations in Lake Michigan have received more attention than deep populations. Investigations of net phytoplankton began as early as 1925 (Eddy 1927). During the late 1960s and early 1970s, Lake Michigan was the focus of studies designed to determine the causes of eutrophication (Schelske and Stoermer 1972), and it was during this time that a shift in the summer (July–

September) phytoplankton assemblage was noted. Prior to the mid-1960s, diatoms were the dominant summer flora, but by the late 1960s and early 1970s, blue-green and green algae were dominant (Schelske and Stoermer 1972). These blue-green and green algae were dominant throughout the summers of the 1970s (Schelske and Stoermer 1972; Rockwell et al. 1980; Bartone and Schelske 1982; S. J. Tarapchak, GLERL/NOAA, pers. comm.). During late July and August 1976–78, blue-green and green algae constituted well over 50% of total phytoplankton biomass and carbon (Bartone and Schelske 1982; S. J. Tarapchak, pers. comm.).

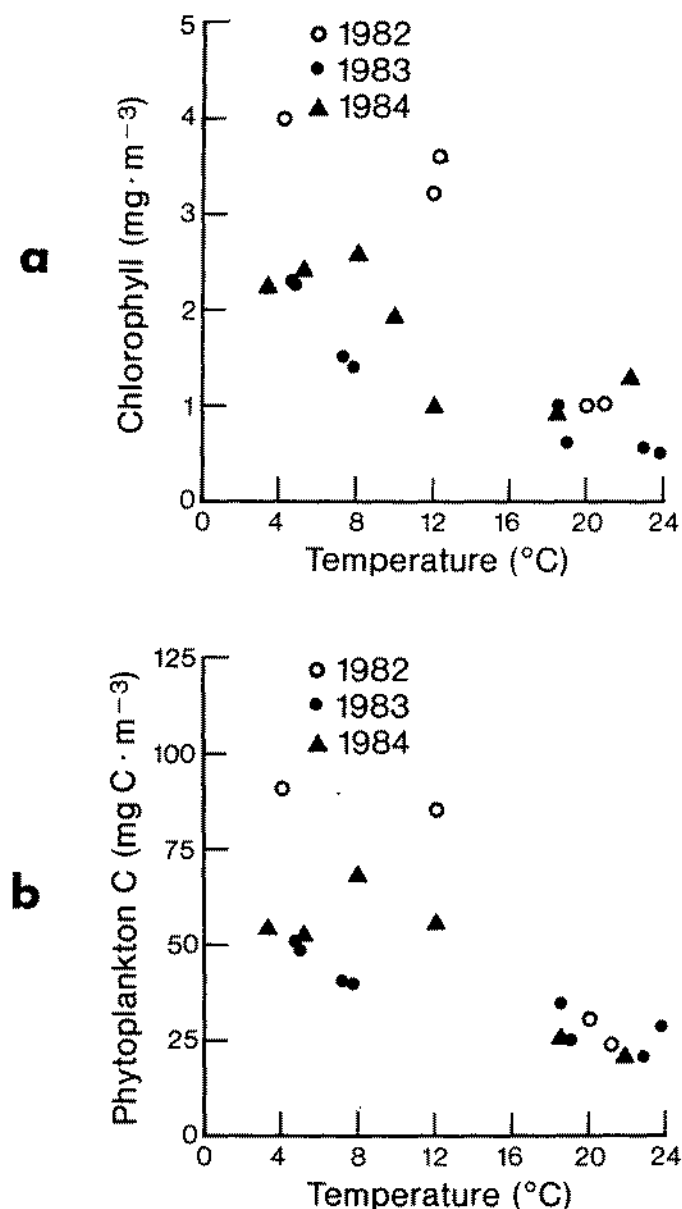


FIG. 2. Average surface mixing layer (epilimnetic) (a) chlorophyll and (b) phytoplankton carbon concentrations plotted against surface mixing layer temperature.

Here, we document a further shift in the summer epilimnetic phytoplankton community. During midstratification, blue-green and green algae constituted 32% (1982) and less than 4% (1983 and 1984) of phytoplankton biomass (Fig. 2), while phytoflagellates constituted 55% (1982), 91% (1983), and 68% (1984). Blue-green and green algae constituted less than 9% of phytoplankton carbon in September 1983 and 1984. Similarly, in July–August 1985, blue-green and green algae constituted only 15% of phytoplankton carbon whereas phytoflagellates accounted for 76% (D. Scavia, unpubl. data). It is clear that the summer community has shifted from blue-green and green dominance in the 1970s to phytoflagellate dominance in the 1980s.

Differences in phytoplankton species composition between the 1970s and 1980s can be attributed to the large-scale ecological changes between those two sets of years. The shift in phytoplankton composition was documented for at least three

years in both the 1970s and 1980s, and it is clear that year-to-year variation is smaller than the documented changes before and after 1982. Thermal conditions, a second potentially important factor, were quite different in 1983 compared with 1984 (Scavia and Fahnenstiel 1987) whereas conditions in 1984 were similar to those in 1970 and 1971 (Fee 1972; Scavia and Fahnenstiel 1987). It is not likely that temperature had an important influence on summer phytoplankton species composition.

At least two factors are likely to have contributed to this recent phytoplankton change: nutrient supply and foodweb interactions. Nutrient supply ratios are important factors controlling the relative abundance of phytoplankton (Tilman et al. 1982), and given the documented changes in phosphorus concentration within Lake Michigan over the past 10 yr (Scavia et al. 1986), it is probable that nutrient supply ratios also have changed. Very little is known about nutrient requirements of cryptophytes and therefore, it is difficult to suggest what change in nutrient ratio would be needed to create a competitive advantage.

Another important factor in regulating phytoplankton composition is foodweb interactions (Carpenter et al. 1985). Major zooplankton shifts occurred in Lake Michigan (Evans and Jude 1986) in the 1980s and these shifts could have influenced the composition of the phytoplankton community. Prior to 1983, the summer zooplankton community was dominated by calanoid copepods that probably would not effectively graze blue-green filaments like *Anabaena flos-aquae* (Richman and Dodson 1983; Knisely and Geller 1986; H. Vanderploeg GLERL/NOAA pers. comm). The summer zooplankton community exhibited an abrupt shift in 1983 when cladocerans, particularly *Daphnia pulex*, became dominant (Scavia et al. 1986). Cladocerans are less selective feeders and probably would graze many of the blue-green and green algae that were abundant (Richman and Dodson 1983; Knisely and Geller 1986). It is possible that the zooplankton shift could have reduced the ability of blue-green and green algae to compete with phytoflagellates by increasing blue-green loss rates.

The timing of the shift from the blue-green and green dominated summer assemblage to the phytoflagellate community may lend some insight into the role of nutrient versus zooplankton control. Gradual compositional shifts would reflect the gradual change in nutrient ratios implied by reduced phosphorus concentrations; however, more abrupt shifts around 1982 and 1983 would reflect the major changes in the zooplankton assemblage. Although we have little data to evaluate the timing of the shift, the composition in 1982 was distinctly different from that during 1983–85, suggesting that the changing zooplankton composition may be at least partially responsible. In July 1982, blue-green and green algae accounted for 32% of phytoplankton carbon, a value significantly higher than 1983–85 levels. If past trends of maximum blue-green and green dominance in late August (Bartone and Schelske 1982) persisted in 1982, we would have expected blue-green and green dominance to increase from the July levels and reach levels comparable with the 1970s by August. If this is true, then a major shift occurred between 1982 and 1983. However, if past trends of blue-green and green dynamics did not persist, and, in 1982, blue-green and green dominance was limited to 32% that we observed in July, then 1982 may have been one year in a more gradual trend of decreasing abundance of blue-green and green algae. More data from the late 1970s and early 1980s are needed to deter-

mine the timing of the shift.

The shift from a diatom-dominated spring community to a nondiatom summer community has been a consistent feature of Lake Michigan for the past 15 yr and has been linked to decreasing supplies of silica (Schelske and Stoermer 1972; Schelske 1985). The observed decrease in SiO_2 concentrations from 15 to 20 μM during spring mixing to $\leq 5 \mu\text{M}$ during midstratification in 1983–84 (D. Scavia and G. Fahnenstiel, unpubl. data) supports this interpretation. Furthermore, during this same period, we found a significant reduction (20–80%) in diatom ^{14}C uptake and growth whereas nondiatoms did not exhibit a decrease in ^{14}C uptake or growth (G. Fahnenstiel, unpubl. data). The largest reductions in ^{14}C uptake and growth were found by spring diatoms such as *Melosira islandica* and *Melosira italica* ssp. *subarctica*.

There can be little doubt that silica limitation is important to the diatom demise, but at least one additional factor is also important. Diatoms, in contrast with other phytoplankton groups, suffer relatively high sedimentation losses during early stratification, 0.17 and 0.07 d^{-1} in 1983 and 1984, respectively. This loss is important in removing diatoms and associated nutrients from the epilimnion. Total phosphorus concentrations decrease by 35–70% from spring mixing to midstratification (D. Scavia and G. Fahnenstiel, unpubl. data). There is also a link between growth and sedimentation rate, as the diatoms that exhibit the largest decreases in growth rate during this period are the same ones that are overrepresented in the sediment traps, i.e. *Melosira islandica*. Thus, the importance of sinking as a loss for spring diatoms appears to be linked to decreasing silica supplies. The interaction between nutritional status and sinking rate has been recognized previously (Titman and Kilham 1976; Walsby and Reynolds 1980).

Deep Chlorophyll Layer

During thermal stratification the dominant feature of the vertical phytoplankton profile is the DCL (Brooks and Torke 1977; Liedle 1978; Schelske et al. 1983; Moll et al. 1984). The DCL represents a relatively broad band of increased chlorophyll where concentrations are often 5–10 times the surface concentrations. Although a persistent feature during thermal stratification, the DCL in 1982 to 1984 was deeper and somewhat broader than those previously described. In the 1970s the DCL formed initially in the 10–30 m region and then deepened to 15–50 m during midthermal stratification (Brooks and Torke 1977; Liedle 1978; Moll et al. 1984). Maximum chlorophyll concentrations of 3–9 $\text{mg} \cdot \text{m}^{-3}$ were found between 20 and 30 m, and chlorophyll concentrations generally decreased dramatically below 40 m. No previous investigator has reported maximum chlorophyll concentrations below 40 m.

After the onset of thermal stratification in 1982–84, chlorophyll concentrations reached a maximum at 15–30 m, similar to the results of previous investigations (see fig. 1 in Fahnenstiel and Scavia 1987). Chlorophyll concentrations in the DCL were approximately 1.75 times the epilimnetic concentrations. However, as thermal stratification progressed, the layer widened and deepened into a broad band of relatively similar chlorophyll concentrations between 25 and 50 m (see fig. 1 in Fahnenstiel and Scavia 1987) and was distinctly different from the DCL in previous years. Integral subsurface chlorophyll concentrations were greater in 1982–84 than prior to 1980. Average subsurface chlorophyll within the region where chlo-

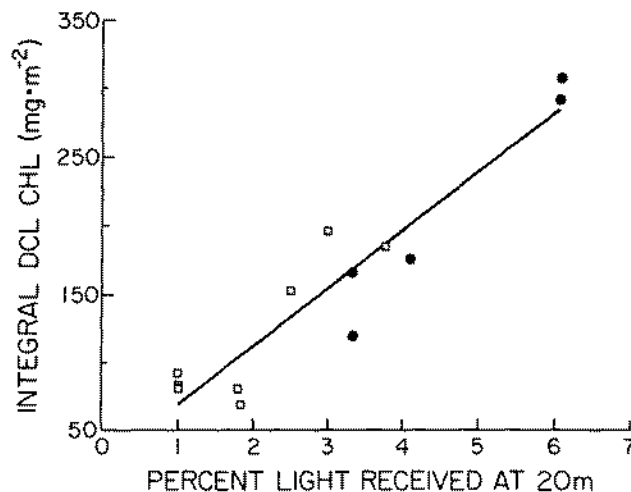


FIG. 3. Regression of integrated chlorophyll concentration within the July DCL and light received at 20 m, calculated from the extinction coefficient for data from 1975–84. Data from 1982–84 are indicated with solid circles. Open squares are from Liedle (1978) and Moll et al. (1984).

rophyll was ≥ 2 times the epilimnetic concentrations averaged 213 $\text{mg} \cdot \text{m}^{-2}$ in July 1982–84 and 142 $\text{mg} \cdot \text{m}^{-2}$ in July 1973–77 (Brooks and Torke 1977; Liedle 1978; Moll et al. 1984). Furthermore, maximum chlorophyll concentrations occasionally occurred as deep as 50 m in July 1982–84. The DCL deepened further during August, with maximum concentrations at or below 50 m. DCL chlorophyll concentrations in July and August 1982–84 were on average 5.7 times but occasionally exceeded 10 times the epilimnetic concentrations.

The recent changes in the Lake Michigan ecosystem have contributed to the deeper and larger DCL. Increased light penetration due to foodweb interactions appears to be a relatively recent event in Lake Michigan (Scavia et al. 1986). Midstratification (July–August) extinction coefficients in 1982–84 range from 0.12 to 0.17 m^{-1} (Scavia et al. 1986) whereas in the 1970s, midstratification extinction coefficients were 0.16–0.23 m^{-1} (Liedle 1978; Moll et al. 1984). With increased light penetration, the DCL could occupy a deeper position within the water column, provided other environmental factors were similar. Furthermore, data collected from 1975 to 1984 demonstrate a direct relationship between subsurface integrated chlorophyll concentrations and irradiance received at depth (Fig. 3). From a previous laboratory study (Fahnenstiel et al. 1984) it is clear that increased light can produce a larger DCL, provided loss rates remain the same. Thus, as light penetration increased in the 1980s, the DCL increased in size in direct proportion to the amount of light received.

In conclusion, we document two significant changes in Lake Michigan phytoplankton dynamics from the 1970s to 1980s. The midsummer epilimnetic phytoplankton community has shifted from the blue-green and green algae dominated community in the 1970s to a phytoflagellate-dominated community in the 1980s. Changing zooplankton community structure appears to be partially responsible for this difference; however, other factors may also be important. The DCL in the 1980s was larger and deeper than the DCL described previously for the 1970s. This difference was attributable to increased light penetration in the 1980s caused by increased epilimnetic zooplankton grazing pressure (Scavia et al. 1986).

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