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The Deep Chlorophyll Maximum in Lake Superior

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ABSTRACT. *Summer surveys conducted on Lake Superior from 1996–2001 indicated that a deep chlorophyll maximum (DCM) is a common feature of the offshore waters. The DCM was usually observed in the upper hypolimnion between 23 and 35 m, a region lacking a pronounced density gradient. Chlorophyll a concentrations in the DCM were typically 1.5–2.5 (median = 2.0) times epilimnetic concentrations, although these were associated with minimal or no increases in particulate organic carbon concentrations. Seston carbon:phosphorus ratios were consistently lower in the DCM than in the epilimnion, indicating increased phosphorus content of DCM phytoplankton. This could have resulted from either improved nutrient conditions or light limitation at depth. A phosphorus-rich phytoplankton community at depth could serve as a resource for the large, deep-living calanoid copepods that constitute the majority of summer zooplankton biomass. The phytoplankton communities at the level of the DCM were taxonomically distinguishable from those in the epilimnion, with the most notable difference being a relative reduction in the abundance of* Cyclotella *species in the DCM.*

INDEX WORDS: *Phytoplankton, nutrient status, phosphorus,* Cyclotella.

INTRODUCTION

Layers of elevated chlorophyll *a* are commonly found below the epilimnion in clear, stratified bodies of water (Fee 1976). Indirect evidence of subepilimnetic phytoplankton accumulations, mostly in the form of increased oxygen concentrations, go back nearly 100 years (e.g., Birge and Juday 1911). The subsequent development of *in situ* fluorescence techniques (Lorenzen 1966) resulted in reports of elevated chlorophyll concentrations at depth in a number of freshwater and marine systems (Fee *et al.* 1977, Kiefer *et al.* 1972, Venrick *et al.* 1973). While the widespread occurrence of deep chlorophyll maxima (DCM) is now generally accepted, there is no consensus on the ecological significance of this phenomenon. If biologically active, a DCM may have a substantial impact on total lake productivity (Moll *et al.* 1984), and may potentially exert an influence on energy and materials transfer by providing a highly concentrated, nutrient-rich food source for grazers.

The existence of a DCM in Lake Superior was first documented by Olson and Odlaug (1966), who recorded maximum chlorophyll *a* concentrations at around 30 m in late July and mid-August 1963. Watson *et al.* (1975) subsequently confirmed the existence of the DCM on the basis of transmissometer profiles; examination of grab samples collected from the depth of minimum transmittance indicated its algal origin. Moll and Stoermer (1982) provided the first continuous chlorophyll profile indicating a DCM in Lake Superior, while Fahnenstiel and Glime (1983) have presented the most temporally detailed work to date on DCM development in Lake Superior. We recently presented the first synoptic survey of the DCM across all five Laurentian Great Lakes (Barbiero and Tuchman 2001), based on data collected during the U.S. EPA's Great Lakes National Program Office (GLNPO) annual surveillance monitoring cruise of 1998. In the present contribution we expand upon that initial report to include an assessment of the in-

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terannual variability in both chemical and biological conditions of the DCM in Lake Superior, using GLNPO data collected from 1996–2001. We were particularly interested in examining whether elevated chlorophyll at depth is a consistent feature of Lake Superior during the stratified period; to what extent the DCM is indicative of an actual increase in phytoplankton biomass at depth; whether species composition in deep communities differs from that of epilimnetic communities; and whether enhanced nutrient availability at depth could explain the existence of these communities.

METHODS

Field Methods

Summer cruises on Lake Superior were conducted between 16 and 24 August during 1996–2001, and included 19 sampling stations distributed throughout the open water of the lake (Fig. 1). At each station, vertical profiles for temperature, *in situ* chlorophyll fluorescence, photosynthetically active radiation (when sampled during daylight), and turbidity (measured as beam attenuation coefficient) were taken using a Seabird STE-911 CTD multi-sensor unit. Integrated (INT) samples for soluble and particulate nutrients, *in vitro* chlorophyll *a*, and phytoplankton enumeration were composited from equal aliquots of water collected at 1 m, 5 m, 10 m, and the lower epilimnion with Niskin bottles mounted on a SeaBird Carousel Water Sampler. Additional samples for chlorophyll *a*, soluble and particulate nutrients and phytoplankton enumeration were taken from the DCM at stations exhibiting maximum chlorophyll concentrations below the epilimnion, based on *in situ* fluorometric profiles.

Samples for total soluble phosphorus (TSP) were filtered in the field through 0.45 µm Millipore filters and preserved with H_2SO_4 for later analysis in the laboratory. Samples for soluble silica (Si) were stored at 4°C. Aliquots of 3–4 L were filtered on station through 0.45 µm membrane filters for particulate organic carbon (POC), which was used as a measure of phytoplankton biomass, and particulate phosphorus (PP). Samples for phytoplankton analysis were preserved in the field with Lugol's solution, and with formalin upon return to the laboratory.

Laboratory Methods

Prior to 1998, chlorophyll *a* was acid-corrected for phaeophytin (APHA 1985); from 1998 on, narrow band filters were used (Welschmeyer 1994). In all years chlorophyll *a* samples were cold extracted in 90% acetone and analyzed using a Turner Designs 10-AU fluorometer. After acid persulfate digestion, TSP and PP were measured on a Lachat QuikChem AE autoanalyzer by the ascorbic acid method (APHA 1985). Si was determined by the molybdate method on a Lachat QuikChem AE autoanalyzer (APHA 1985). POC was determined by the combustion-infrared method on a Carlo Erba carbon analyzer (APHA 1985). Phytoplankton were identified and abundances were estimated using the Utermöhl technique (Lund *et al.* 1958) at a magnification of 500x, with diatoms other than *Rhizosolenia* identified as either centrics or pennates. Diatoms were identified, and relative abundances determined, from permanent slide mounts at 1250x. Relative proportions of each taxon of centrics and pennates were then multiplied by the respective Utermöhl counts. Primary taxonomic references included Prescott (1962), Kramer and Lange-Bertalot (1991, 1997), Patrick and Reimer (1966, 1975), Germain (1981), Huber-Pestalozzi (1941, 1968, 1983), and Drouet and Daily (1972). At least 10 individuals of each taxon were measured per sample

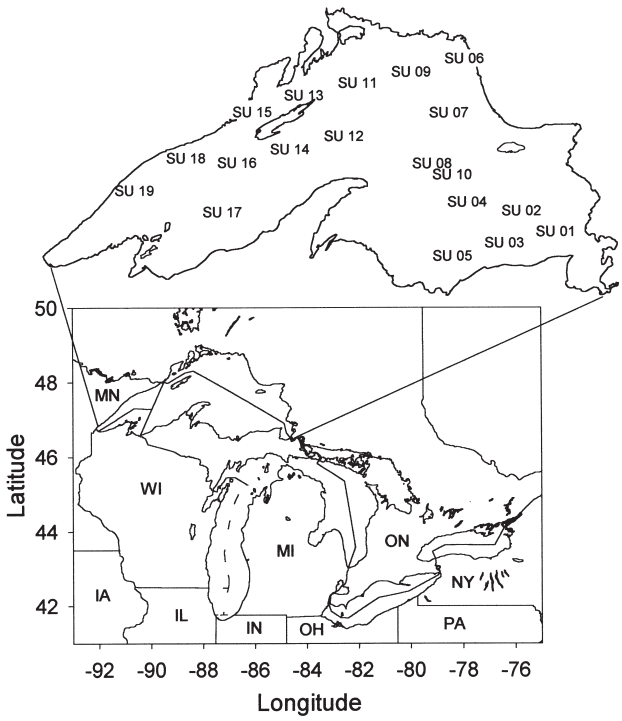

FIG. 1. Map of Lake Superior indicating location of the sampling stations.

and cell volumes computed using geometric formulae that most closely approximate their shape.

As an indication of the timing of thermal development in different years, surface water temperature data were obtained from NOAA's National Data Buoy Center (http://www.ndbc.noaa.gov) for three sites in Lake Superior (buoys 45001, 45004, 45006), and the first date at which lake surface temperature remained above 8ºC determined. This is referred to as the first date of stratification, although the choice of 8ºC as an indication of stratification was somewhat arbitrary.

Data Analysis

Differences between epilimnetic and DCM variables were assessed with paired *t*-tests, using integrated (INT) samples to represent the epilimnion. In all cases the following one-tailed null hypothesis was tested for each year of available data:

$$H_0 : \mu_d \leq 0$$

$$\text{where: } \mu_d = \mu_{INT} - \mu_{DCM}$$

In cases where assumptions of normality and homoscedasticity were not met, a non parametric test, the Wilcoxon Signed Rank Test, was used. In all cases, $\alpha = 0.05$. To explore potential differences in phytoplankton species composition between integrated samples and those from the DCM, detrended correspondence analysis (DCA: Hill and Gauch 1980) was employed using the program CANOCO (Ter Braak 1988). Only species contributing > 2% biovolume to any sample were used, and biovolumes were converted to natural logarithms prior to analysis.

RESULTS

Occurrence of DCM in Lake Superior

Maximum chlorophyll concentrations, as measured by *in situ* fluorescence, occurred below the epilimnion at most stations in almost all years (Fig. 2). Most exceptions to this were seen in 1996 at stations where thermal stratification had not yet developed at the time of sampling in that unusually cold year. Depths of the DCM, as well as the distinctness and magnitude of the peaks, exhibited considerable spatial and interannual variation. Annual median depths of the DCM ranged from about 27 m in 2001 to 31 m in 1998, with most values falling between 23 m and 35 m (Fig. 3a). In most cases the DCM was located below the metalimnion, either in an area of gradual thermal change in the upper hypolimnion, or more typically in a deeper, more or less isothermal region. More than half of the deep chlorophyll peaks were between 11 and 18 m (median = 15 m) below the depth stratum of greatest density change (Fig. 2).

The lower limit of the photic zone is usually assumed to correspond to the depth at which light = 1% of surface illumination (I_0). Average light levels at the depth of the DCM for the different years ranged from 3.3 to 7.1% I_0, except in 1998 when the average light level was 1.4% I_0 (Fig. 3b). A highly significant ($F = 11.6$, $P < 0.001$) negative relationship existed between the depth of the DCM and the turbidity of the upper 20 m (Fig. 4), although this relationship explained a relatively low amount of the variance in DCM depth as indicated by a low r^2. A nearly identical relationship was found between extinction coefficient and DCM depth.

Magnitude of DCM

When *in situ* fluorometric chlorophyll values at the depth of the DCM were compared to average values from the upper 20 m, annual medians of the ratio of the two values (DCM:20 m) ranged from 1.7 (1997) to 2.7 (1998), with 50% of all ratios falling within this range. DCM:INT ratios, measured as *in vitro* chlorophyll *a*, were only slightly less, with annual medians falling between 1.5 (2001) and 2.4 (1998). Overall, the median ratio between DCM and INT chlorophyll *a* was 2.0. The median differences between *in vitro* DCM and INT chlorophyll *a* values for the different years ranged from 0.10 µg Chl *a*/L in 1996 to 0.85 µg Chl *a*/L in 2000, with a maximum difference of 1.82 µg Chl *a*/L seen in 2000 at station SU 07 (Fig. 5). Overall, where a DCM existed, the median increase in *in vitro* chlorophyll *a* at depth compared to INT samples was 0.40 µg Chl *a*/L. The difference between DCM and INT *in vitro* chlorophyll *a* concentrations was highly statistically significant ($P < 0.01$) in all years. At least part of the variation in the relative increase in chlorophyll *a* at depth could be explained by epilimnetic temperature and number of days of stratification preceding the sampling date (Fig. 6). Highly significant ($P < 0.001$) relationships were found between both of these variables and the ln-transformed relative increase in chlorophyll *a* at depth.

POC concentrations, which we used as a mea-

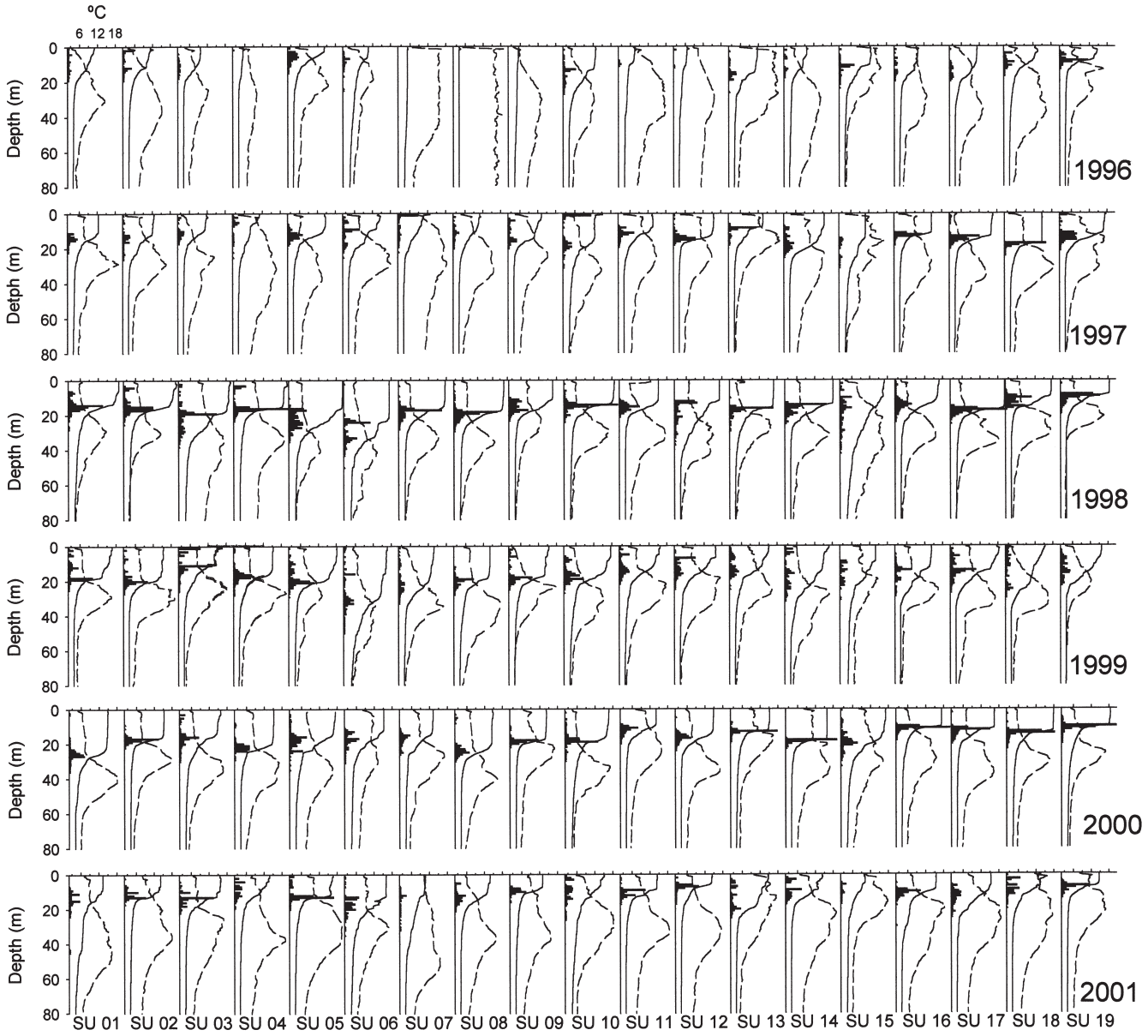

FIG. 2. Temperature (—) and* in situ *chlorophyll (------) profiles in Lake Superior during summer cruises, 1996–2001. Horizontal bars indicate density differences per meter increase in depth. Temperature and density scales are the same for all graphs, fluorometric units are relative. Station names are indicated at the bottom.

sure of phytoplankton biomass, were only slightly elevated in the DCM compared to the epilimnion between 1997 and 1999, with the annual median ratio of POC_{DCM}:POC_{INT} ranging between 1.07 and 1.29. In 2000 and 2001, POC tended to be slightly lower in the DCM than in the epilimnion (Fig. 7a). Paired *t*-tests indicated significantly ($P = 0.007$) higher POC in the DCM for 1998 only, although sample size during 1999–2001 was very small ($n = 3$). Chlorophyll *a*:POC ratios were consistently elevated in the DCM, compared to the epilimnion (Fig. 7b). These differences were statistically significant ($\alpha = 0.05$) in all years but 2001, when the probability (0.054) was only marginally higher than α. Annual median values varied between 2.6 and 6.2 μg Chl:mg POC for integrated samples and between 4.7 and 13.1 μg Chl:mg POC for DCM samples.

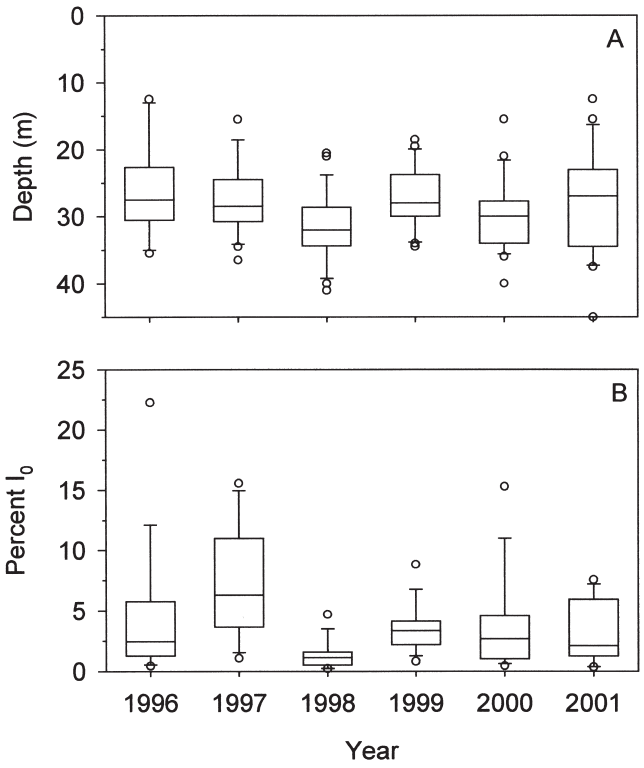

FIG. 3. Box plots of A) Depth of chlorophyll maxima, as indicated by* in situ *fluorometric profiles; and B) Percent of surface light intensity (I_0) at depth of the chlorophyll maximum. Boxes indicate 25th and 75th percentiles; lines indicate median; whiskers indicate 10th and 90th percentiles, circles indicate outliers.

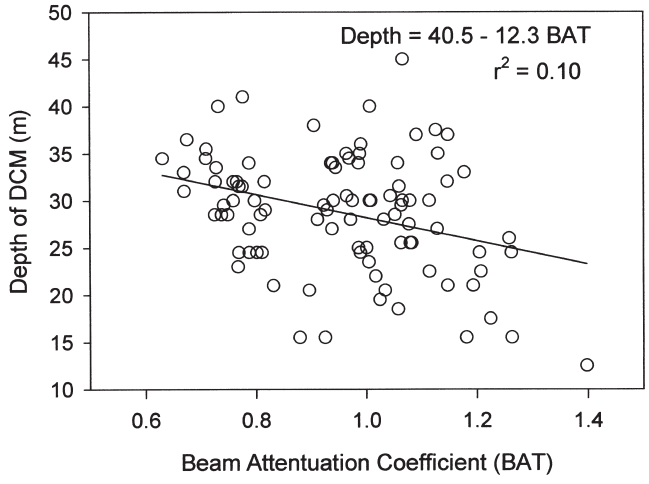

FIG. 4. Least squares regression showing relationship between turbidity, measured as beam attenuation coefficient (BAT), and depth of the DCM.

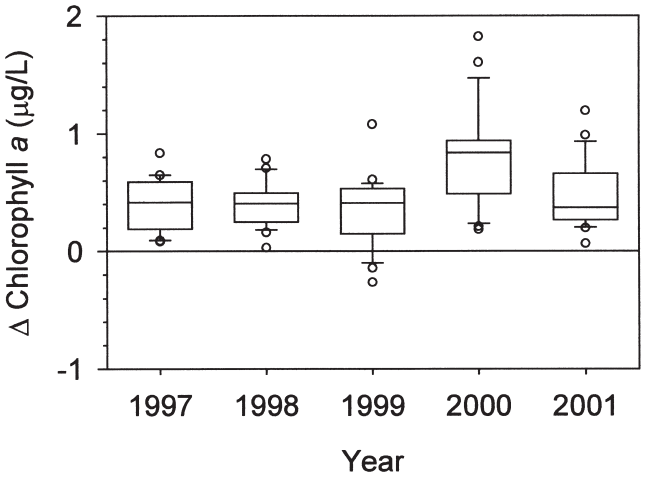

FIG. 5. Box plots of differences between* in vitro *chlorophyll concentration at the depth of the DCM and in the epilimnion, 1997–2001. Boxes as in Figure 3.

Nutrient Conditions

In most years, TSP concentrations were not higher at the depth of the DCM than in the epilimnion (Fig. 8a). A statistically significant increase in TSP in DCM samples was seen only in 1998 ($P = 0.001$), although even in this year the observed increases were extremely small, on the order of 1 μg P/L. In contrast, SiO_2 concentrations were significantly greater at the DCM in all study years (Fig. 8b). In spite of the lack of increased TSP at the depth of the DCM, in all years particulate matter had significantly lower POC:PP (C:P) ratios in the DCM than in the epilimnion, suggesting that phytoplankton cells were relatively enriched with respect to phosphorus at depth (Fig. 9). Annual average C:P ratios in the DCM ranged from 147 to 222 (atomic), while in the epilimnion these ranged from 227 to 291. Healey and Hendzel (1980) have suggested that C:P ratios greater than 130 and 260 are indicative of moderately and severely P-limited phytoplankton, respectively. Between 1997 and 2001, 47% of epilimnetic samples were severely P-limited by this criterion, while only 13% of DCM samples fell into this category.

Species Composition

DCA ordination analysis of phytoplankton communities from 1997–1999 resulted in nearly complete separation of DCM and epilimnetic communities (Fig. 10). With the exception of a sin-

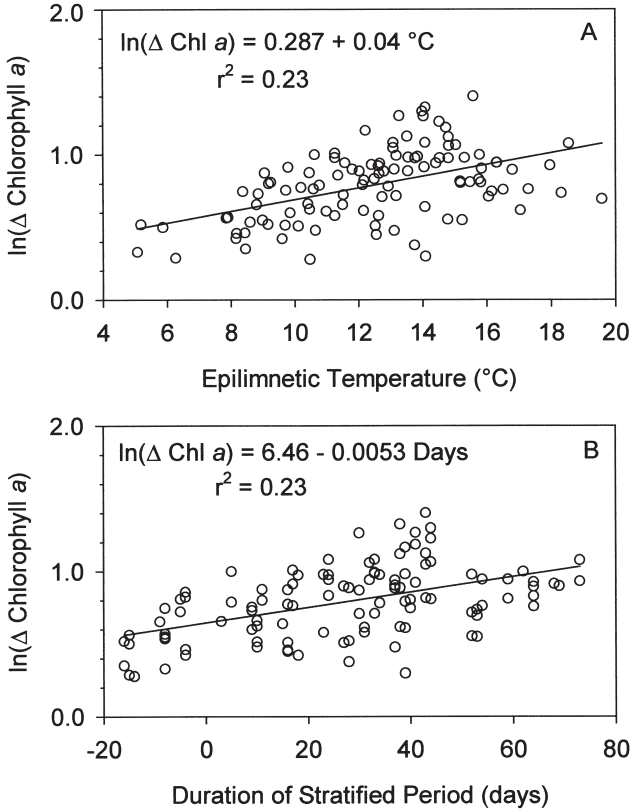

FIG. 6. A) Least squares regression showing relationship between epilimnetic temperature and the natural log of the difference between* in situ *DCM and epilimnetic chlorophyll; and B) Least squares regression showing relationship between the approximate Julian day of first stratification and the natural log of the difference between* in situ *DCM and epilimnetic chlorophyll.

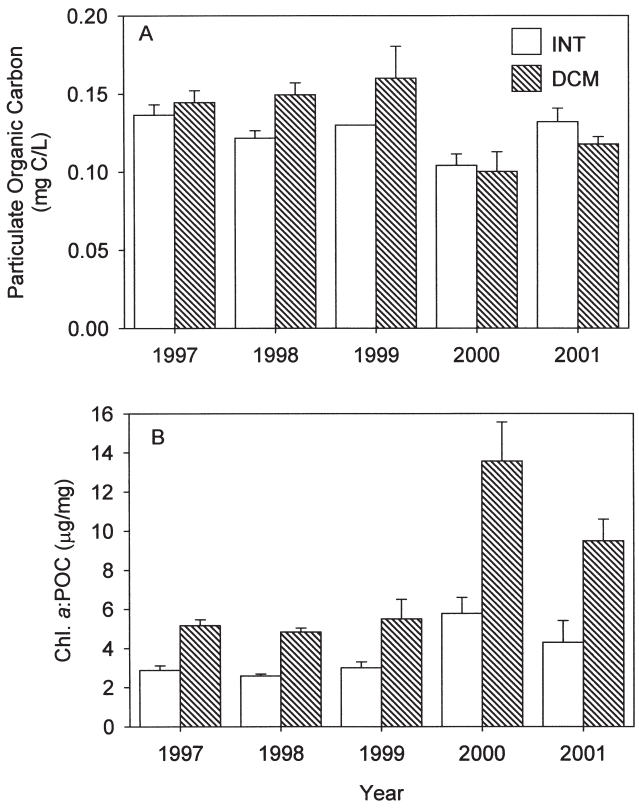

FIG. 7. A) Average particulate organic carbon; and B) Average chlorophyll* a*:particulate organic carbon ratio, for DCM and integrated (INT) samples. Error bars indicate one standard error.

gle sample, the two groups could be separated from each other entirely by first axis scores in all years, while interannual variation within the community types was expressed primarily on the second ordination axis.

While species composition varied considerably in both epilimnetic and DCM communities over the three years for which data are available, some general differences between the two communities can be discerned. Broadly, DCM samples had notably less centric diatoms, and usually relatively more pennate diatoms, cryptophytes and pyrrophytes (Fig. 11). The most notable species level difference was the reduced abundance of the summer epilimnetic dominant, *Cyclotella comta*, in DCM communities, a trend that was both marked and consistent (Table 1). Several other common epilimnetic species of *Cyclotella* (*C. ocellata*, *C. delicatula,* and *C. comensis*), were also less abundant in the DCM, and no centric diatoms were more abundant in the DCM compared to the epilimnion. Of the several species of *Dinobryon*, the other typical summer dominant seen in this study, *D. cylindricum* was consistently more abundant at depth.

The majority of species found in greater abundance in the DCM were flagellated, and included the cryptophyte genera *Cryptomonas* and *Rhodomonas* and the pyrrophyte genera *Gymnodinium* and *Glenodinium*. The pennate diatom *Fragilaria crotonensis* was also found in increased numbers in the DCM in all 3 years examined, and was apparently the only diatom with increased abundances at depth. With the exception of *C. comta*, though, relative differences in species abundances between the epilimnion and DCM tended to be small.

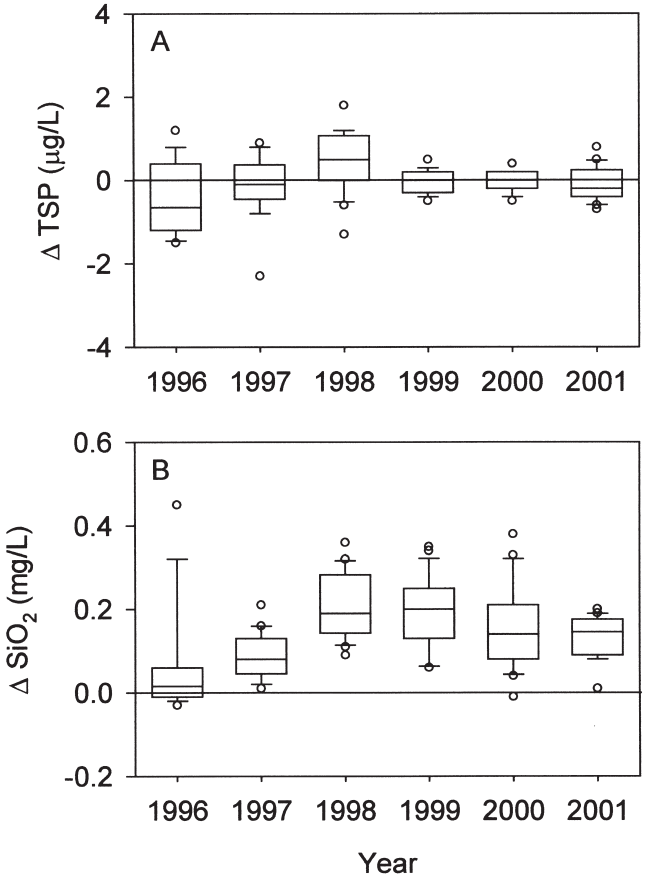

FIG. 8. Box plots of differences between concentrations in DCM and integrated samples of A) Total soluble phosphorus; and B) Soluble silica. Boxes as in Figure 3.

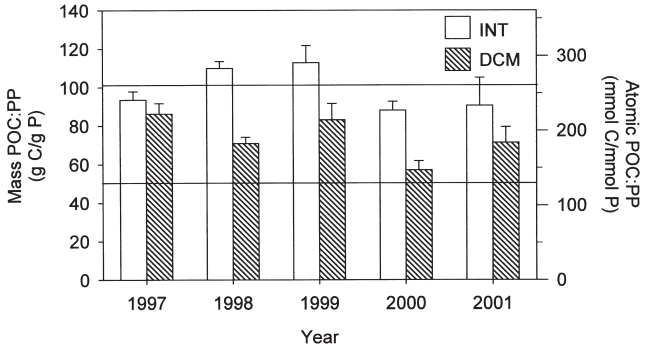

FIG. 9. Particulate organic carbon: particulate phosphorus ratios in DCM and integrated (INT) samples. Error bars indicate one standard error; reference lines indicate moderate and severe P limitation, according to Healey and Hendzel (1980).

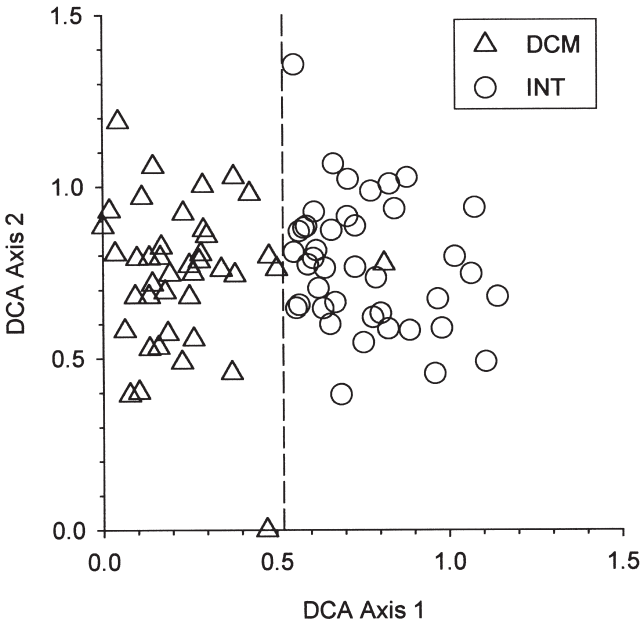

FIG. 10. Results of detrended correspondence analysis of summer phytoplankton communities in the epilimnion (INT) and DCM, 1997–1999.

DISCUSSION

The data presented here were collected during a 1-week period in late August in each year, and are therefore only representative of a restricted period in the development of the DCM. The DCM, however, is a dynamic phenomenon. The depth of the DCM and the relative importance of *in situ* growth, sedimentation, and shade adaptation to its maintenance can change markedly over the course of the stratified period (Fahnenstiel and Scavia 1987b). Uptake by algae can alter nutrient profiles over the course of a season, and in turn alter the vertical distribution of chlorophyll over time (Barbiero and McNair 1996). Shorter-term phenomena, such as seiche activity, can impact the vertical distribution of chlorophyll on a smaller time scale (Moll and Stoermer 1982, Moll *et al.* 1984). The dynamic nature of the DCM must be borne in mind when comparing our results with those of other studies.

Magnitude of the DCM

Where thermal structure had developed, chlorophyll maxima at depth were a near constant feature of Lake Superior during GLNPO's summer cruises. In spite of the sometimes dramatic peaks seen in *in situ* chlorophyll profiles, though, concentrations of

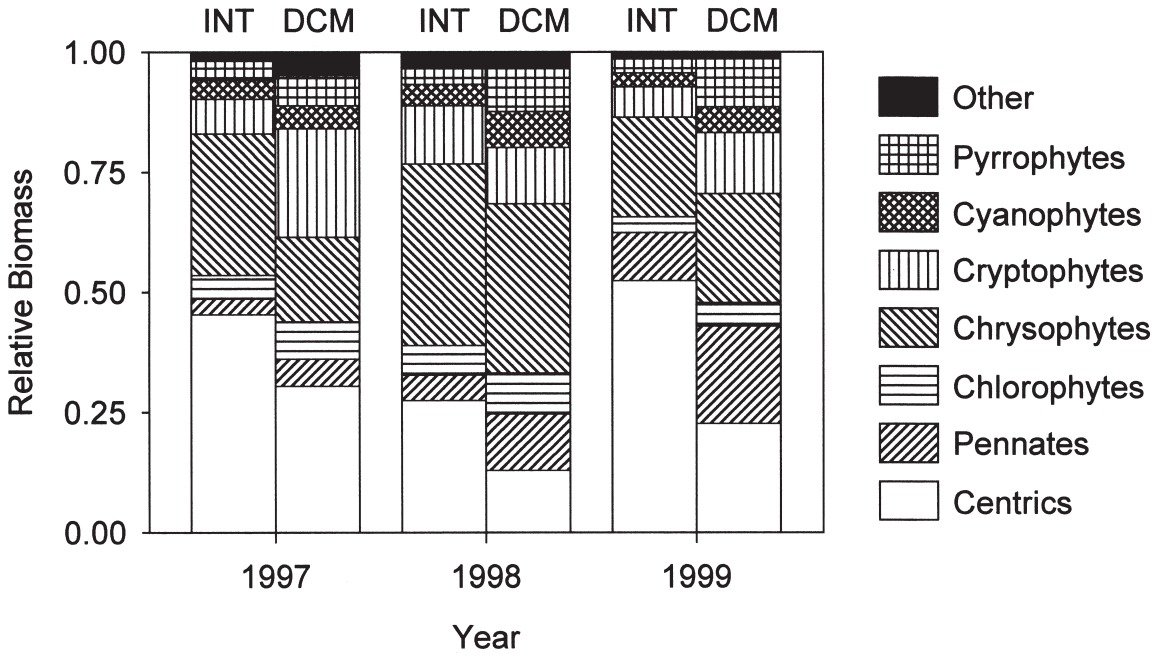

FIG. 11. Taxonomic composition by major group of epilimnetic (INT) and deep (DCM) phytoplankton communities, 1997–1999.

POC in the DCM were usually not substantially higher than epilimnetic concentrations, and during two of the five years examined, were less than those in the epilimnion. Previous studies have also found that increases in phytoplankton biomass in the DCM tend to be less pronounced than chlorophyll increases. Olson and Odlaug (1966) reported a DCM at 30 m in early August in which chlorophyll *a* values were nearly three times higher than epilimnetic values. Biomass (estimated by phytoplankton cell counts), however, was only 1.24 times higher than in the epilimnion. Munawar and Munawar (1978) reported a subthermocline phytoplankton biomass peak at an open water station in western Lake Superior sampled in September 1973. Judging from data presented, however, biomass at this depth (25 m) was slightly less than that observed at 3 m. Fahnenstiel and Glime (1983) reported a chlorophyll *a* concentration at 20 m, corresponding to the base of the metalimnion, that was nearly three times the surface water concentration in early September, 1979. Biomass at that depth appeared to be somewhat less that double that of surface waters, as indicated by their figure 4.

Given that most reports of the DCM in Lake Superior indicate chlorophyll concentrations 2–3.5 times higher than epilimnetic concentrations (Olson and Odlaug 1966, Watson *et al.* 1975, Moll and Stoermer 1982, Fahnenstiel and Glime 1983, this study), while increases in biomass at depth, when reported, are much smaller if present at all, it appears that the DCM in Lake Superior can be explained to a large extent by shade adaptation (i.e., increases in chlorophyll per unit carbon) of deep-living phytoplankton, rather than by increases in phytoplankton biomass. Chl:C ratios were always significantly higher at the depth of the DCM than they were in the epilimnion in our study. A similar conclusion was reached by Fahnenstiel and Scavia (1987a) for Lake Michigan, who found Chl:C ratios in the DCM of that lake roughly double those of the epilimnion.

Potential Contribution of DCM to Overall Productivity

It is possible that even modestly elevated levels of biomass in the DCM could be important to the overall trophic functioning of the lake, although a lack of available primary productivity data makes this difficult to evaluate. The stratified period of Lake Superior is relatively short—approximately 4 months (Bennett 1978)—and given its great mixing depth, phytoplankton productivity is thought to be light limited during most of the year (Guildford *et al.* 2000). Most primary production, therefore, is

TABLE 1. Percent difference in phytoplankton species composition (measured as biovolume) between communities in the DCM and those in the epilimnion, 1997–1999.

Taxa Less Common in DCM	% diff.	Taxa More Common in DCM	% diff.
1997		1997	
Cyclotella comta	15.9%	*Cryptomonas erosa* var. *reflexa*	4.2%
Dinobryon sociale	5.0%	*Cryptomonas erosa*	3.7%
Oscillatoria minima	1.7%	*Gymnodinium* spp.	3.2%
Cyclotella ocellata	1.6%	*Cryptomonas pyrenoidifera*	3.1%
		Unidentified ovoid Chrysophyta	2.9%
		Rhodomonas minuta	2.4%
		Ulothrix spp.	2.4%
		Oscillatoria spp.	2.2%
		Fragilaria crotonensis	2.0%
		Cryptomonas ovata	2.0%
		Anacystis montana f. *minor*	1.7%
		Unidentified flagellate ovoid	1.5%
		Glenodinium spp.	1.5%
1998		1998	
Cyclotella comta	13.2%	*Gymnodinium* spp.	5.3%
Dinobryon bavaricum	5.9%	*Fragilaria crotonensis*	3.5%
Cyclotella delicatula	5.3%	*Oscillatoria* spp.	3.0%
Dinobryon divergens	1.8%	*Dinobryon sociale*	2.4%
Cyclotella comensis	1.6%	*Dinobryon cylindricum*	2.0%
Dinobryon bavaricum v. *vanhoeffenii*	1.5%	*Ulothrix* spp.	1.6%
		Glenodinium spp.	1.6%
		Dinobryon sertularia	1.6%
1999		1999	
Cyclotella comta	56.6%	*Gymnodinium helveticum* f. *achroum*	2.6%
Cyclotella delicatula	9.1%	*Fragilaria crotonensis*	2.0%
Cyclotella comensis	4.8%	*Dinobryon cylindricum*	2.0%
Dinobryon sociale v. *americanum*	2.6%	*Gymnodinium* spp.	1.7%
Dinobryon bavaricum	2.6%	*Glenodinium* spp.	1.6%
Dinobryon sertularia	2.3%		
Peridinium spp.	2.2%		
Dinobryon sociale	2.0%		
Dinobryon bavaricum v. *vanhoeffenii*	1.5%		

confined to the stratified period, during which time conditions are suitable for DCM development. In Lake Michigan, peaks in primary productivity have been found just above the level of the DCM (Moll and Stoermer 1982), and it has been estimated that over 60% of total areal primary productivity in July can take place below the epilimnion in that lake (Moll *et al.* 1984). Fahnenstiel and Scavia (1987b) found that the DCM contributed 30% of total water column productivity in Lake Michigan.

Light levels at the depth of the DCM in our study tended to be higher than the 1% I_0 usually taken as the limit of the photic zone, which, because of the lake's high transparency, typically extends to 25–30 m (Schertzer *et al.* 1978), so some degree of *in situ* production is likely. However, there are few estimates of productivity for the DCM in Lake Superior. Watson *et al.* (1975) addressed the viability of algae in the DCM in Lake Superior by measuring phaeophytin content, ATP content and ^{14}C incorporation. Phaeophytin content, a measure of chlorophyll degradation, was not higher in the DCM compared to the upper 20 m, while ATP content was somewhat higher at depth. When ^{14}C incorporation of DCM samples was measured in a shipboard incubator at non-ambient light levels, it was comparable to that of epilimnetic samples, confirming the viability of algae in the DCM. However, the proximity of the DCM to the 1% light level led the authors to conclude that there was most likely little *in situ* productivity in this layer. Fahnenstiel and Glime (1983), on the other hand, found maximum

rates of primary production associated with a subthermocline chlorophyll peak in early September. This peak was substantially shallower (15–20 m) than any of those seen in our study, however. Fee *et al.* (1992) presented model results of carbon fixation versus depth for Lake Superior showing minimal production below 20 m. This model, however, averaged production over the ice free season, and did not take into account increased chlorophyll or the possibility of low-light adaptation at depth. The potential contribution of the DCM to overall primary production in Lake Superior, therefore, remains unknown.

Nutrient Characteristics of the DCM

One of the most consistent differences found in our study between epilimnetic and DCM phytoplankton communities was the increased cellular phosphorus content of the latter. Cellular phosphorus content (as indicated by seston C:P) was higher at depth in all years of our study, and suggests that phytoplankton in the DCM were less nutrient deficient than epilimnetic phytoplankton. The C:P ratios seen in our study indicate moderate to severe P limitation (Healey and Hendzel 1980). Other physiological indicators of P status, such as alkaline phosphotase activity and P debt, have also shown Lake Superior to be highly P limited during the stratified period (Guildford *et al.* 1994, Guildford and Hecky 2000), although it has also been pointed out that P deficiency is not as severe as would be expected on the basis of P concentration in the lake (Nalewajko *et al.* 1981, Guildford *et al.* 1994).

In spite of the difference in phosphorus status between epilimnetic and DCM phytoplankton, vertical gradients in soluble phosphorus were by and large not seen in our study. It is likely that in this extremely low nutrient lake, ecologically important gradients of limiting nutrients are too small to be measurable. Total soluble phosphorus in our study was typically < 3.0 µg P/L, and often below the detection limit of 2 µg P/L. Moreover, nutrient availability is a function of supply rate (via grazing, mineralization, advection of nutrients from the hypolimnion, etc.), rather than concentration *per se*. Uptake, especially under conditions of high nutrient deficiency, could prevent limiting nutrients from accumulating at the depth of the DCM. The relatively low thermal stability of the water column in Lake Superior (Guildford *et al.* 2000) suggests at least the potential for movement of nutrients into the upper hypolimnion from deeper levels, and thus an increased nutrient supply rate at the level of the DCM compared to the epilimnion. Silica levels were consistently higher 10 m above the bottom than at the level of the DCM in 1997–2001 (mean $\Delta Si = 0.16$ mg Si/L), although as noted TSP values were too low to enable meaningful comparisons.

If differences in nutrient condition are a determinant of DCM development, then one would expect a longer period of strong summer thermal stratification to produce a larger difference in biomass between the surface and DCM, due to the longer period of time for nutrient depletion to occur in the epilimnion. We found that the size of the DCM was strongly influenced by interannual variation in thermal regime, as manifested by both surface temperature and length of the period of stratification. The length of the stratification period could also influence the position of the DCM, since with time nutrient uptake at the depth of the DCM should lead to a progressive deepening of any nutriclines, and consequently a deepening of the DCM. Sinking rate in many phytoplankton decreases with improved nutrient status (Titman and Kilham 1976, Davey 1988, Jackson *et al.* 1990) so even non-motile algae can track a deepening nutricline (Barbiero and McNair 1996). The effects of temperature and length of stratification was most clearly seen in 1998 when surface water temperatures were approximately 5°C warmer than is typical, and stratification occurred more than a month earlier than usual. Consequently, the DCM was markedly deeper in 1998 than in other years. This was also the only year in which statistically significant increases in POC were seen at depth, compared to the epilimnion.

An alternative explanation for the lower cellular C:P at depth is decreased light availability, and hence light limitation, rather than increased nutrient supply. Nalewajko *et al.* (1981) have argued that even epilimnetic phytoplankton in Lake Superior can be light limited during the stratified period. They found that *Chlorella* cultures adapted to low light levels and grown at phosphate levels approximating those found in Lake Superior exhibited reduced P uptake rates and had a per cell P content 2.8 times higher than that of those grown in a high light environment. This was interpreted as evidence of light, rather than P, limitation.

Implications for Higher Trophic Levels

Regardless of their cause, algal nutrient ratios can have important consequences for the demographics of higher trophic levels (Sterner and Hes-

sen 1994). Algal C:P and C:N ratios tend to be relatively high compared to those of zooplankton, thus presenting nutritional challenges to zooplankton grazers. Variations in the biochemical composition of algae can therefore have a strong influence on zooplankton growth and reproduction (Sterner *et al.* 1993). Consequently, a fairly concentrated layer of P-enriched phytoplankton, such as occurs in the DCM, could have a greater impact on higher trophic levels than simple considerations of biomass might imply, given some degree of spatial overlap between the DCM and zooplankton grazers in Lake Superior. There are numerous reports from the marine literature of increased populations of herbivorous zooplankton associated with the DCM (Anderson *et al.* 1972, Longhurst 1976, Ortner *et al.* 1980, Herman *et al.* 1981). Crustacean biomass in Lake Superior is dominated by the calanoid copepods *Limnocalanus macrurus* and *Leptodiaptomus sicilis*, with the cladocerans *Daphnia galeata mendotae* and *Holopedium gibberum* also abundant in the summer (Barbiero *et al.* 2001, Barbiero and Tuchman 2002). M. Evans, (pers. comm. in Fahnenstiel and Glime 1983) found that zooplankton abundances in central Lake Superior were 5–10 times greater in the epilimnion than at the depth of the DCM. Similar results were reported by Olson and Odlaug (1966), which led them to speculate that a lack of grazing pressure in the DCM was in fact responsible for its development. Their tows, however, only extended to 30 m, a depth which would not sample effectively the deep living calanoids that predominate in Lake Superior. Barbiero *et al.* (2000) compared abundances estimated from 20 m and 100 m tows throughout the lake and found that cladocerans were largely confined to the top 20 m at all times, while estimates of *L. macrurus* and *L. sicilis* abundance were always greater from deeper tows. Swain *et al.* (1970) and Conway *et al.* (1973) similarly found shallow populations of cladocerans and deep populations of large calanoids. In Lake Michigan, populations of *L. sicilis* and *L. macrurus* exhibit maxima between 20 and 40 m at midnight and/or dusk (Barbiero *et al.* 2004), a stratum which would include most of the DCM seen both in that lake (Barbiero and Tuchman 2001) and in Lake Superior. During the day, populations of these organisms occupy much deeper levels. It seems possible, therefore, that the larger calanoids in the lake could be taking advantage of the nutrient-rich algae in the DCM, whereas cladoceran grazers most likely are not.

Species Composition of the DCM

Ordination results showed a clear difference in community composition between epilimnetic and DCM phytoplankton communities. The most obvious species level difference between the two communities was the relative lack of *Cyclotella* at depth. Barbiero and Tuchman (2001) also noted reduced abundances of *Cyclotella* in the DCM of Lake Huron, although these observations are at odds with previous reports. Both Fahnenstiel and Glime (1983) and Moll and Stoermer (1982) reported a DCM in Superior composed almost exclusively of *Cyclotella* species. In the only other report on species composition in the DCM of Lake Superior, Munawar and Munawar (1978) did not report large differences in species composition between epilimnetic and deep communities. The other notable difference between epilimnetic and DCM communities was the increased abundances of flagellated species in the latter. This would be consistent with a community actively maintaining its position at a desired depth, particularly given the lack of a pronounced density gradient at the depth of the DCM. So while our measures of biomass indicate that the DCM community is not *larger* than the epilimnetic community, the species differences, coupled with the differences in cellular nutrient content seen, suggest that the community is nonetheless *different*.

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