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Results from the U.S. EPA's Biological Open Water Surveillance Program of the Laurentian Great Lakes: II. Deep Chlorophyll Maxima

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ABSTRACT. *Deep chlorophyll maxima (DCM) were found in all five Laurentian Great Lakes during August, 1998. Chlorophyll profiles were consistent over large areas in Lakes Superior and Michigan, while distinct inter-site differences were apparent in the other three lakes. Shade adaptation appeared to be primarily responsible for increases in chlorophyll at depth in Lakes Huron and Ontario, while in Lake Superior increases in phytoplankton biovolume were also noted. Deep living phytoplankton populations in the latter lake exhibited improved nutrient status at depth, where concentrations of both soluble phosphorus and silica were higher. Phytoplankton community composition in the DCM differed from that previously reported for the lakes, most notably in the reduced populations of* Cyclotella, *relative to the epilimnion, seen at most sites. Filamentous chlorophytes were often more abundant at depth, as were certain species of* Dinobryon.

INDEX WORDS: *Phytoplankton, nutrients, chlorophyll maximum,* Cyclotella.

INTRODUCTION

Subsurface layers of elevated chlorophyll concentration are a common feature of many lakes that develop thermal stratification and possess adequate light penetration. The existence of these deep chlorophyll maxima (DCM) has long been recognized in the Great Lakes (Putnam and Olson 1966, Watson *et al.* 1975), and they have been particularly well studied in Lakes Superior and Michigan (Fahnenstiel and Glime 1983; Fahnenstiel and Scavia 1987a, 1987b; Moll and Stoermer 1982). Only limited information is available on the existence of DCM in Lakes Huron, Erie, and Ontario, however. In addition, previous studies have usually been limited to one or several sites. As a result, little is known about the spatial variability of DCM in the Great Lakes.

The Great Lakes National Program Office (GLNPO) of the United States Environmental Protection Agency (U.S. EPA) has conducted regular surveillance monitoring of physical, chemical, and biological aspects of the offshore waters of the Great Lakes since 1983, providing extensive spatial coverage of all five lakes during two annual surveys. This monitoring has included sampling for phytoplankton community composition and biomass. While initially directed solely toward epilimnetic communities, recognition of the potential importance of deep-living phytoplankton populations in Great Lakes ecosystem functioning led, in 1996, to the inclusion of regular sampling of these communities in GLNPO's routine monitoring program. Here, in a continuing series of papers presenting results from the 1998 surveys, a comparative description is presented for the first time of deep chlorophyll maxima from all five lakes during a single season. The goals of this paper are: 1) To document the spatial variability of deep chlorophyll maxima within each lake; 2) To examine differences in nutrient status between surface and deep phytoplankton communities; and 3) To describe differences in community make-up between these two communities.

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METHODS

Field Methods

DCM sampling was conducted during GLNPO's summer survey, which in 1998 ran from 2 August to 5 September. A total of 72 stations were sampled, and at each station water column profiles for temperature, *in vivo* chlorophyll fluorescence, and photosynthetically active radiation (when sampled during daylight) were taken using a Seabird STE-911 CTD multi-sensor unit. Extinction coefficients (η) were calculated by regressing ln-transformed light with depth. Integrated samples (INT) for soluble nutrients, *in vitro* chlorophyll *a*, and phytoplankton enumeration were created from a composite of water samples taken at discrete depths (surface, 5 m, 10 m, and 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 deep chlorophyll maximum (DCM) at stations exhibiting marked horizontal discontinuities in chlorophyll concentration. The depth of collection for DCM samples was determined at each site on the basis of 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 lab. Samples for soluble silica (Si) were stored at 4°C. Aliquots of 3 to 4 L were filtered on station through 0.45 µm membrane filters for particulate organic carbon (POC) 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. Further details on field methods for the 1998 survey, including station locations, are available elsewhere (Barbiero and Tuchman 2001).

Laboratory Methods

Chlorophyll *a*, uncorrected for pheophytin, was determined on a Turner Designs 10-AU fluorometer following the method of Welschmeyer (1994). 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 500×, with diatoms other than *Rhizosolenia* identified as either centrics or pennates. Diatoms were identified, and relative abundances determined, from permanent slide mounts at 1,250×. Relative proportions of each taxon of centrics and pennates were then multiplied by the appropriate Utermöhl counts. Primary taxonomic keys used were Prescott (1962), Krammer and Lange-Bertalot (1991, 1997), Patrick and Reimer (1966, 1975), Germain (1981), Huber-Pestalozzi (1941, 1968, 1983), and Drouet and Daily (1973). At least 10 individuals of each taxon were measured per sample, and cell volumes computed using geometrical formulae that most closely approximated their shape. Cell volumes were converted to biomass assuming a specific gravity of 1.

Data Analysis

Differences in biological and chemical variables between epilimnetic and DCM communities were assessed using paired *t*-tests for lakes which had sufficient sample sizes (Lakes Superior, Huron and Ontario), using integrated (INT) samples to represent the epilimnion. In all cases the following one-tailed hypothesis was tested:

$$H_0: \mu_d \le 0;\ \mu_d = \mu_{INT} - \mu_{DCM} \tag{1}$$

To test for potential differences in species composition between integrated samples and those from the DCM, Whittaker's (1952) percent similarity (PSC) index was used:

$$PSC = 100 - 0.5\sum_{i=1}^{K} |a - b| \tag{2}$$

where *a* and *b* are, for a given species, percentages of the total integrated and DCM samples *A* and *B*, respectively, which that species represents. The absolute value of their difference is then summed over all species. PSC values from each lake were then compared to the PSC values generated from pairs of replicate quality control (QC) samples. QC counts, in which a single sample is counted by two analysts as a check on inter-analyst accuracy, are routinely done on approximately 10% of all samples. A *t*-test was conducted of the following one-tailed hypothesis:

$$H_0: PSC_{INT} - PSC_{DCM} \le 0 \tag{3}$$

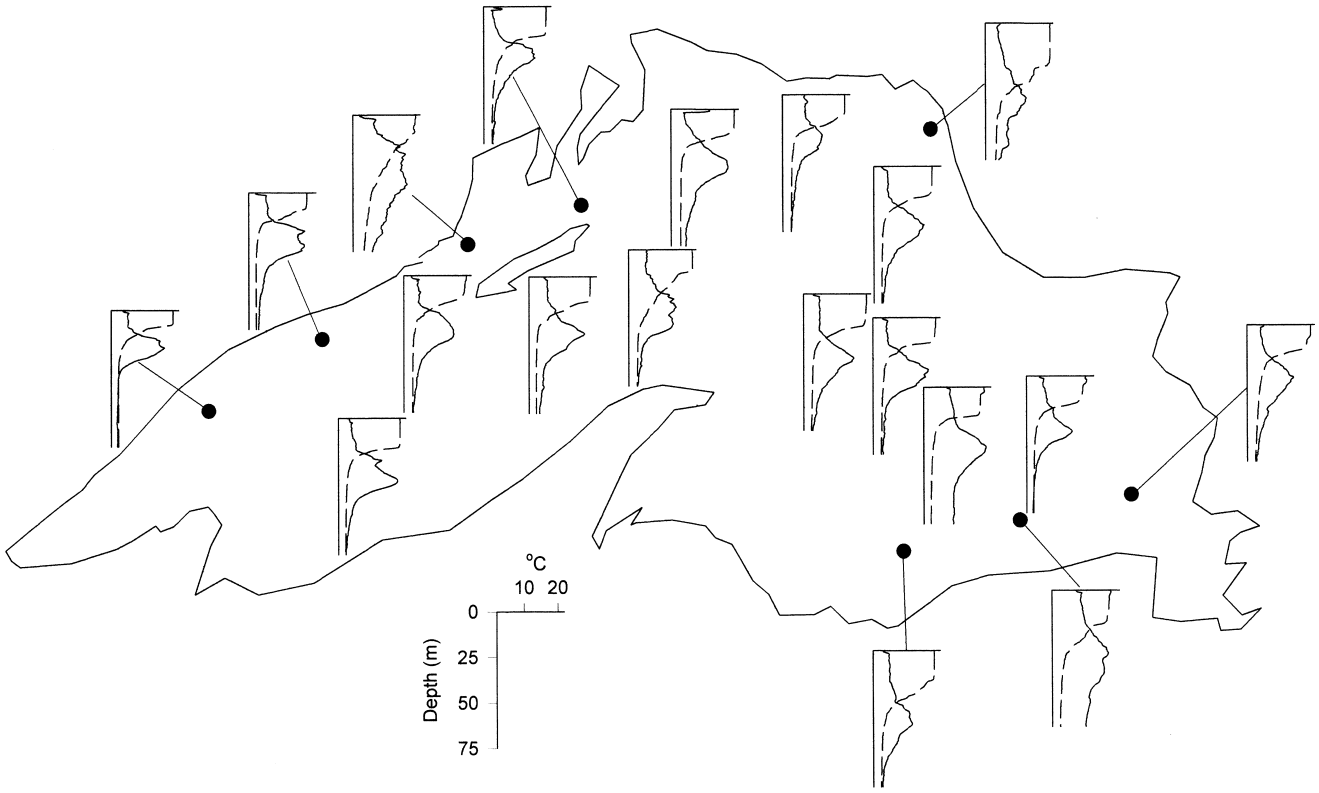

FIG. 1. **In vivo** ***chlorophyll (——) and temperature (------) profiles across Lake Superior, summer, 1998. Fluorometric units are relative.***

Each lake was tested individually against the same set of QC comparisons generated from the whole study. In all cases data conformed to assumptions of normality and homoscedasticity.

RESULTS

Occurrence of DCM

Stable stratification was apparent at nearly all open water sites in all lakes at the time of the summer survey, except for Lake Erie, where strong stratification was only evident in the deeper eastern basin. The depth of the epilimnion (delimited by a temperature difference greater than 1°C within a depth of 1 meter) ranged from 5.5 m in western Lake Ontario to 23.5 m in northern Lake Superior, and averaged between 14 and 17 m for the upper lakes and 19 and 11 m for Lakes Erie and Ontario, respectively. *In situ* fluorometer profiles revealed DCMs at all sites in Lake Superior, nearly all sites in Lake Michigan, and at about half the sites examined in Lakes Huron and Ontario. All three sites examined in the deeper eastern basin of Lake Erie exhibited DCMs, as did some sites in the central basin, although in some cases these were not pronounced.

In Lake Superior, chlorophyll maxima were located well below the metalimnion, occurring between 20 and 40 m (Fig. 1). Development of the DCM was very consistent from site to site, with only a small number of sites exhibiting poorly defined maxima, and these at sites where thermal structure was not as well developed. In Lake Michigan, DCM invariably occurred at the interface of the epilimnion and metalimnion, at a depth of about 23 m (range 21 to 26 m), and occupied a narrower depth range than in Lake Superior (Fig. 2). This was especially the case in the southern basin, where chlorophyll peaks were particularly pronounced.

A greater degree of variability existed in Lake Huron. Sites in the southern part of the lake tended to have chlorophyll maxima at the base of the epilimnion, at a depth of about 20 m, as in Lake Michigan, although these maxima were not as pronounced as in the latter lake (Fig. 3). At a number of these sites, secondary peaks were apparent at the top of the hypolimnion. At some mid-lake and

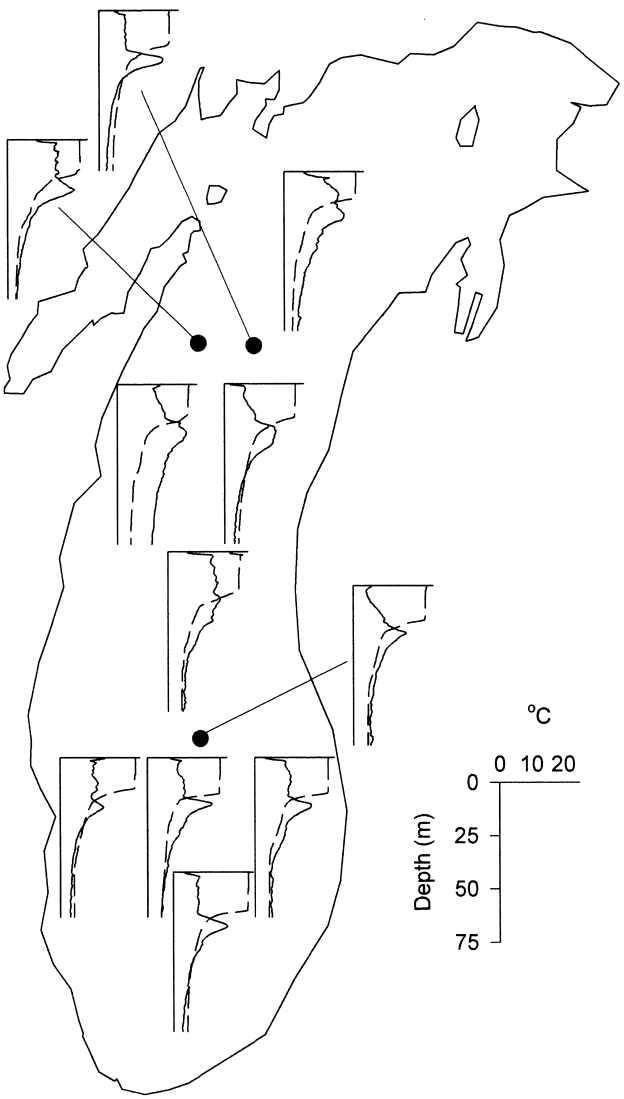

FIG. 2. **In vivo *chlorophyll (——) and temperature (------) profiles across Lake Michigan, summer, 1998. Fluorometric units are relative.***

northern sites, maxima were well below the epilimnion, usually at about 40 m, and tended to be more pronounced than those in the south of the lake. In general, fluorometric profiles showed a greater degree of variability within each site than in either Lake Superior or Lake Michigan, and appeared more "ragged" than in the other upper lakes.

Chlorophyll profiles in Lake Ontario differed greatly between the western and eastern basins of the lake. Sites in the western basin exhibited dramatic peaks in chlorophyll at 16 to 18 m, a depth corresponding to the bottom of the metalimnion (Fig. 4). Thermal structure was not highly developed at these sites, and the epilimnion typically extended to a depth of less than 10 m. Epilimnion depth was substantially greater in the eastern basin, (14 to 16 m), but DCM were largely lacking. Instead, at some sites a small increase in chlorophyll was seen at a depth of about 30 m, corresponding to the top of the hypolimnion.

The position of DCM in Lake Erie was much more variable, sometimes occurring at the base of the epilimnion or in the metalimnion, and sometimes forming a very diffuse band that extended through the bottom half of the epilimnion (Fig. 5). At a number of central basin sites, fluorometer profiles exhibited a gradual increase through much of the epilimnion, to peak at its base. More clearly defined chlorophyll peaks were seen at the base of the epilimnion in the eastern basin.

When the depth of the *in vivo* chlorophyll maximum was regressed against extinction coefficient (η) for sites at which both were available, a strong negative relationship was found ($F = 85.8$; $p < 0.001$), indicating that clearer water permitted the establishment of a deeper DCM (Fig. 6). This relationship appeared to be consistent across all five lakes, and also appeared to explain a substantial amount of the within-lake variation in the depth of the DCM. In particular, differences in the depth of the DCM at different sites in Lake Huron and Lake Erie appeared to be due to differences in water transparency.

Chemical Characteristics of DCM

Judging from *in situ* fluorometer values, chlorophyll maxima were, on average, 2 to 2.5 times greater than mean epilimnetic values for all lakes except for Superior, where DCM values were, on average, 3.25 times epilimnetic values. Chlorophyll concentrations measured *in vitro*, however, showed lesser differences between the DCM and epilimnion, and in some cases deep values were not elevated compared to integrated epilimnetic samples. Of the three lakes with sufficient samples to permit statistical testing, paired *t*-tests indicated that *in vitro* chlorophyll concentrations in both Lakes Superior and Huron were significantly higher in the DCM, compared to the epilimnion (using values from integrated samples). While concentrations were somewhat higher in the DCM in Ontario, this difference was not statistically significant (Table 1).

To determine if the differences in chlorophyll between these two habitats were due to actual differ-

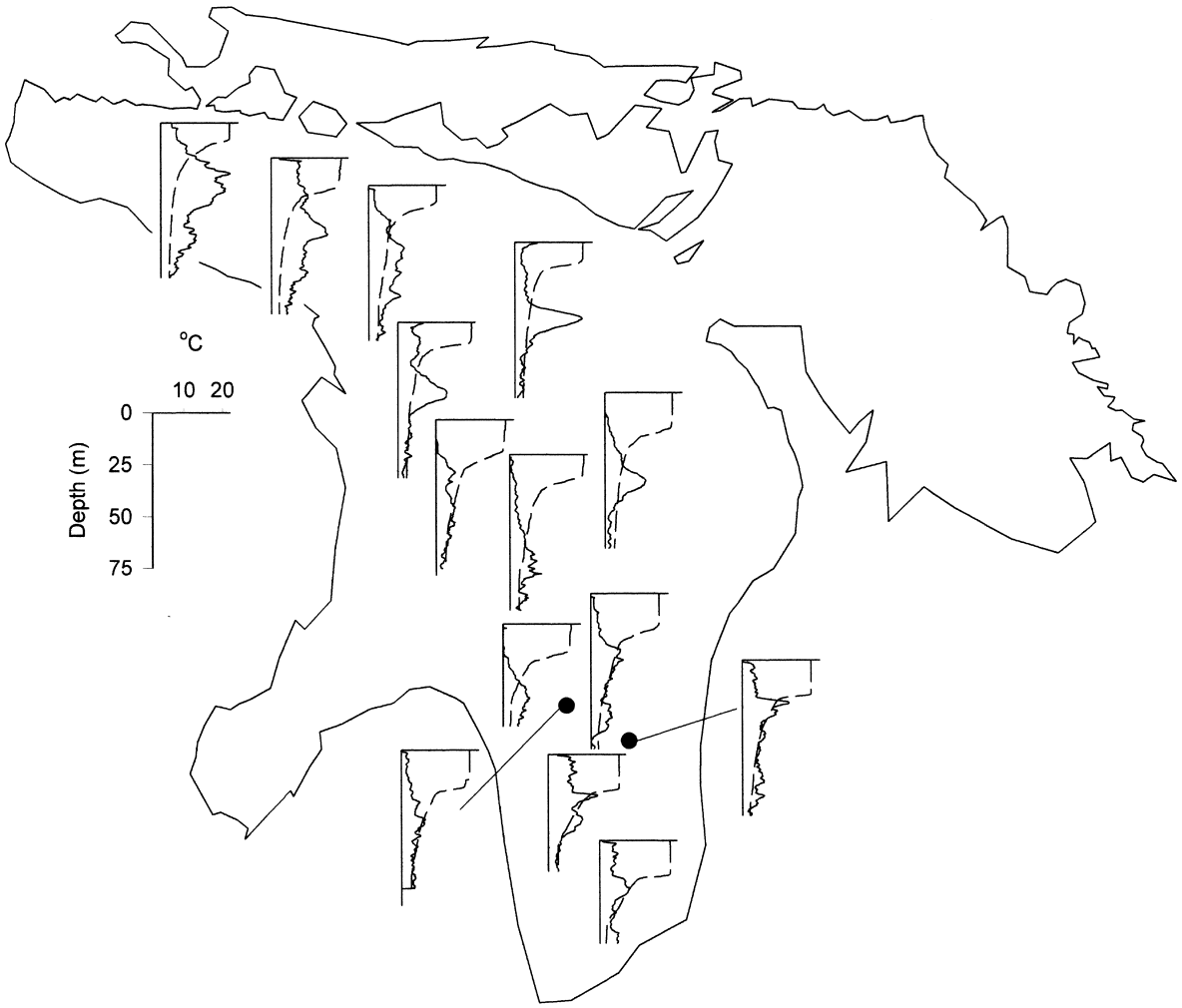

FIG. 3. **In vivo *chlorophyll (——) and temperature (------) profiles across Lake Huron, summer, 1998. Fluorometric units are relative.***

ences in phytoplankton biomass, as indicated by particulate carbon (PC), or due simply to increases in cellular concentrations of chlorophyll, both PC values and chlorophyll:carbon ratios of integrated and DCM samples were compared. Statistically significant differences in PC concentrations between DCM and integrated samples were found in only in Lake Superior, and not in Lakes Huron or Ontario (Table 1). Statistically significant differences in chlorophyll:carbon ratios, however, were found in both Lakes Superior and Huron, suggesting that shade adaptation was occurring in the deeper phytoplankton populations in these lakes. No significant difference was found in Lake Ontario, although the low p value and small sample size suggest that the lack of a statistical difference could have been due to low power of the test performed.

The real increases in phytoplankton biovolume seen in Lake Superior could have been fostered by improved nutrient concentrations at depth. This could be apparent both in higher concentrations of available nutrients at the depth of the DCM, and in improved nutrient status of phytoplankton at depth, as indicated, for example, by increased particulate phosphorus:particulate carbon (PP:PC) ratios. Ratios of PP:PC in the DCM were, in fact, statistically significantly higher than integrated values in Lake Superior, but not in the other two lakes (Table 1), suggesting an improved nutrient status of deep-living phytoplankton populations with regard to phos-

FIG. 4. **In vivo *chlorophyll (——) and temperature (------) profiles across Lake Ontario, summer, 1998. Fluorometric units are relative.***

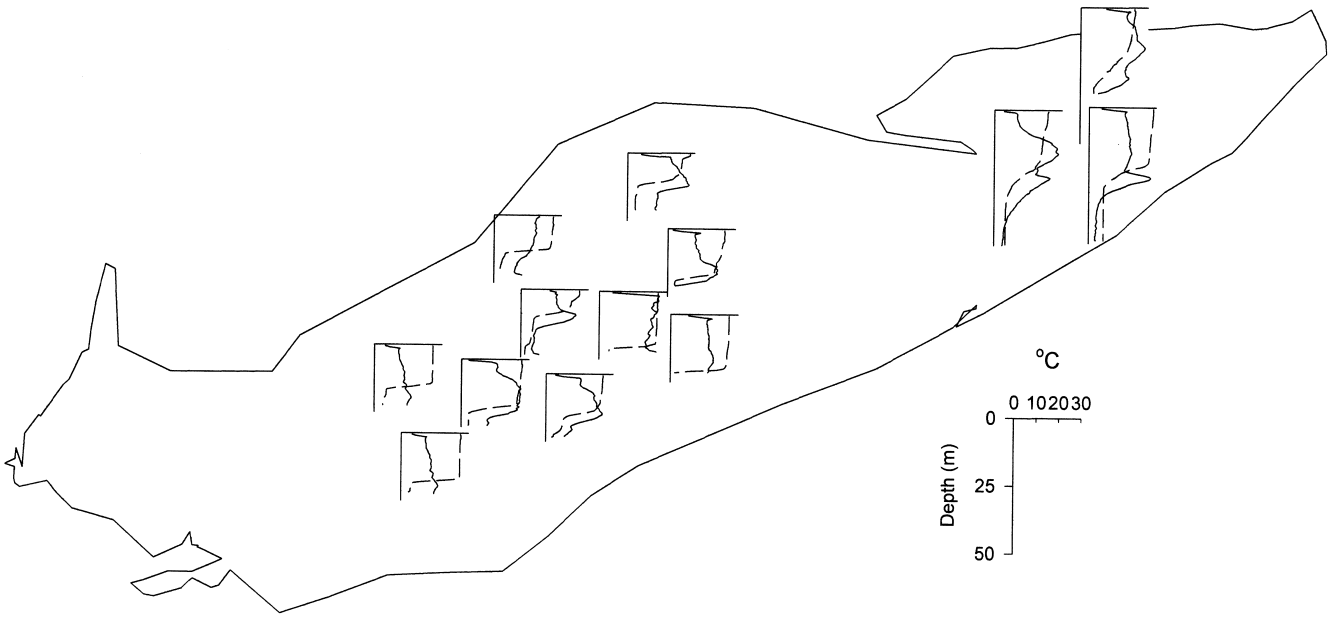

FIG. 5. **In vivo *chlorophyll (——) and temperature (------) profiles across Lake Erie, summer, 1998. Fluorometric units are relative.***

phorus in the former lake. Both soluble phosphorus and soluble silica concentrations were also statistically significantly higher at depth than in the epilimnion in Lake Superior, although the overall mean differences were relatively small (0.996 µg P/L, 0.098 mg Si/L).

Community Composition

Comparisons of percent similarity (PSC) values calculated between pairs of integrated and DCM samples with those calculated from QC samples indicated that DCM communities were statistically

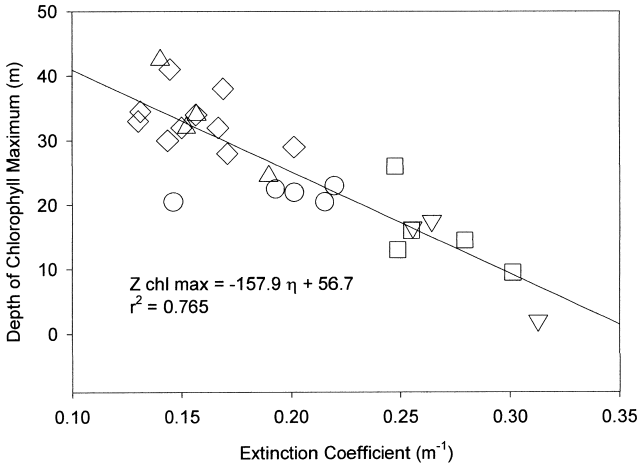

FIG. 6. Regression of extinction coefficient (η) against depth of maximum* in vivo *chlorophyll. ◇ = Superior; ○ = Michigan; △ = Huron; □ = Erie; ▽ = Ontario.

significantly less similar to each other than replicate QC samples were to each other in the case of all three lakes tested (Table 2). While these differences were all highly significant ($p < 0.0001$ in all cases), they should be interpreted with some caution since replicate QC counts are done on laboratory splits as a test of inter-analyst accuracy, rather than on actual field duplicates.

While differences in species composition between epilimnetic and DCM communities were highly variable, and probably incorporated at least to some degree sampling variability, some broad trends were apparent. In Lake Superior, DCM samples had substantially smaller populations of *Cyclotella* species, including *Cyclotella comta* (Ehr.) Kütz., *Cyclotella delicatula* Hust., and *Cyclotella comensis* Grun., compared to epilimnetic samples (Table 3). Deep samples in turn had larger populations of *Fragilaria crotonensis* Kitton (Table 4).

TABLE 1. Results of paired t-tests comparing chemical and biological characteristics of deep (DCM) and epilimnetic (INT) phytoplankton communities. In all cases, the following one-tailed hypothesis was tested: $H_0 : \mu_d \leq 0$; $\mu_d = \mu_{int} - \mu_{DCM}$. Significant differences ($\alpha = 0.05$) are shown in bold.

Lake Superior Variable	$\bar{x}$ INT	$\bar{x}$ DCM	Diff	t	p
***in vitro* Chl**	0.31	0.72	–0.41	–9.03	**0.001**
PC	0.12	0.15	–0.03	–3.06	**0.004**
Chl:C	2.59	4.78	–2.19	–10.46	**0.001**
PP:PC	9.26	14.35	–5.09	–7.00	**0.001**
TSP (µg/L)	1.12	2.12	–1.00	–11.29	**0.001**
Si (mg/L)	1.05	1.15	–0.10	–11.40	**0.001**
Lake Huron Variable	$\bar{x}$ INT	$\bar{x}$ DCM	Diff	t	p
***in vitro* Chl**	0.42	0.87	–0.45	–3.31	**0.011**
PC	0.16	0.18	–0.03	–1.11	0.159
Chl:C	2.73	4.63	–1.90	–3.71	**0.007**
PP:PC	12.57	14.19	–1.63	–0.56	0.300
TSP (µg/L)	1.99	2.50	–0.52	–1.02	0.177
Lake Ontario Variable	$\bar{x}$ INT	$\bar{x}$ DCM	Diff	t	p
in vitro Chl	1.30	1.55	–0.25	–1.26	0.149
PC	0.34	0.26	0.08	1.28	0.146
Chl:C	3.89	6.44	–2.56	–1.98	0.071
PP:PC	18.66	18.20	0.46	0.21	0.424
TSP (µg/L)	6.26	4.80	1.46	1.14	0.169

TABLE 2. Results of t-tests comparing percent similarity (PSC) values between quality control samples with those between DCM and integrated samples. In all cases, the following one-tailed hypothesis was tested: $H_0 : PSC_{QC} - PSC_{Int,\ DCM} \leq 0$.

Lake	$\bar{x}$ QC	$\bar{x}$ Int:DCM	Diff	t	p
Superior	0.572	0.353	0.219	6.69	< 0.001
Huron	0.572	0.226	0.346	6.41	< 0.001
Ontario	0.572	0.315	0.257	4.28	< 0.001

Two species of *Dinobryon*, *Dinobryon bavaricum* Imhof and *Dinbryon divergens* Imhof, were also less abundant at depth, and were apparently replaced by the congeners *Dinobryon sociale* Ehr., *Dinobryon cylindricum* Imhof, and *Dinobryon sertularia* Ehr. in the deep samples. Larger populations of an unidentified *Oscillatoria* species were also found in Lake Superior DCM samples.

Differences between the two communities in Lake Huron exhibited some similarities with Lake Superior. Populations of *C. comensis* and *C. comta* were reduced in DCM samples compared to epilimnetic samples, while those of *F. crotonensis* were increased. Also as in Lake Superior, *D. bavaricum* appeared to be replaced by *D. sertularia*, as well as the variety *Dinobryon sertularia* var. *protruberans* (Lemm.) Kreig. in DCM communities. In addition, *Chrysosphaerella longispina* Laut. emend. Nich., which was the dominant species in the eplimnion in Lake Huron in summer, was notably absent from DCM samples, although an unidentified species of *Chrysosphaerella* was recorded in the DCM at one site, to which it contributed a large amount of biomass. Large populations of a species of the filamentous chlorophyte *Ulothrix* were the most notable additions to the DCM communities at most sites in Lake Huron.

In Lake Ontario, increased biomass of *Ulothrix* and *F. crotonensis* were found in DCM samples, in comparison to epilimnetic samples. Large populations of the centric diatom *Stephanodiscus alpinus*

TABLE 3. Average lake-wide percent decrease in species biomass in the DCM compared to the epilimnion.

Lake Superior		Lake Huron	
Cyclotella comta (Ehr.) Kutz.	–8.77%	*Chrysosphaerella longispina* Laut. emend. Nich.	–17.41%
Dinobryon bavaricum Imhof	–7.15%	*Ceratium hirundinella* (O.F. Mull.) Schr.	–7.93%
Cyclotella delicatula Hust.	–5.37%	*Peridinium* spp.	–5.93%
Rhodomonas minuta Skuja	–1.93%	*Dinobryon bavaricum* Imhof	–4.91%
Dinobryon divergens Imhof	–1.63%	*Cyclotella comensis* Grun.	–3.34%
Cyclotella comensis Grun.	–1.55%	*Cyclotella comta* (Ehr.) Kutz.	–2.30%
Dinobryon bavaricum var. *vanhoeffenii* (Bachm.) Krieg.	–1.53%	*Rhizochrysis* spp.	–1.95%
Cryptomonas marssonii Skuja	–1.22%	*Ochromonas* spp.	–1.70%
Ochromonas spp.	–1.08%	*Cryptomonas reflexa* Skuja	–1.59%
Chromulina spp.	–0.96%	*Mallomonas* spp.	–1.47%
Aphanothece clathrata W. & G.S. West	–0.82%	*Trachelomonas* spp.	–1.08%
Cryptomonas erosa Ehr.	–0.71%	*Spiniferomonas* spp.	–0.94%
Lake Michigan		**Lake Ontario**	
Chrysosphaerella spp.	–16.28%	*Ceratium hirundinella* (O.F. Mull.) Schr.	–14.47%
Dinobryon divergens Imhof	–9.21%	*Peridinium* spp.	–4.86%
Planktonema lauterborni Schm.	–7.43%	*Dinobryon divergens* Imhof	–4.01%
Cryptomonas erosa Ehr.	–4.57%	*Tetraedron minimum* (A. Braun) Hansg.	–3.11%
Mallomonas spp.	–3.59%	*Cosmarium depressum* (Nag.) Lund	–2.97%
Peridinium spp.	–3.50%	*Scenedesmus ecornis* (Ralfs) Chod.	–2.66%
Gomphosphaeria lacustris Chod.	–2.38%	*Oocystis borgei* Snow	–2.15%
Cryptomonas phaseolus Skuja	–1.72%	*Cryptomonas erosa* Ehr.	–2.02%
Dinobryon bavaricum Imhof	–1.33%	*Haptophyceae*	–1.55%
Cryptomonas marssonii Skuja	–1.15%	*Oocystis crassa* Witt.	–1.39%
Dinobryon sociale var. *americanum* (Brunnth.) Bachm.	–1.07%	*Anacystis montana* f. *minor* Dr. & Daily	–1.38%
Cryptomonas spp.	–0.73%	*Oocystis parva* W. & G.S. West	–1.33%

TABLE 4. Average lake-wide percent increase in species biomass in the DCM compared to the epilimnion.

Lake Superior		Lake Huron	
Gymnodinium spp.	4.99%	*Fragilaria crotonensis* Kitton	10.42%
Fragilaria crotonensis Kitton	3.82%	*Ulothrix* spp.	9.52%
Oscillatoria spp.	2.93%	*Chrysosphaerella* spp.	9.07%
Dinobryon sociale Ehr.	2.21%	*Synedra ulna* var. *chaseana* Thomas	3.35%
Dinobryon cylindricum Imhof	1.89%	*Rhizosolenia longiseta* Zach.	2.43%
Ulothrix spp.	1.51%	*Tabellaria flocculosa* (Roth) Knud.	2.31%
Dinobryon sertularia Ehr.	1.41%	*Asterionella formosa* Hass.	2.17%
Glenodinium spp.	1.34%	*Dinobryon sertularia* var. *protuberans* (Lemm.) Kreig.	2.07%
Tabellaria flocculosa (Roth) Knud.	1.26%	*Dinobryon sertularia* Ehr.	1.95%
Gymnodinium helveticum f. *achroum* Skuja	1.21%	*Cryptomonas rostratiformis* Skuja	1.59%
Cryptomonas curvata Ehr.	1.14%	*Rhizosolenia eriensis* H.L. Sm.	1.44%
Pseudokephyrion attenuatum Hill	1.12%	*Cryptomonas ovata* Ehr.	1.39%
Lake Michigan		**Lake Ontario**	
Cosmarium depressum (Nag.) Lund	10.13%	*Ulothrix* spp.	11.41%
Chroococcus limneticus Lemm.	4.44%	*Stephanodiscus alpinus* Hust.	9.63%
Rhodomonas minuta Skuja	3.94%	*Gymnodinium helveticum* Pen.	7.16%
Rhodomonas minuta var. *nannoplanctica* Skuja	3.48%	*Fragilaria crotonensis* Kitton	6.20%
Aphanocapsa delicatissima W. & G.S. West	2.82%	*Diatoma tenue* var. *elongatum* Lyngb.	5.28%
Aphanothece clathrata W. & G.S. West	2.56%	*Tabellaria flocculosa* (Roth) Knud.	2.28%
Cyclotella comensis Grun.	2.44%	*Closteriopsis longissima* (Lemm.) Lemm.	1.81%
Aulacoseira subarctica (O. Mull.) Haworth	2.29%	*Cryptomonas erosa* var. *reflexa* Marss.	1.47%
Gloeocystis gigas (Kutz.) Lag.	1.96%	*Asterionella formosa* Hass.	1.21%
Chrysophyte unicell	1.89%	*Gymnodinium* spp.	1.11%
Dinobryon sociale Ehr.	1.65%	*Cyclotella comta* (Ehr.) Kutz.	1.05%
Cryptomonas erosa var. *reflexa* Marss.	1.62%	*Phacus* spp.	0.70%

Hust. were also found in the DCM; this species was common in the eplimnion in the spring, and could thus have represented a relict population from the previous season. As in Lake Superior, *D. divergens* was less abundant at depth than in the epilimnion, although it did not appear that any congener took its place in the DCM. The pennate diatoms *Diatoma tenue* Ag. and *Tabellaria flocculosa* (Roth) Knud. were also more common in deep communities than in the epilimnion. In all lakes members of the cryptophyta, in particular *Rhodomonas minuta* Skuja, were notably common in both the epilimnion and the DCM.

DISCUSSION

Chlorophyll *a* concentrations, as measured by *in vivo* fluorometry, were higher at depth than in the eplimnion at most sites in the upper lakes examined in this study. Chlorophyll maxima in Lake Superior occurred at depths of between 20 and 40 m, which agrees well with the results of previous workers (Watson *et al.* 1975, Moll and Stoermer 1982, Fahnenstiel and Glime 1983). The depth of the DCM in Lake Michigan were substantially more shallow and remarkably consistent, averaging about 23 m. Reports from the 1970s placed the deep chlorophyll maxima between 20 and 30 m in Lake Michigan (Brooks and Torke 1977, Moll *et al.* 1984), while during the 1980s the depth of the chlorophyll maximum apparently increased to between 40 and 70 m during August mid-stratification (Fahnenstiel and Scavia 1987a). This was attributed to an increase in water clarity brought about by increased zooplankton grazing. The results of this study are more consistent with earlier reports; extinction coefficients in Lake Michigan during the summer of 1998 ranged from –0.15 to –0.22/m, and were more similar to those reported from the 1970s (0.16 to 0.23/m: data from Fahnenstiel and Scavia 1987a) than the early 1980s (0.12 to 0.17/m: Scavia *et al.* 1986). However, extinction coefficients increased again in the late 1980s (pers. comm. G. Fahnenstiel, NOAA GLERL, April

2000), and so it is likely that the increased water clarity, and consequent increased DCM depth, witnessed in the early 1980s was the result of normal inter-annual variability in phytoplankton population size and/or zooplankton community structure, rather than indicative of any fundamental change in the Lake Michigan ecosystem.

Virtually no historical information is available on the existence of DCM in Lake Huron. A study of southern Lake Huron in 1974 found little consistency in the vertical distribution of phytoplankton, and in particular little correlation with thermal structure (Stoermer and Kreis 1980), although sampling resolution in that study was limited to four depths (surface, 5, 10, and 20 m). The results of this study also suggest a lack of spatial consistency; vertical distributions of chlorophyll were highly variable from site to site. Part of this variability appeared to be due to differences in water transparency in different parts of the lake. Interestingly, vertical chlorophyll profiles showed little similarity with those from Lake Michigan in spite of a general similarity in water chemistry and phytoplankton community composition between the two lakes (Barbiero and Tuchman 2001).

As might be expected from considerations of depth and water clarity, DCM in the lower lakes were not as pronounced or consistent as those in the upper lakes. Nonetheless, they were found at a number of sites in both Lake Erie and Lake Ontario. There is almost no information available from the literature, however, to indicate how consistent a phenomenon this is. Stoermer *et al.* (1974) provided some evidence of increased total phytoplankton cell counts in Lake Ontario at a depth of 5 or 10 m during July and August, 1972, although this was highly variable among the five stations examined. Munawar *et al.* (1974), reporting on a single mid-lake station, showed a very pronounced peak in both biomass and chlorophyll at 10 m in July of the same year. There appears to be no information available on vertical distribution of phytoplankton in Lake Erie.

In spite of the existence of DCM in all five Great Lakes, the ecological significance of this phenomenon differed from lake to lake. While large peaks of *in vivo* chlorophyll were seen at depth in Lake Ontario, statistically significant increases were not seen in either *in vitro* chlorophyll or Chl:C ratios. Therefore it appears that the DCM observed in fluorometer profiles was largely due to differences in the ratio of *in vivo* fluorescence to chlorophyll *a* concentration with depth. This could be a result of differences in chloroplast conformation, species composition or nutrient status (Keifer 1973a, Kiefer 1973b, Harris 1980). This contrasts with Munawar *et al.*'s (1974) results which found maxima of both biomass and *in vitro* chlorophyll *a* at depth. In Lake Huron, increased *in vitro* chlorophyll at depth could entirely be accounted for by shade adaptation (increased chlorophyll per cell), as evidenced both by increases in Chl:C ratios and a lack of increase in PC at depth.

The situation seems to have been different in Lake Superior. Chlorophyll was on average 3 times higher at depth than in the epilimnion, which is consistent with the 3.0 to 3.5-fold difference reported by Moll and Stoermer (1982) for Lake Superior in 1978. However, increases in the cellular chlorophyll content of deep phytoplankton populations, as suggested by high Chl:C ratios at depth, rather than actual increases in phytoplankton biomass, probably accounted for most of the elevated deep chlorophyll concentrations seen in the present study. Fahnenstiel and Scavia (1987b) similarly found DCM chlorophyll:carbon ratios in Lake Michigan to be about double those in the epilimnion, while Munawar and Munawar (1978), in an extensive survey of Lake Superior phytoplankton, did not notice substantial increases in phytoplankton biovolume at depth.

Phytoplankton in the DCM in Lake Superior did appear to be benefiting from improved nutrient conditions at depth, relative to epilimnetic communities, as evidenced by P:C ratios which averaged 14.3 µg/mg in the DCM, compared to 9.3 in the epilimnion. Healey and Hendzel (1980) have suggested a P:C ratio of 10 to delimit moderate and severe nutrient deficiency, with P:C < 10 a sign of severe deficiency. According to this criterion, phytoplankton communities at depth were, on average, under considerably less nutrient stress than epilimnetic communities. Similar results have been found for both metalimnetic cyanobacterial populations (Konopka 1982, Konopka 1989) and mixed metalimnetic and hypolimnetic communities (Healey and Hendzel 1980, Barbiero and McNair 1996). Both TSP and Si were higher at depth than in the epilimnion, though these differences were slight. Even so, the extreme nutrient deficiency in the epilimnion of Lake Superior could make even modest increases in soluble nutrients at depth ecologically significant.

It should be borne in mind that deep-living algal communities can be highly dynamic, and the results of this study represent only a single sampling

date for each site. Where nutrient concentrations play a role in determining DCM extent and position, uptake by the algae themselves will alter nutrient profiles, thus in turn effecting changes in vertical chlorophyll distribution over time (Barbiero and McNair 1996). In Lake Michigan, both the depth of the DCM and the relative importance of *in situ* growth, sedimentation, and shade adaptation to its maintenance have been shown to change markedly over the course of the stratified period (Fahenstiel and Scavia 1987b). Physical disturbance, such as seiche activity, can alter vertical profiles of chlorophyll on a shorter-term basis, as has been shown in both Lakes Michigan and Superior (Moll and Stoermer 1982, Moll *et al.* 1984). Such short-term alterations might be more pronounced in the less thermally stable lower lakes. Differences between the results of this study and those of previous studies must therefore be viewed in the context of this potential temporal variation, which the data in this study cannot address.

Differences in species composition between epilimnetic and deep-living communities were apparent in all cases, although these differences were for the most part at variance with those previously reported in the literature. Both Fahnenstiel and Glime (1983) and Moll and Stoermer (1982) reported DCM in Superior composed almost exclusively of *Cyclotella* species, while in this study abundances of this genus were found to be notably reduced in deep samples in both Lakes Superior and Huron. Large differences in species composition between epilimnetic and deep communities were not apparent in data presented from open lake stations in Lake Superior by Munawar and Munawar (1978), neither did they find increases in biomass at depth. Brooks and Torke (1977) found the DCM community of Lake Michigan to be dominated by *Dinobryon sociale, Tabellaria fenestrata, Fragilaria crotonensis,* and green and blue-green filaments. The former two species were also dominant in the epilimnion. In Lake Ontario, the most notable difference in deep communities was the increase in the green filamentous genus *Ulothrix*, smaller increases of which were also noted in Lakes Huron and Superior. Moll *et al.* (1984) presented data from Lake Michigan that showed increases in "green filaments" at a depth coincident with the DCM. In addition, in their study, populations of *Cyclotella stelligera*, which was apparently a dominant taxon in the upper waters, were notably reduced at the depth of the DCM. Among the only other Great Lakes reports of species composition in a DCM, Munawar and Munawar (1982) indicated this community in Lake Ontario was dominated by cryptophytes, in contrast to the results reported here.

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REFERENCES

APHA (American Public Health Association). 1985. *Standard Methods for the Examination of Water and Wastewater*. 16th ed. Washington, D.C.: American Public Health Association.

Barbiero, R.P., and McNair, C.M. 1996. The dynamics of vertical chlorophyll distribution in an oligomesotrophic lake. *J. Plankton. Res.* 18:225–237.

_____, and Tuchman, M.L. 2001. Results from the U.S. EPA's biological open water surveillance program of the Laurentian Great Lakes: I. Introduction and phytoplankton results. *J. Great Lakes Res.* 27(2): 134–154.

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.

Drouet, F., and Daily, W.A. 1973. *Revision of the Coccoid Myxophyceae*. New York, NY: Hafner Press.

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: recent changes in surface and deep communities. *Can. J. Fish. Aquat. Sci.* 44:509–514.

_____, and Scavia, D. 1987b. Dynamics of Lake Michigan phytoplankton: the deep chlorophyll layer. *J. Great Lakes Res.* 13:285–295.

Germain, H. 1981. *Flore des Diatomées Eaux Douces et Saumâtres*. Paris: Société Nouvelle des Éditions Boubée.

Harris, G.P. 1980. The relationship between chlorophyll *a* fluorescence, diffuse attenuation changes and photosynthesis in natural phytoplankton populations. *J. Plankton Res.* 2:109–126.

Healey, F.P., and Hendzel, L.L. 1980. Physiological

indicators of nutrient deficiency in lake phytoplankton. *Can. J. Fish. Aquat. Sci.* 37:442–453.

Huber-Pestalozzi, G. 1941. *Die Binnengenwasser: Band XVI. Das Phytoplankton Des Süßwassers. Systematik und Biologie. Teil 2, 1. Hälfte: Chrysophyceen, Farblose Flagellaten, Heterokonten*. Stuttgart: E. Schweizerbart`sche Verlagsbuchhandlung.

_____. 1968. *Die Binnengenwasser: Band XVI. Das Phytoplankton Des Süßwassers. Systematik und Biologie. Teil 3. Cryptophyceae, Chloromonadophyceae, Dinophyceae. 2. Aufl. Mit Neubearbeitung der Chloromonadophyceae und neuestem Literaturverzeichnis von B. Fott*. Stuttgart: E. Schweizerbart`sche Verlagsbuchhandlung.

_____. 1983. *Die Binnengenwasser: Band XVI. Das Phytoplankton Des Süßwassers. Systematik und Biologie. Teil 7, 1. Hälfte. Chlorophyceae (Grünalgen), Ordnung Chlorococcales von Jiri Komarek und Bohuslav Fott.* Stuttgart: E. Schweizerbart`sche Verlagsbuchhandlung.

Keifer, D.A. 1973a. Chlorophyll a fluorescence in marine centric diatoms: responses of chloroplasts to light and nutrient stress. *Mar. Biol*. 23:39–46.

_____. 1973b. Fluorescence properties of natural phytoplankton populations. *Mar. Biol*. 22:263–269.

Konopka, A. 1982. Physiological ecology of a metalimnetic *Oscillatoria rubescens* population. *Limnol. Oceanogr.* 27:1154–1161.

_____. 1989. Metalimnetic cyanobacteria in hard-water lakes: Buoyancy regulation and physiological state. *Limnol. Oceanogr.* 34:1174–119–84.

Krammer, K., and Lange-Bertalot, H. 1991. *Süßwasserflora von Mitteleuropa, II:2 Bacillariophyceae. 3.Teil: Centrales, Fragilariaceae, Eunotiaceae*. NY, New York: Gustav Fischer Verlag.

_____, and Lange-Bertalot, H. 1997. *Süßwasserflora von Mitteleuropa, II:2 Bacillariophyceae. 2.Teil: Bacillariaceae, Epithemiaceae, Surirellaceae*. New York, NY: Gustav Fischer Verlag.

Lund, J.W.G., Kipling, C., and LeCren, E.D. 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. *Hydrobiologia* 11:143–170.

Moll, R.A., and Stoermer, E.F. 1982. A hypothesis relating trophic status and subsurface chlorophyll maxima of lakes. *Arch. Hydrobiol.* 94:425–440.

_____, Brahce, M.Z., and Peterson, T.P. 1984. Phytoplankton dynamics within the subsurface chlorophyll maximum of Lake Michigan. *J. Plankton Res*. 6:751–766.

Munawar, M., and Munawar, I.F. 1978. Phytoplankton of Lake Superior 1973. *J. Great Lakes Res.* 4:415–442.

_____, and Munawar, I.F. 1982. Phycological studies in lakes Ontario, Erie, Huron, and Superior. *Can. J. Bot.* 60:1837–1858.

_____, Stadelman, P., and Munawar, I.F. 1974. Phytoplankton biomass, species composition and primary production at a nearshore and a midlake station of Lake Ontario during IFYGL. In *Proc. 17th Conf. Great Lakes Res.*, pp. 629–652. Internat. Assoc. Great Lakes Res.

Patrick, R., and Reimer, C.W. 1966. *The Diatoms of the United States, Exclusive of Alaska and Hawaii. Volume One: Fragilariaceae, Eunotiaceae, Achnanthaceae, Naviculaceae.* Philadelphia, PA: The Academy of Natural Sciences.

_____, and Reimer, C.W. 1975. *The Diatoms of the United States, Exclusive of Alaska and Hawaii. Volume Two, Part One: Entomoneidaceae, Cymbellaceae, Gomphonemaceae, Epithemiaceae*. Philadelphia, PA: The Academy of Natural Sciences.

Prescott, G.W. 1962. *Algae of the Western Great Lakes Area*. Koenigstein, Germany: Otto Koeltz Science Publishers.

Putnam, H.D., and Olson, T.A. 1966. Primary productivity at a fixed station in western Lake Superior. In *Proc. 9th Conf. Great Lakes Res.*, pp. 119–128. Internat. Assoc. Great Lakes Res.

Scavia, D., Fahnenstiel, G.L., Evans, M.S., Jude, D.J., and Lehman, J.T. 1986. Influence of salmonine predation and weather on long term water quality trends in Lake Michigan. *Can. J. Fish. Aquat. Sci.* 43:435–443.

Stoermer, E.F., and Kreis, R.G., Jr. 1980. *Phytoplankton Composition and Abundance in Southern Lake Huron*. U.S. EPA, Duluth, MN. EPA-600/3-80-061.

_____, Bowman, M.M., Kingston, J.C., and Schaedel, A.L. 1974. *Phytoplankton composition and abundance in Lake Ontario During IFYGL*. Univ. Mich., Great Lakes Res. Div. Spec. Rep. 53.

Watson, N.H.F., Thomson, K.P.B., and Elder, F.C. 1975. Sub-thermocline biomaass concentration detected by transmissometer in Lake Superior. *Verh. Internat. Verein. Limnol.* 19:682–688.

Welschmeyer, N. 1994. Fluorometric analysis of chlorophyll *a* in the presence of chlorophyll *b* and pheopigments. *Limnol. Oceanogr.* 39:1985–1992.

Whittaker, R.H. 1952. A study of summer foliage insect communities in the Great Smoky Mountains. *Ecol. Monogr*. 22:1–44.

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