

DYNAMICS OF LAKE MICHIGAN PHYTOPLANKTON: THE DEEP CHLOROPHYLL LAYER

Gary L. Fahnenstiel and Donald Scavia

Great Lakes Environmental Research Laboratory
National Oceanic and Atmospheric Administration
2205 Commonwealth Blvd.
Ann Arbor, Michigan 48105

ABSTRACT. *The dynamics of the Lake Michigan deep chlorophyll layer (DCL) were studied from the period of late spring isothermal mixing (May) through mid-stratification (July-August) in 1982-1984. After the onset of thermal stratification, the DCL developed in the 15-30 m region and deepened to 25-50 m in July and 40-70 m in August. Chlorophyll and phytoplankton carbon concentrations in the DCL averaged, respectively, 1.80X and 1.34X epilimnetic concentrations during early stratification (June). Those factors increased to 5.70X and 2.60X during mid-stratification. Although phytoplankton carbon concentrations within the DCL changed on average only 31% from May through July-August, phytoplankton species composition exhibited pronounced shifts. Measured phytoplankton growth, sedimentation, and zooplankton grazing rates suggest DCL formation was attributable to in situ growth and to a lesser extent to sedimentation and shade adaptation. By July, sedimentation resulted in a net loss from the DCL. With the deepening of the DCL during mid-stratification, the importance of in situ growth decreased while the importance shade adaptation increased. In situ growth was only important in the upper part of the DCL. Zooplankton grazing increased during mid-stratification and was at least partially responsible for phytoplankton concentrations decreases in the 20-50 m region.*

INTRODUCTION

With the establishment of the seasonal thermocline, a deep chlorophyll layer (DCL) develops in Lake Michigan (Brooks and Torke 1977, Fahnenstiel *et al.* 1984, Moll *et al.* 1984). The DCL occupies the region below the thermocline and is represented by a broad band of increased chlorophyll concentrations. Most of water column chlorophyll (Brooks and Torke 1977) and a large portion of the primary production (Fahnenstiel and Scavia 1987a) are found within the DCL. Phytoplankton composition in the DCL is somewhat similar to the spring composition (Brooks and Torke 1977, Moll *et al.* 1984); however, the quantitative and qualitative changes that occur within the DCL during thermal stratification are not well understood. In fact, while it is clear that surface phytoplankton biomass concentration decreases during thermal stratification (Bartone and Schelske 1982, Fahnenstiel and Scavia 1987b), no clear trend in phyto-

plankton biomass within the DCL has been established.

The factors that contribute to the formation and maintenance of the DCL also are not well known. The only process that has been measured is *in situ* growth (Moll *et al.* 1984), but its importance relative to other processes such as phytoplankton sedimentation, shade adaptation, and zooplankton grazing has not been established. These other processes may also be important in the establishment and maintenance of the DCL (Steele and Yentsch 1960, Kiefer *et al.* 1976, Longhurst 1976, Richardson *et al.* 1978).

The accumulation of chlorophyll in the DCL after the onset of thermal stratification may be from phytoplankton cells sinking from the epilimnion rather than from *in situ* growth within the layer. Diatoms dominate the spring phytoplankton assemblage (Parker *et al.* 1977, Bartone and Schelske 1982, Fahnenstiel and Scavia 1987b) and their abundance above the DCL decreases dramati-

cally after the onset of thermal stratification. Brooks and Torke (1977) and Moll *et al.* (1984) suggested that sinking could be important based on the similarity of phytoplankton composition within the DCL and the previous spring diatom maximum; however, no comparisons to *in situ* growth were made.

If shade adaptation is significant within the DCL, then increased chlorophyll concentrations within the DCL during mid-stratification (Brooks and Torke 1977) may not represent an actual increase in phytoplankton biomass. That is, increased chlorophyll:carbon ratios alone may be sufficient to produce the DCL (Kiefer *et al.* 1976). Previous results on the importance of shade adaptation are inconclusive. Moll *et al.* (1984) did not find evidence for increased chlorophyll:biovolume ratios within the DCL; however, shade adaptation was an important process contributing to the DCL in another study (Fahnenstiel *et al.* 1984).

In this paper we evaluate the relative importance of phytoplankton growth, sinking, shade adaptation, and zooplankton grazing to the dynamics of the Lake Michigan DCL from the onset of thermal stratification through mid-stratification.

METHODS

An offshore station (depth = 100 m), located 25 km from Grand Haven, Michigan, 43° 01' 11"N, 86° 36' 48"W, was sampled twenty times from 1982 through 1984. The sampling period was from late spring isothermal mixing (May) to mid-thermal stratification (July-August) of each year.

Temperature and incident and underwater irradiation were determined as described in Fahnenstiel and Scavia (1987a). Chlorophyll concentrations were determined fluorometrically on 90% acetone extracted samples (Strickland and Parsons 1972). Phytoplankton samples were preserved with Lugol's solution, settled (Crompton and Wetzel 1981) or filtered (Stoermer and Kreis 1980) onto slides, and counted. Biovolume for each species was calculated from estimates of cell shape and dimensions. These biovolume estimates were converted to carbon using the formulae of Strathman (1966). Separate conversions were used for diatoms and non-diatoms because of fundamental differences in the biovolume:carbon ratios (Sicko-Goad and Ladewski 1977). Primary production was measured with 24-h *in situ* ¹⁴C incubations (Fahnenstiel and Scavia 1987a). ¹⁴C uptake was

combined with phytoplankton carbon estimates to determine exponential growth rates.

Phytoplankton loss rates due to zooplankton grazing were determined by combining zooplankton clearance rates and zooplankton abundance estimates (Scavia *et al.* 1986, Scavia and Fahnenstiel 1987). Zooplankton abundance was determined by vertical net hauls of a 0.5-m diameter, 153- μ m closing plankton net through the depth region of interest. Animals were preserved in sugar-formalin after narcotization with club soda. Zooplankton dry weights were determined by converting abundance estimates with taxon-specific dry weight values from either published values for Lake Michigan (Hawkins and Evans 1979) or by weight measurements on the 1983 and 1984 samples (M.S. Evans, Great Lakes Research Division, Univ. Michigan, Ann Arbor, Michigan, and D. Scavia, unpubl. data).

Clearance rates were determined from grazing experiments modelled after those described by Lehman (1980) and Lehman and Sandgren (1985). Water pumped from depth through a high-speed, high capacity pump was passed through a 153- μ m mesh plankton net to remove animals before dispensing into a 1,000-L tank. Experimental animals were then collected from the water column by vertical net haul through the DCL. These animals were added to the tank at approximately natural densities. After filling, the tank was covered and shaded during transport to shore.

At shore, tank contents were mixed and siphoned into plastic pails for preparation. For "no-zooplankton" treatments (0X), siphoned water was passed through a 153- μ m Wisconsin-type plankton net to remove crustaceans. These animals were saved and added to unscreened water for the 2X treatment. Unscreened water was used for the 1X treatment and an appropriate volume of water was passed through a 153- μ m net to collect animals for the 4X treatment. Water and animals from the pails were gently poured into replicate 20-L clear, polycarbonate carboys which were capped with neoprene stoppers. To minimize differences in the effect of zooplankton-recycled nutrients at the different zooplankton abundances (Lehman 1980), carboys were spiked with PO₄, the limiting nutrient (Schelske 1979, Fahnenstiel and Scavia 1987a), to a final P concentration of 0.23 μ M. Carboys were then placed on rotating racks in water-cooled incubators and exposed to screened natural light and appropriate ambient temperatures. Incubation time was usually 24 hours but never longer than 36

hours. Samples, taken before and after incubation, were processed for chlorophyll as described above. At the end of the incubation and after chlorophyll sampling, animals were collected by pouring the entire contents of each 20-L carboy through a 153- μm net and preserved as described above.

If plots of specific algal growth rates versus zooplankton abundance in each carboy from this type of experiment (e.g., Fig. 4) are linear, then the slope of the plot is an estimate of the zooplankton weight-specific clearance rate, and the intercept is an estimate of algal intrinsic growth rate (Lehman 1980).

Sediment traps, similar to those described by Eadie *et al.* (1984) were placed at the base of the epilimnion and at three deeper depths in 1984 (Scavia and Fahnenstiel 1987). The depths of deployment in 1984 varied from 10 to 50 m to include the region of the DCL. Traps were deployed in the lake for periods of 4 to 29 days. All traps were 20 cm in diameter and had a height to diameter ratio of 5:1 and Lugol's poisoned collection bottles. Phytoplankton sedimentation flux was determined from microscopic counts of samples from the collection bottles and conversion to phytoplankton carbon. Phytoplankton sinking rate was calculated by dividing the carbon flux into the trap (F , $\text{mg C}\cdot\text{m}^{-2}$) by phytoplankton concentration in the water above the trap (C , $\text{mg C}\cdot\text{m}^{-3}$) and duration of deployment (T , days).

Sedimentation exponential net loss rate (d^{-1}) was calculated from fluxes into and out of the DCL with the following equation:

$$L = \frac{\ln \left(1 + \frac{NF}{A \cdot Z} \right)}{T}$$

where Z = thickness of the layer (m) and NF = the net flux to the DCL, and A = algal carbon concentration in the DCL, and T = time (days).

RESULTS

For the purpose of clarity, thermal stratification was divided into two periods, early and mid, based on epilimnetic temperature (Fahnenstiel and Scavia 1987a). Early stratification applies to the period (primarily June) when epilimnetic temperatures were less than 15°C , whereas mid stratification applies to the period (July-August) when epilimnetic temperatures were greater than 17°C . Also, the DCL is defined as the region where sub-

surface chlorophyll concentrations exceed 2.0X epilimnetic concentrations. This definition results in a DCL of approximately 30–50 m wide during mid-stratification. Because chlorophyll differences between surface and deep communities were not as pronounced during early stratification, the DCL during early stratification was defined as the region where chlorophyll concentrations exceed 1.5X epilimnetic concentrations.

During each year, the DCL developed in the 15–30 m region during early stratification and deepened to 25–70 m by mid-stratification (Fig. 1). Average chlorophyll concentrations within the DCL averaged 1.80X epilimnetic chlorophyll concentrations during early stratification and increased to an average of 5.70X epilimnetic concentrations during mid-stratification. Phytoplankton carbon concentration differences between the DCL and epilimnion were not as pronounced as chlorophyll differences. Average DCL carbon concentrations never exceeded 4X epilimnetic concentrations and averaged 1.3X epilimnetic concentrations in early stratification and 2.6X epilimnetic concentration in mid-stratification. These differences in phytoplankton carbon and chlorophyll can be seen in seasonal carbon:chlorophyll ratios for epilimnetic and DCL communities (Fig. 2). Phytoplankton carbon:chlorophyll ratios during mid-stratification averaged 36.8 mg C:mg Chl for the epilimnetic community and 16.7 mg C:mg Chl for the DCL community.

Although the DCL was very pronounced during thermal stratification, phytoplankton carbon concentrations within the DCL were not unlike average concentrations in that region during spring mixing (Fig. 3). For the 2-to 3-month period from isothermal mixing to mid-stratification, average phytoplankton carbon concentrations within DCL remained within 40% of spring mixing concentrations in all but one case, and coefficients of variations were 17.6% in 1982, 26.5% in 1983, and 9.7% in 1984. Maximum phytoplankton carbon concentrations within the DCL were higher than spring mixing concentrations in 1983 and 1984, but lower in 1982.

Phytoplankton species composition changed within the DCL as summer progressed. Diatoms constituted 67–72% of total phytoplankton carbon during early stratification and 48–58% during mid-stratification. More importantly, large shifts occurred within the diatom community. *Melosira islandica* constituted 31–53% of phytoplankton carbon during spring mixing but only 9–14% in

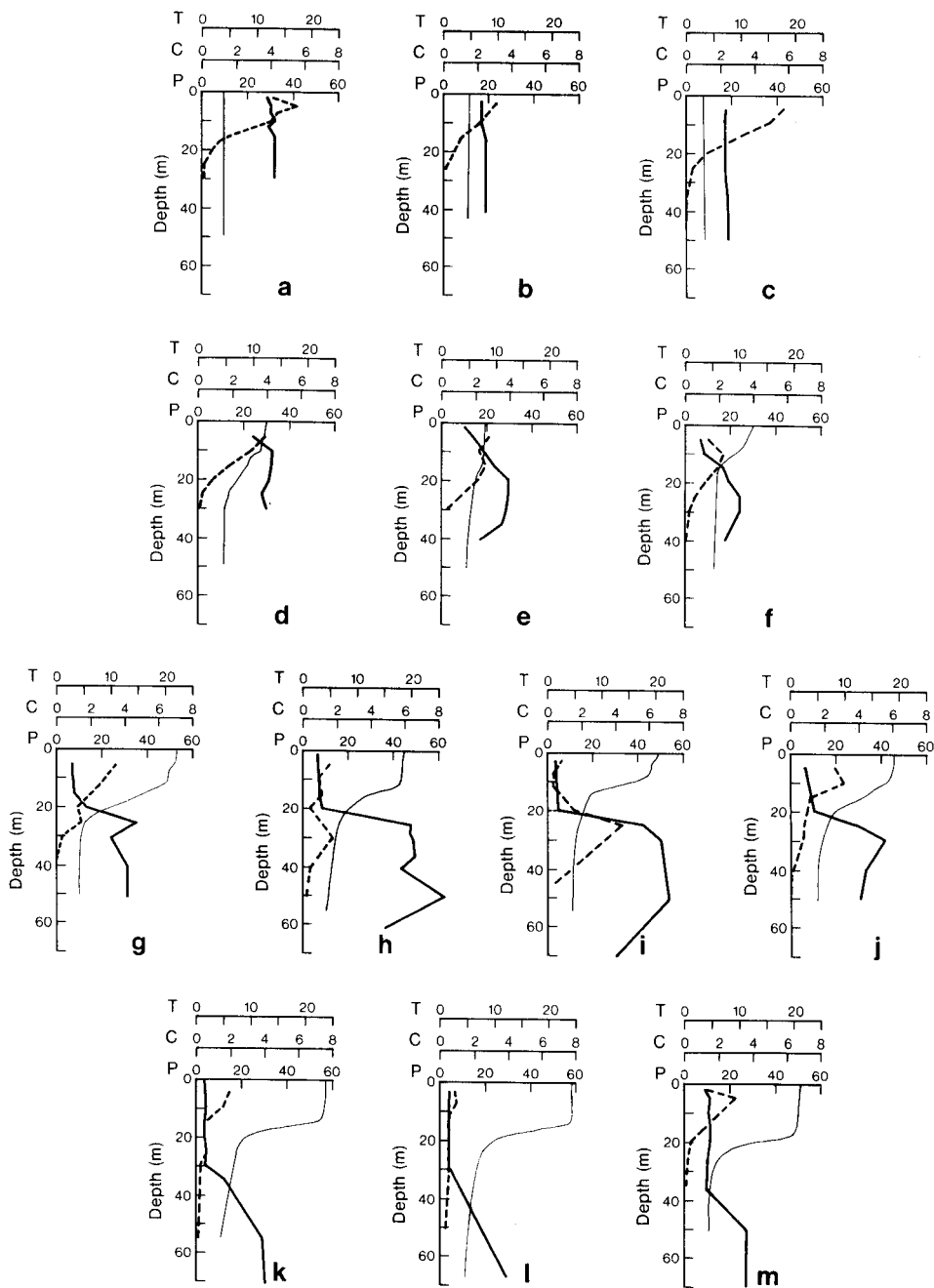


FIG. 1. Examples of temperature ($^{\circ}\text{C}$, —), chlorophyll ($\text{mg}\cdot\text{m}^{-3}$, —), and primary production ($\text{mg C}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$, ---) during spring isothermal mixing (a-c), early stratification (d-f), July mid stratification (g-j), and August mid stratification (k-m). a) 22 May 1982, b) 16 May 1983, c) 21 May 1984, d) 24 June 1982, e) 9 June 1983, f) 5 July 1984, g) 22 July 1982, h) 11 July 1983, i) 13 July 1983, j) 23 July 1984, k) 2 August 1983, l) 4 August 1983, and m) 23 August 1984. From Fahnenstiel and Scavia 1987a.

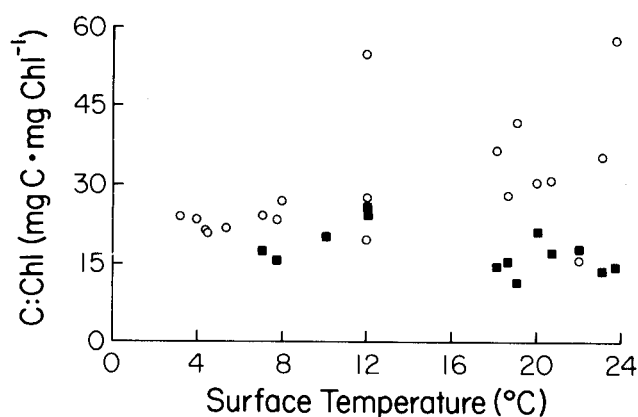


FIG. 2. Phytoplankton carbon: chlorophyll ratios of surface mixing-layer and DCL communities versus surface mixing-layer temperature. Surface temperature was used rather than calendar date because the timing of thermal stratification was different for the 3 years. DCL ratios are indicated by solid boxes and surface mixing-layer ratios are indicated by open circles.

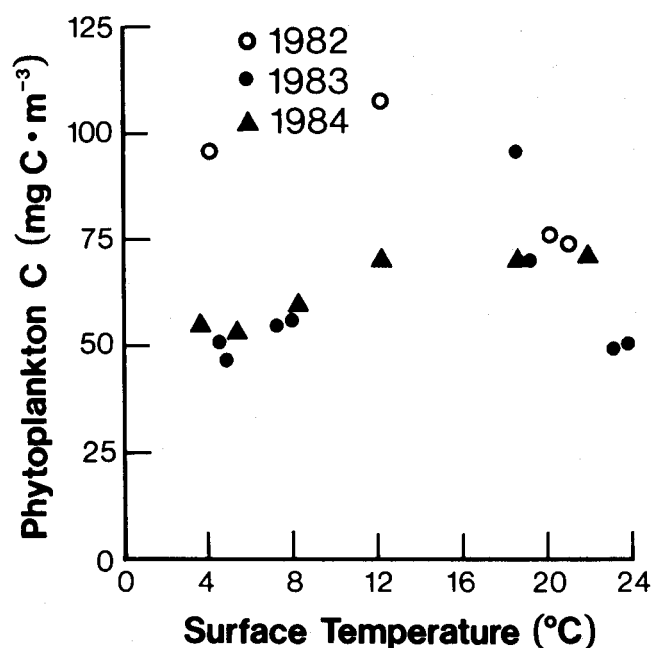


FIG. 3. Phytoplankton carbon concentration within DCL versus surface mixing-layer temperature. Surface temperature was used rather than calendar date because the timing of thermal stratification was different for the 3 years.

TABLE 1. Phytoplankton growth rates (d^{-1}) within the DCL determined from ^{14}C uptake and phytoplankton carbon concentrations.

Date	Depth (m)	Growth rate
9 June 1983	20, 25	0.23, 0.15
23 June 1982	17, 25	0.11, 0.05
25 June 1984	25	0.10
5 July 1984	15, 25	0.16, 0.05
11 July 1983	30, 40	0.13, 0.04
13 July 1983	25, 45	0.29, 0.05
21 July 1982	25, 30	0.10, 0.05
22 July 1982	25, 30	0.15, 0.03
23 July 1984	25, 30	0.11, 0.06
2 August 1983	35, 55	0.07, 0.02
4 August 1983	50	0.07
24 August 1984	35	0.02

July, whereas *Fragilaria crotonensis* accounted for only 4–6% of spring phytoplankton carbon but 17–37% in July. Blue-green filaments such as *Oscillatoria redekei* and *O. bornettii* were also abundant within the DCL. Blue-green filaments accounted for only 3% of spring phytoplankton carbon but 17% in July and at one depth in the July 1983 DCL accounted for 44%.

Two distinct phytoplankton assemblages existed within the broad July DCL. In the upper portion, 25–35 m, cosmopolitan diatoms such as *Fragilaria crotonensis*, *Asterionella formosa*, and *Tabellaria* spp. were abundant. Spring diatoms such as *Melosira islandica* were not abundant, accounting for only 1–4% of phytoplankton carbon. In the deeper portion of the DCL (40–60 m) the opposite conditions existed, with spring diatoms more abundant and cosmopolitan species less abundant. In the deep region of the DCL, *Melosira islandica* accounted for 17–29% of phytoplankton carbon.

The highest growth rates in the DCL were typically 0.1 to 0.3 d^{-1} in June and July and less than 0.1 d^{-1} in August (Table 1). In June, these growth rates were representative of most of the DCL whereas in July and August they represented only the upper part of the DCL. For example, while maximum growth rates in the DCL on 5 and 23 July 1984 were 0.16 and 0.11 d^{-1} , average growth rates in the DCL were only 0.055 and 0.035 d^{-1} .

Phytoplankton carbon sedimentation loss rates associated with the DCL were measured in 1984. For the period 25 June–5 July, mean sedimentation flux into the DCL, determined from two sediment

traps placed above the DCL, was $228 \text{ mg}\cdot\text{m}^{-2}$. This represents a mean sinking rate of $0.36 \text{ m}\cdot\text{d}^{-1}$. During the same period, sedimentation flux out of the DCL, determined from a trap at its base, was $94 \text{ mg}\cdot\text{m}^{-2}$. This represents a sinking rate of $0.14 \text{ m}\cdot\text{d}^{-1}$ for the DCL community. From these two flux estimates, sedimentation produced a net source of cells to the DCL at a rate of 0.010 d^{-1} . However, for the period 5–24 July, sedimentation resulted in a net loss. Sedimentation into the DCL was $86 \text{ mg}\cdot\text{m}^{-2}$, while flux out was $441 \text{ mg}\cdot\text{m}^{-2}$. These fluxes yield sinking rates for communities above and within the DCL of $0.10 \text{ m}\cdot\text{d}^{-1}$ and $0.35 \text{ m}\cdot\text{d}^{-1}$, respectively. The net loss of phytoplankton carbon from the DCL during this period was 0.009 d^{-1} .

Zooplankton grazing losses were also calculated in 1984 by combining clearance rate and abundance estimates. Zooplankton clearance rates, determined with DCL phytoplankton and zooplankton assemblages (15–40 m), were $2.91 \text{ mL}\cdot\mu\text{g}^{-1}\cdot\text{d}^{-1}$ for a night assemblage on 4 July, $1.87 \text{ mL}\cdot\mu\text{g}^{-1}\cdot\text{d}^{-1}$ for a day assemblage on 5 July, and $0.25 \text{ mL}\cdot\mu\text{g}^{-1}\cdot\text{d}^{-1}$ for a day assemblage on 23 July (Fig. 4). Zooplankton biomass within the DCL was relatively low in July but increased dramatically in August (Fig. 5). Calculated loss rates due to zooplankton grazing were 0.037 d^{-1} on 4 July, 0.033 d^{-1} on 5 July, and 0.01 d^{-1} on 23 July. Using the mean clearance rate from July ($1.69 \text{ mL}\cdot\mu\text{g}^{-1}\cdot\text{d}^{-1}$) as a clearance rate estimate for the 22 August assemblage yields a loss rate of 0.39 d^{-1} for 22 August. The actual loss rate for the August community was probably much higher because the August zooplankton community was dominated by *Daphnia* (Fig. 5) and not *Diaptomus* as in July. Lake Michigan *Daphnia*-dominated communities were found to have significantly higher clearance rates than *Diaptomus*-dominated communities (Scavia *et al.* 1986).

DISCUSSION

In the past, much information regarding the formation and maintenance of the DCL has been inferred from vertical chlorophyll profiles (Hobson and Lorenzen 1972, Longhurst 1976, Brooks and Torke 1977, Cullen 1982). However, chlorophyll profiles must be interpreted with great care if the dynamics of the DCL are to be clearly understood. For example, in Lake Michigan, a substantial increase in phytoplankton abundance from spring through mid summer thermal stratification had been suggested by the large increases in

subsurface chlorophyll (Brooks and Torke 1977). This notion is not supported by our data. Our results demonstrate that phytoplankton carbon concentrations in the region of the DCL changed only slightly from spring isothermal conditions through mid stratification (Fig. 3). In all but one case, maximum phytoplankton carbon concentrations in the DCL were within 40% of spring-mixing carbon concentrations. Even a systematic increase in carbon concentration of 40% over that time period corresponds to net growth rate of only 0.004 to 0.006 d^{-1} .

Small changes in DCL phytoplankton carbon concentrations may be surprising in light of the pronounced differences in epilimnetic and deep chlorophyll concentrations. As illustrated from averages of 3 years of data, two factors contributed to the pronounced vertical chlorophyll profile. The first was the decreased epilimnetic chlorophyll concentrations after the onset of thermal stratification. Epilimnetic chlorophyll concentrations typically exhibited a 2 to 4-fold decrease from spring mixing to mid-stratification (Fahnenstiel and Scavia 1987b). The second factor was shade adaptation, the increase in pigment per unit biomass that accompanies growth at low irradiances (Cullen 1982). The average carbon:chlorophyll ratio of epilimnetic phytoplankton during mid-stratification was 36.8:1 whereas the ratio for DCL phytoplankton was 16.7:1. Therefore, DCL chlorophyll concentrations would be approximately 4–8X epilimnetic concentrations, based only on these two factors. Increased DCL phytoplankton carbon concentration is not necessary.

From these data, it is tempting to suggest that the DCL was merely a remnant of the spring phytoplankton bloom. This was not the case. While some remnants of the spring phytoplankton bloom were abundant in the DCL, the majority of the community was composed of new biomass. Many species in the DCL increased dramatically from spring mixing through mid-stratification; most notably, *Fragilaria crotonensis* and *Oscillatoria* spp. Conversely, dominant spring diatoms (e.g., *Melosira islandica*) exhibited clear and predictable decreases.

Because DCL phytoplankton concentrations exhibit little change over the 2-to 3-month period, their growth and loss rates must balance. To test this, we estimated phytoplankton growth and several loss rates for the period 3–26 July 1984 when average phytoplankton carbon concentrations and DCL thickness exhibited little change (Figs. 1 and

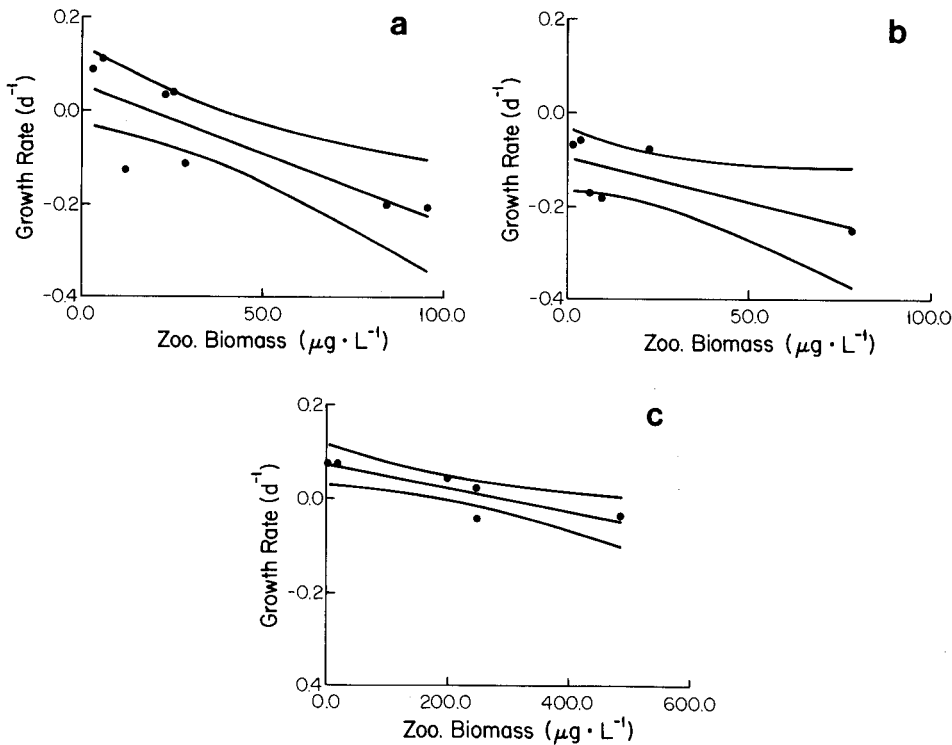


FIG. 4. Effects of zooplankton abundance ($\mu\text{g}\cdot\text{L}^{-1}$) on phytoplankton growth rates (d^{-1}) in manipulation experiments. Regression results and 90% confidence intervals are plotted. The slope represents the clearance rate ($\text{L}\cdot\mu\text{g}^{-1}\cdot\text{d}^{-1}$) and the intercept represents the algal growth rate (d^{-1}). Zooplankton experiments were conducted on (a) a nighttime assemblage 4 July ($y = 0.0537 - 0.0029X$; $R^2 = 0.64$, $p = 0.02$), (b) a daytime assemblage 5 July ($y = -0.0969 - 0.0019X$; $R^2 = 0.50$, $p = 0.12$), and (c) a daytime assemblage 23 July ($y = 0.0722 - 0.0002X$; $R^2 = 0.73$, $p = 0.03$).

3). Phytoplankton growth rates, integrated over the DCL, averaged 0.045 d^{-1} , loss rates due to crustacean grazing averaged 0.027 d^{-1} , and net sedimentation loss was 0.009 d^{-1} . Balancing these mean estimates yields a net growth rate of 0.009 d^{-1} . This estimate, while a relatively small portion of total growth and loss processes, must represent either experimental error or an unmeasured loss rate. While a net rate of 0.009 d^{-1} is very small it may be attributable to grazing by *Mysis relicta*. *M. relicta* has been suggested as an important DCL herbivore capable of significant grazing on large diatoms (Bowers and Grossnickle 1978). The effect of this crustacean was not determined in our experiments because it was not included within our zooplankton grazing enclosures. With a mean filtering rate of $187 \text{ mL}\cdot\text{mysid}^{-1}\cdot\text{d}^{-1}$ and abundance estimates of 30–60 animals m^{-3} within the DCL (Bowers and Grossnickle 1978), the loss rate due to *M. relicta*

would be $0.006\text{--}0.011 \text{ d}^{-1}$ which could account for the unidentified loss. Cell mortality may also contribute to the unaccountable loss rate but its importance is more difficult to evaluate.

Our evaluation of the importance of various mechanisms in the formation and maintenance of the Lake Michigan DCL suggest that *in situ* growth and shade adaptation were primarily responsible for the Lake Michigan DCL. *In situ* growth, as opposed to sedimentation (see below), was important in maintaining phytoplankton carbon concentrations within the DCL. Primary production within the DCL averaged 30% of total water column production (Fahnenstiel and Scavia 1987a) and growth rates were as high as 0.3 d^{-1} (Table 1). Environmental conditions within the DCL were particularly favorable for the growth of many species such as blue-green filaments (G. Fahnenstiel, unpubl. data) and *Fragilaria crotonensis* (Lin and

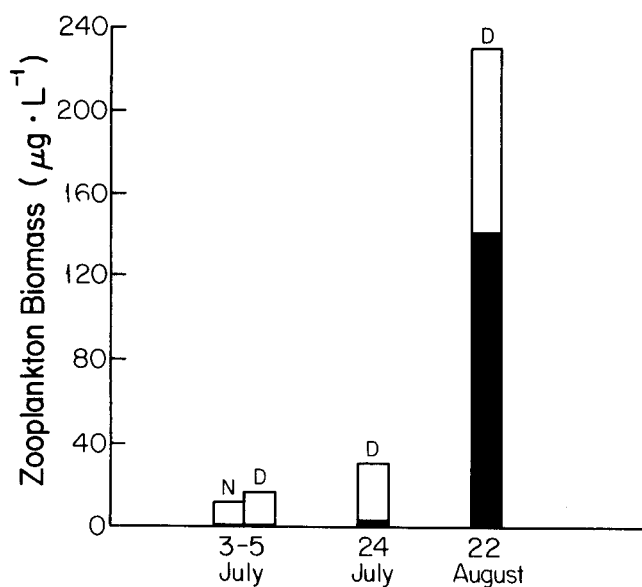


FIG. 5. Zooplankton abundance within the DCL for 3-5 July (15-30 m), 24 July (25-40 m), and 22 August (20-40 m) (D = daytime assemblage and N = nighttime assemblage). Shaded areas represent contribution of *Daphnia* spp.

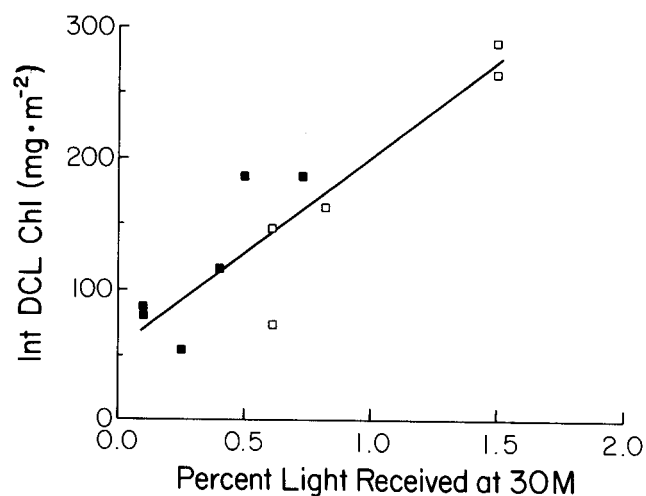


FIG. 6. Regression of integrated chlorophyll content ($\text{mg}\cdot\text{m}^{-2}$) in the July DCL and percent surface light received at 30 m, calculated from extinction coefficient, for data from 1975 to 1984. The DCL was defined as the region where chlorophyll concentrations exceeded $2 \text{ mg}\cdot\text{m}^{-3}$. Data from 1982-1984 are indicated by open squares. Black squares are from Liedle (1978) and Moll et al. (1984).

Schelske 1979) which exhibited 10- to 30-fold abundance increases.

In situ growth has been important to the Lake Michigan DCL for at least the past 10 years. During the period 1975-1984, the amount of chlorophyll within the July DCL was related directly to amount of subsurface irradiance as demonstrated by the highly significant regression ($y = 144.0X + 55.7$, $R^2 = 0.81$, $N = 11$, $p < 0.001$) of integrated DCL chlorophyll and percent of surface light received at 30 m, calculated from extinction coefficient (Fig. 6). To remove potential bias in the above relationship due to the possible relationship between epilimnetic chlorophyll concentrations and extinction coefficient, we redefined the DCL for this analysis as the region where chlorophyll concentrations exceeded $2 \text{ mg}\cdot\text{m}^{-3}$ rather than in relation to epilimnetic chlorophyll. The strong relationship between chlorophyll content of the DCL and light received in the DCL most likely exists because of the very strong relationship between subsurface primary production and irradiance (Fahnenstiel and Scavia 1987a). Thus, phytoplankton growth within the DCL was a primary factor determining the size of the DCL, in agreement with laboratory studies (Fahnenstiel et al. 1984).

Shade adaptation is also an active process performed by light-limited phytoplankton and was responsible for accentuating chlorophyll differences between surface and deep populations. The importance of shade adaptation was related to the depth of the DCL; the shallower the layer the less important was shade adaptation. While the average effect of shade adaptation was to double chlorophyll concentrations in the DCL, carbon:chlorophyll ratios at 50 m were approximately 4-5X lower than epilimnetic ratios. Shade adaptation was not very important during early stratification because the DCL was shallower in the water column (15-30 m) and carbon:chlorophyll ratios were not very different from those in the epilimnion.

The importance of *in situ* growth and shade adaptation for the Lake Michigan DCL has been confirmed in laboratory experiments with a natural DCL assemblage. These two processes were found to produce a phytoplankton assemblage which resembled the DCL (Fahnenstiel et al. 1984). Earlier field investigations also supported the role of *in situ* growth as evidenced by significant ^{14}C uptake within the DCL (Liedle 1978, Moll et al. 1984). These processes were also important for the Lake Superior DCL (Fahnenstiel and Glime 1983,

Fahnenstiel *et al.* 1984); however, the importance of other processes such as sedimentation and grazing relative to *in situ* growth has not been determined.

Phytoplankton sinking has been suggested as an important mechanism for the Lake Michigan DCL (Brooks and Torke 1977) and in other environments (Steele and Yentsch 1960). Yet, there has been little field evidence to test its importance. Two aspects of sinking are considered here. The first is sedimentation as a net source of cells to the DCL. This was evaluated by comparing sedimentation fluxes into and out of the layer. Sedimentation resulted in a significant net increase of cells only during early stratification and then at a rate significantly lower than *in situ* production. The net growth rate from sedimentation was 0.01 d^{-1} , which was considerably less than the average *in situ* growth rates of $0.05\text{--}0.17 \text{ d}^{-1}$. As epilimnetic diatom abundance decreased during thermal stratification, so did the role of sedimentation as a source of phytoplankton to the DCL. By mid-stratification, sedimentation resulted in a net loss of phytoplankton from the DCL at a rate of 0.01 d^{-1} .

The second aspect of sedimentation was its role in regulating the depth of the DCL. The DCL deepened throughout thermal stratification (Fig. 1) and this can be at least partially attributed to sinking phytoplankton populations. The importance of sinking can be seen most easily by following the vertical abundance of a spring diatom population from spring-mixing through thermal stratification (Fig. 7). *Melosira islandica* is a large net diatom that was not grazed in the epilimnion and exhibited minimal growth during thermal stratification (G. Fahnenstiel, unpubl. data). Thus, changes in abundance in the upper 10 m in June and upper 20 m in July can be attributed primarily to sinking. Abundance within the epilimnion gradually decreased during thermal stratification and by July there were very few cells left above 25 m; however, abundance in the 50–60 m region was still high and similar to spring-mixing abundance.

Although previously neglected, zooplankton grazing also played an important role in determining the size and structure of the DCL. As suggested by Ortner *et al.* (1980), if significant depth-differential grazing pressure exists and phytoplankton sedimentation rates are low within the epilimnion, then the upper boundary of the DCL could be maintained by reduced grazing pressure. Epilimnetic sedimentation rates were very low dur-

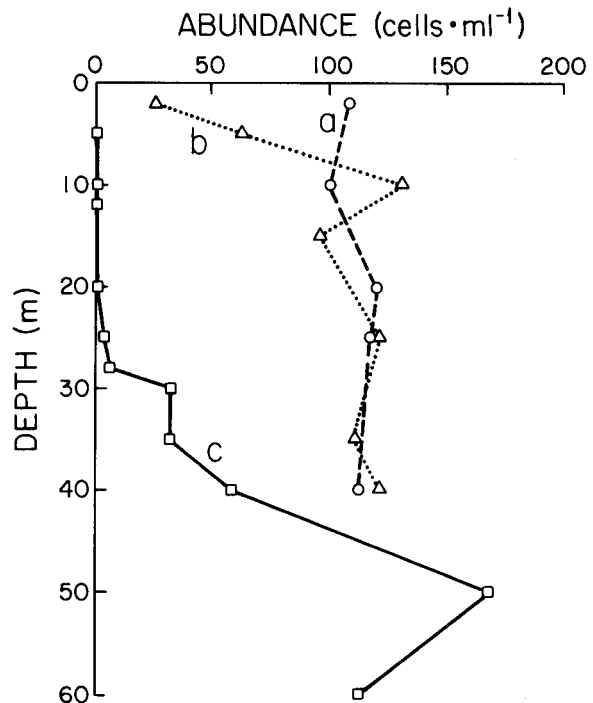


FIG. 7. Vertical profile of *Melosira islandica* abundance during spring mixing (May, a), early stratification (June, b), and mid stratification (July, c) in 1983.

ing mid-stratification and epilimnetic zooplankton clearance rates were at least an order of magnitude higher than similar DCL clearance rates (Scavia and Fahnenstiel 1987). There can be no doubt that zooplankton grazing was important in determining the depth and shape of the DCL during mid-stratification. For in August 1984, when zooplankton grazing loss rate increased dramatically to approximately 0.38 d^{-1} in the 20–40 m region, phytoplankton concentrations within that region decreased. Thus, the relatively rapid decrease in phytoplankton abundance in the 20–40 m region in August can be ascribed to increased zooplankton grazing pressure. Intense grazing activity in this depth region in August 1983 is also suggested from analysis of regenerated nutrients (D. Scavia, unpubl. data).

The importance of various processes in the DCL vary temporally and spatially. In early stratification the formation of the DCL was attributable to *in situ* growth and to a lesser extent to sedimentation and shade adaptation. By July, sedimentation no longer contributed to the layer and *in situ* growth was important in the upper part of the DCL while shade adaptation was important in the

lower part. In August, when most of the DCL was below 50 m, the importance of *in situ* growth decreased and shade adaptation increased. Zooplankton grazing pressure increased and was at least partially responsible for the decrease in phytoplankton concentrations in the 20–50 m region.

The Lake Michigan DCL was not only a highly dynamic feature seasonally but also annually. Recent changes within the Lake Michigan ecosystem have brought about profound changes in the DCL. In the 1980s the DCL was much larger and located deeper in the water column than in the 1970s due to increases in light penetration in the 1980s (Fahnenstiel and Scavia 1987b). Increased epilimnetic zooplankton grazing pressure caused by a shift in zooplankton composition was responsible for this increase in light penetration (Scavia *et al.* 1986). As the zooplankton community continues to change in Lake Michigan (D. Scavia, unpubl. data), it is likely that future changes will also occur within the DCL.

ACKNOWLEDGMENTS

This manuscript benefitted greatly from the comments of A. Beeton, J. Cullen, E. Fee, W. Gardner, C. Schelske, E. Stoermer, and N. Watson. Technical assistance was provided by W. Burns, S. Fortner, J. Gauvin, J. Grimes, T. Heatlie, G. Laird, D. Morse, L. Strong, and B. Wharlam. Phytoplankton samples were counted by L. Feldt, R. Kreis, and E. Theriot. Contribution No. 560 Great Lakes Environmental Research Lab.

REFERENCES

- Bartone, C. R., and Schelske, C. L. 1982. Lake-wide seasonal changes in limnological conditions in Lake Michigan in 1976. *J. Great Lakes Res.* 8:413–427.
- Bowers, J. A., and Grossnickle, N. E. 1978. The herbivorous habits of *Mysis relicta* in Lake Michigan. *Limnol. Oceanogr.* 23:767–776.
- Brooks, A. S., and Torke, B. G. 1977. Vertical and seasonal distribution of chlorophyll *a* in Lake Michigan. *J. Fish. Res. Board Can.* 34:2280–2287.
- Crumpton, W. G., and Wetzel, R. G. 1981. A method for preparing permanent amounts of phytoplankton for critical microscopy and cell counting. *Limnol. Oceanogr.* 26:976–980.
- Cullen, J. J. 1982. The deep chlorophyll maximum: comparing vertical profiles of chlorophyll *a*. *Can. J. Fish. Aquat. Sci.* 39:791–803.
- Eadie, B. J., Chambers, R. L., Gardner, W. S., and Bell, G. L. 1984. Sediment trap studies in Lake Michigan: Resuspension and chemical fluxes in the southern basin. *J. Great Lakes Res.* 10:307–321.
- Fahnenstiel, G. L., and Glime, J. M. 1983. Subsurface chlorophyll maximum and associated *Cyclotella* pulse in Lake Superior. *Int. Revue ges. Hydrobiol.* 68:605–618.
- _____, and Scavia, D. 1987a. Dynamics of Lake Michigan phytoplankton: Primary production and growth. *Can. J. Fish. Aquat. Sci.* 44: 499–508.
- _____, and Scavia, D. 1987b. Dynamics of Lake Michigan phytoplankton: Recent changes in surface and deep communities. *Can. J. Fish. Aquat. Sci.* 44:509–514.
- _____, Scavia, D., and Schelske, C. L. 1984. Nutrient-light interactions in the Lake Michigan subsurface chlorophyll layer. *Verh. Internat. Verein. Limnol.* 22:440–44.
- Hawkins, B. E., and Evans, M. S. 1979. Seasonal cycles of zooplankton biomass in southeastern Lake Michigan. *J. Great Lakes Res.* 5:256–263.
- Hobson, L. A., and Lorenzen, C. J. 1972. Relationships of chlorophyll maxima to density structure in the Atlantic Ocean and Gulf of Mexico. *Deep-Sea Res.* 19:297–306.
- Kiefer, D. A., Olson, R. J., and Holm-Hansen, D. 1976. Another look at the nitrite and chlorophyll maxima in the central North Pacific. *Deep-Sea Res.* 23:1199–1208.
- Lehman, J. T. 1980. Release and cycling of nutrients between planktonic algae and herbivore. *Limnol. Oceanogr.* 25:620–632.
- _____, and Sandgren, C. D. 1985. Species-specific rates of growth and grazing loss among freshwater algae. *Limnol. Oceanogr.* 30:34–46.
- Liedle, S. D. 1978. Seasonal and vertical determinations of primary production at a deep Lake Michigan station. M. S. thesis, Univ. Wisconsin-Milwaukee.
- Lin, C. K., and Schelske, C. L. 1979. *Effects of nutrient enrichment, light intensity, and temperature on growth of phytoplankton from Lake Huron*. U.S. Env. Prot. Agency report. EPA-600/3-79-049. Duluth, Minnesota.
- Longhurst, A. L. 1976. Interactions between zooplankton and phytoplankton profiles in the eastern tropical Pacific Ocean. *Deep-Sea Res.* 23: 729–754.
- Moll, R. A., Brahe, M. Z., and Peterson, T. P. 1984. Phytoplankton dynamics within the subsurface chlorophyll maximum of Lake Michigan. *J. Plankton Res.* 6:751–766.
- Ortner, P. B., Wiebe, P. H., and Cox, J. L. 1980. Relationships between oceanic zooplankton distributions and the seasonal deep chlorophyll maximum in the Northwestern Atlantic Ocean. *J. Mar. Res.* 38:507–531.
- Parker, J. I., Conway, H. L., and Yaguchi, E. M. 1977. Seasonal periodicity of diatoms, and silicon limita-

- tion in offshore Lake Michigan, 1975. *J. Fish. Res. Board Can.* 34:552-558.
- Richerson, P. J., Lopez, M. M., and Coon, T. 1978. The deep chlorophyll maximum layer of Lake Tahoe. *Verh. Internat. Verein. Limnol.* 20: 426-433.
- Scavia, D., and Fahnenstiel, G. L. 1987. Dynamics of Lake Michigan phytoplankton: Mechanisms controlling epilimnetic communities. *J. Great Lakes Res.* 13:103-120.
- _____, Fahnenstiel, G. L., Evans, M. S., Jude, D. J., and Lehman, J. T. 1986. The influence of salmonid predation and weather on long-term water-quality trends in Lake Michigan. *Can. J. Fish. Aquat. Sci.* 43:435-443.
- Schelske, C. L. 1979. Role of phosphorus in Great Lakes eutrophication: Is there a controversy? *J. Fish. Res. Board Can.* 36:286-288.
- Sicko-Goad, L., and Ladewski, B. G. 1977. A morphometric method for correcting phytoplankton cell volume estimates. *Protoplasma* 93:147-163.
- Steele, J. H., and Yentsch, C. S. 1960. The vertical distribution of chlorophyll. *J. Mar. Biol. Ass. U.K.* 39:217-226.
- Stoermer, E. F., and Kreis, R. G. Jr. 1980. *Phytoplankton composition and abundance in southern Lake Huron*. EPA report-EPA-600/3-80-161. Duluth, Minnesota.
- Strathman, R. R. 1966. Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. *Limnol. Oceanogr.* 11:411-418.
- Strickland, J. D. H., and Parsons, T. R. 1972. *A Practical Handbook of Seawater Analysis*, 2nd ed. Bull. Fish. Res. Bd. Can. No. 167.