

Phototrophic Picoplankton in Lakes Huron and Michigan: Abundance, Distribution, Composition, and Contribution to Biomass and Production

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The phototrophic picoplankton communities of Lakes Huron and Michigan were studied from 1986 through 1988. Abundances in the surface-mixed layer ranged from 10 000 to 220 000 cells·mL⁻¹ with a seasonal maximum during the period of thermal stratification. During thermal stratification, maximum abundances were generally found within the metalimnion/hypolimnion at depths corresponding to the 0.6–6.0% isolumes. The picoplankton community was dominated by single phycoerythrin-containing (PE) *Synechococcus* (59%) with lesser amounts of chlorophyll fluorescing cells (21%), PE colonial *Synechococcus*-like cells (11%), other PE colonial Chroococcales (6%), and other cells (3%). Single PE *Synechococcus* was abundant throughout the year whereas chlorophyll-fluorescing and colonial cyanobacteria were more abundant during the periods of spring isothermal mixing and summer stratification, respectively. Picoplankton accounted for an average of 10% (range 0.5–50%) of phototrophic biomass. Phototrophic organisms that passed 1-, 3-, and 10- μ m screens were responsible for an average of 17% (range 6–43%), 40% (21–65%), and 70% (52–90%) of primary production. Maximum contributions of <1, <3, and <10 μ m size fractions occurred during the period of thermal stratification. Primary production by phototrophic picoplankton was found to equal production in the <1 μ m size fraction.

De 1986 à 1988, on a étudié les communautés de picoplancton phototrophe des lacs Huron et Michigan. Dans la couche de brassage de surface, l'abondance variait de 10 000 à 20 000 cellules·mL⁻¹ et atteignait son maximum lors de la période de stratification thermique, en particulier dans le métalimnion et l'hypolimnion à des profondeurs correspondant aux isovolumes allant de 0,6 à 6,0 %. La communauté picoplanctonique était en grande partie composée de *Synechococcus* unicellulaires (59 %) contenant de la phycoérythrine (PE); elle comprenait aussi de moindres quantités de cellules fluorescentes (21 %), de cellules coloniales semblables à *Synechococcus* contenant de la PE, d'autres Chroococcales coloniales contenant de la PE (6 %) ainsi que d'autres types de cellules (3 %). Les populations de *Synechococcus* unicellulaires contenant de la PE étaient abondantes pendant toute l'année, tandis que les populations de cyanobactéries fluorescentes et coloniales étaient plus abondantes pendant les périodes de brassage printanier de l'isotherme et de la stratification estivale, respectivement. Le picoplancton représentait en moyenne 10 % (écart 0,5 à 50 %) de la biomasse planctonique. Les organismes phototrophes non retenus dans des cribles de 1, 3 et 10 μ m étaient à l'origine, en moyenne, de 17 % (écart 6 à 43 %), 40 % (écart 21 à 65 %) et 70 % (écart 52 à 90 %) de la production primaire, respectivement. L'apport maximum des classes dimensionnelles de <1, <3 et <10 μ m a été décelé lors de la période de stratification thermique. On a noté que la production primaire par le picoplancton phototrophe était égale à la production de la classe dimensionnelle de <1 μ m.

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During the past decade, the importance of phototrophic picoplankton as significant contributors to primary production and phototrophic biomass in a wide variety of environments has been realized (see reviews by Stockner and Antia 1986; Stockner 1988). The contribution of picoplankton to primary production and phototrophic biomass increases in oligotrophic environments where it can be as much as 90% of total primary production (Li et al. 1983; Stockner and Antia 1986). Picoplankton communities are generally dominated by cyanobacteria of the genus *Synechococcus* and chlorophyll-fluorescing cells of a more uncertain taxonomic origin (Waterbury et al. 1979; Caron et al. 1985; Murphy and Haugen 1985; Glover et al. 1986; Chisholm et al. 1988). *Synechococcus* typ-

ically are abundant throughout most of the photic zone whereas chlorophyll-fluorescing cells become more abundant at the base (Murphy and Haugen 1985; Glover et al. 1986). Much of this picoplankton production appears to be consumed within the photic zone by small heterotrophic protozoans (Fahnenstiel et al. 1991a).

Most information regarding phototrophic picoplankton is from studies in the marine environment (Stockner and Antia 1986). In freshwater systems, previous studies have focused primarily on a specific component of the community (Caron et al. 1985; Fahnenstiel et al. 1986; Weisse 1988; Weisse and Munawar 1989; Fahnenstiel et al. 1991a, 1991b), on the contribution of picoplankton to biomass or production (Craig 1984;

Pick and Caron 1987; Stockner 1987), or the role of picoplankton in the food web (Stockner and Shortreed 1989). Only one study has described the abundance, distribution, and composition of the entire phototrophic picoplankton community (Nagata 1986).

The large, deep, oligotrophic nature of Lakes Michigan and Huron make them particularly good environments to study phototrophic picoplankton communities for comparisons with the marine environment. The microbial food web of Lake Michigan has received much attention in the past 5 yr with studies on the role of heterotrophic picoplankton (Scavia et al. 1986; Scavia and Laird 1987) as well as on the abundance, composition, and biomass of nanoplankton and microplankton communities (Carrick and Fahnenstiel 1989, 1990). Information on phototrophic picoplankton is needed to conceptualize carbon flow within the microbial food web of Lake Michigan. This study was initiated to describe the phototrophic picoplankton community of Lakes Huron and Michigan with a focus on abundance, composition, and contribution to primary production.

Materials and Methods

Sampling was conducted on 26 days at two offshore stations in Lake Huron (northern: 45°25'N, 82°55'W, maximum depth 150 m; southern: 43°54'N, 82°21'W, maximum depth 70 m) and on 15 days at a single station in Lake Michigan (43°1'N, 86°36'W, maximum depth 100 m) from March 1986 to November 1988. The biological, chemical, and physical conditions at these offshore stations are representative of general offshore conditions in both lakes (Lesht and Rockwell 1985; Makarewicz 1985, 1987; Laird et al. 1987). Total phosphorus concentrations range from 0.1 to 0.3 μM and soluble reactive phosphorus concentrations are at or below the detection level ($<0.01 \mu\text{M}$) during summer thermal stratification (Lesht and Rockwell 1985; Laird et al. 1987). Nitrate concentrations in both lakes generally exceed 15 μM throughout the year. Silica concentrations decrease from approximately 15–30 μM during the spring mixing period to ≤ 5 –15 μM in Lake Michigan and 5–15 μM in Lake Huron during thermal stratification (Lesht and Rockwell 1985; Laird et al. 1987). Phytoplankton chlorophyll concentrations in the surface-mixed layer range from 0.5 to 3.0 $\text{mg}\cdot\text{m}^{-3}$ with highest values during the spring mixing period (Lesht and Rockwell 1985; Fahnenstiel et al. 1989).

Water samples were collected with 5- or 10-L PVC Niskin bottles. Water column temperature profiles were measured with an electronic bathythermograph, and underwater scalar irradiation was measured with a Licor LI-193SB sensor and LI-188B integrating meter. Chlorophyll concentrations were determined fluorometrically from 90% acetone extracted samples (Strickland and Parsons 1972).

For this study, picoplankton were defined by microscopic analysis as organisms $<3 \mu\text{m}$ in all dimensions. This size is slightly larger than the 2- μm definition used by Sieburth et al. (1978) but similar to the size used by Stockner and Antia (1986). Because almost all phototrophic picoplankton in Lakes Huron and Michigan are significantly $<2 \mu\text{m}$, either definition could be used in this study with similar results.

Water samples for microscopic analysis were transferred into 250-mL amber bottles and preserved with either glutaraldehyde (1% final concentration) buffered with sodium cacodylate (0.1 M final concentration) for picoplankton or with 0.3% Lugol's acid iodine for phytoplankton. Picoplankton samples were then cooled ($\sim 5^\circ\text{C}$) until duplicate slides were prepared

within 24 h (Waterbury et al. 1979) and then frozen (-20°C). These slides were counted within a few days to minimize the fading of autofluorescence. Picoplankton biomass and composition on each slide were estimated by enumerating a minimum of 500 units ($<5\%$ counting error assuming Poisson statistics, Lund et al. 1958) using a Leitz Laborlux microscope (magnification 1250 \times) equipped to distinguish the dominant bright autofluorescent emission of an individual cell. To examine abundance and composition of picoplankton within thermal regions of the water column (surface-mixed layer, metalimnion, and hypolimnion) on a given date, individual values (typically three to five) from specific depths were averaged within each layer.

The dominant fluorescence of a cell allowed us to determine the general taxonomic position of each cell (Tsuji et al. 1986). Specifically, chlorophyll-dominant cells emitted far-red light ($>660 \text{ nm}$) when excited with blue light (450 nm) or green light (530–560 nm). Phycoerythrin-dominant cells were characterized by yellow emission following blue excitation and by bright red fluorescence (600–660 nm) when excited with green light. Phycocyanin-rich cells were detected by very faint or no emission in the red (600–660 nm) and far-red ($>660 \text{ nm}$) when excited with blue light and by very bright red emission with green excitation. The length and breadth of 20 individuals of each taxon were measured twice during each major season from projections of photomicrographs. Cell volumes were calculated for each taxon assuming geometric configurations, and these estimates were subsequently converted to carbon using the conversion factor of 121 fg $\text{C}\cdot\mu\text{m}^{-3}$ (Watson et al. 1977).

Our procedure for preparing and counting picoplankton cells may underestimate total picoplankton abundance due to fading of very weak chlorophyll-fluorescing cells (Chisholm et al. 1988) or destruction of delicate cells (Murphy and Haugen 1985). To examine these possibilities, on several occasions we compared picoplankton counts using our standard approach with counts made immediately on live samples. We did not detect any difference for phycobilin-containing cells, but some differences were noted for chlorophyll-fluorescing cells, as counts from our standard procedure were on average 83% of counts from live samples (range 65–118%). Also, on two occasions we compared our routine counts of phototrophic picoplankton with counts from a flow cytometer and detected no significant differences (Fahnenstiel et al. 1991b). Thus, we consider our estimates of picoplankton abundance to be reasonably accurate.

Phytoplankton were prepared and enumerated using the technique of Dozier and Richerson (1975). Subsamples (5–25 mL) of the preserved phytoplankton samples were filtered onto 0.22- μm filters, placed on microscope slides, and subsequently cleared with glutaraldehyde under low heat. Cleared filters were then permanently mounted with Permount and a coverslip. The dimensions of each taxon encountered was measured and converted to biovolume by applying appropriate geometric shapes. These estimates were subsequently converted to carbon using the formula of Strathman (1966) with separate conversions for diatoms and nondiatoms.

Primary production was estimated using the ^{14}C technique (Vollenweider 1974) following modifications outlined in Fahnenstiel et al. (1989). Water collected from either the surface mixing layer or in the vicinity of the deep chlorophyll layer was immediately dispensed into duplicate shaded 2-L polycarbonate bottles, inoculated with 2–220 μCi (1 $\mu\text{Ci} = 37 \text{ kBq}$) of ^{14}C as NaHCO_3 , and incubated for a short time (1–2 h) at ambient

temperature in a shipboard photosynthesis-irradiance incubator. Following the incubation, subsamples from the high-activity 2-L bottles were postfractionated through 1- and 3- μm Nuclepore membranes and 10- μm Nitex screen; a portion of unfractionated water was retained to serve as an estimate of total primary production. Very low vacuum pressure was used for all of the fractionations (<50 mm Hg (1 mm Hg = 133.322 Pa)). Three subsamples from each fraction (<1, <3, and <10 μm) were filtered onto membranes (0.22- μm Millipore), decontaminated with 0.5 mL of 0.5 N HCl for 4–6 h, placed in scintillation vials with 12 mL of scintillation cocktail, and assayed with a Packard Tri-Carb spectrometer. Counting efficiencies were determined by external standards.

Results

Seasonal Temperatures and Light Extinction Coefficients

Surface-mixed layer temperatures were similar in Lakes Huron and Michigan. In 1986–88 the spring isothermal mixing period lasted from March to late May/early June in the southern regions of the lakes and into June in the northern regions. The period of thermal stratification began in May/June and lasted into December when fall turnover occurred. Maximum surface temperatures occurred in the late July/August period in the southern regions of the lakes and in August in the northern regions. At this time, the surface-mixed layer temperatures were 20–24°C and the depth of the surface-mixed layer was approximately 10–15 m. For the purposes of discussion, thermal stratification was divided into two periods: intermediate stratification when surface-mixed layer temperatures were from 4 to 15°C and midstratification when surface-mixed layer temperatures were >15°C (Fahnenstiel and Scavia 1987).

In both lakes, the light extinction coefficient (PAR) ranged from 0.14 to 0.23 m^{-1} ; minimum values (0.14–0.17 m^{-1}) occurred in the July/early August period.

Picoplankton Abundance and Distribution

Although the study covered 3 yr, limited sampling in some years prevented us from examining annual variability. However, since major thermal periods were sampled several times during the study, representative conditions can be described (Table 1). In both lakes, picoplankton were abundant in the

surface-mixed layer (10^3 – 10^5 cells·mL⁻¹) and demonstrated marked seasonal variability (Fig. 1 and 2; Table 1). Mean surface picoplankton abundance was 5.96×10^4 cells·mL⁻¹ in Lake Michigan and 4.27×10^4 cells·mL⁻¹ in Lake Huron whereas maximum surface abundance was 2.26×10^5 cells·mL⁻¹ in Lake Michigan and 1.21×10^5 cells·mL⁻¹ in Lake Huron. Generally, surface picoplankton abundances were low during isothermal mixing periods or during weak inversely stratified periods and then increased during thermal stratification (Fig. 1 and 2; Table 1). Abundances were similar in the northern and southern Lake Huron stations (Fig. 1), suggesting that horizontal variation in the offshore regions of the lake was minimal.

During summer thermal stratification, distinct vertical variation in picoplankton abundance was found with maximum abundance generally located at approximately 20–30 m within the metalimnion or upper hypolimnion (Fig. 3 and 4). With light extinction coefficients ranging from 0.14 to 0.17 m^{-1} , the depths of these maxima received 0.6–6.0% of surface irradiance. Maximum picoplankton abundances in both lakes (2.27×10^5 cells·mL⁻¹ in Lake Michigan and 2.15×10^5 cells·mL⁻¹ in Lake Huron) were found within the metalimnion. With one exception (Lake Huron, 5 August 1986), all vertical profiles of picoplankton abundance exhibited a subsurface maximum severalfold higher than the abundance of surface populations (deep to surface ratio 2.0–11.0) with the most pronounced maxima occurring in July/August.

Community Structure

We divided the picoplankton community into five groups based on pigment fluorescence, morphology, size of cell, and mode of growth (Table 2). The structure of the picoplankton communities was similar in both lakes (Fig. 1 and 2; Table 2) and was dominated by phycoerythrin-rich cyanobacteria of approximately 0.9 to 1.6 μm , which constituted approximately 80% of the total picoplankton community.

The most abundant cyanobacteria were single coccoid phycoerythrin-rich cyanobacteria of approximately 1.0 μm (Table 3), which constituted, on average, 50–60% of total abundance in both lakes (Fig. 1 and 2; Table 2). The maximum abundance of these cells was 1.89×10^5 cells·mL⁻¹ in Lake Michigan and 1.78×10^5 cells·mL⁻¹ in Lake Huron, with both

TABLE 1. Mean abundance of phototrophic picoplankton from major thermal periods and layers at two stations in Lake Huron and at a single station in Lake Michigan (n = number of sampling dates).

Lake	Thermal period	Layer	Mean abundance ^a	n
Michigan	Isothermal	Surface	26 000	7
	Stratification	Surface	70 900	8
		Metalimnion	105 200	7
		Hypolimnion	12 200	7
Mean			59 600	15
Huron	Isothermal	Surface	38 400	8
	Stratification	Surface	53 500	18
		Metalimnion	65 400	15
		Hypolimnion	15 500	10
Mean			42 700	26
Grand mean both lakes			51 150	41

^aUnits are cells·mL⁻¹.

LAKE HURON

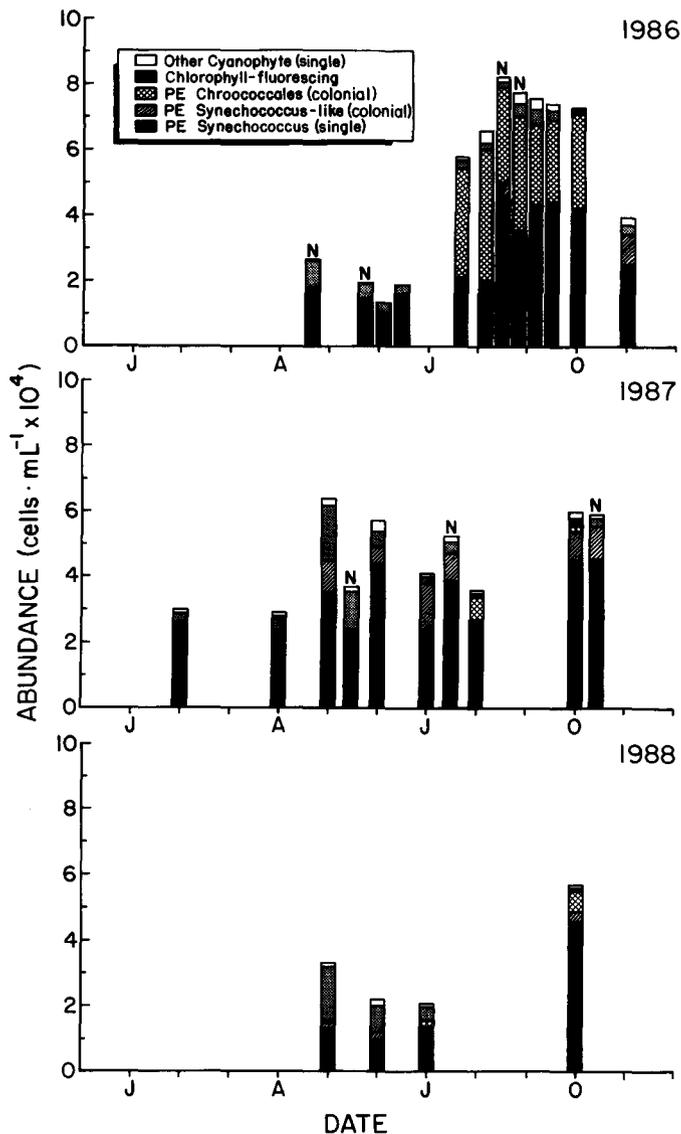


FIG. 1. Seasonal abundance and composition of phototrophic picoplankton from the surface-mixed layer at two stations in Lake Huron. N indicates data from northern Lake Huron station. The five groups of picoplankton are phycoerythrin-containing (PE) single *Synechococcus*, PE colonial *Synechococcus*-like cells, other PE colonial Chroococcales cells, chlorophyll-fluorescing cells, and other cyanophytes.

maxima occurring within the metalimnion during thermal stratification. In culture, an isolate of these cells divided in one plane; therefore, we tentatively assigned these cells to the genus *Synechococcus* (Stanier et al. 1971). *Synechococcus* dominance was not confined spatially or temporally in either lake, but rather dominated at all stations throughout the study (Table 2).

Although picoplankton communities were dominated generally by single-celled *Synechococcus*, other phycoerythrin-containing cyanobacteria became abundant at specific times of the year (Fig. 1 and 2; Table 2). During thermal stratification, colonial or aggregate cyanobacteria become abundant, and in some cases, even dominant. The percent contribution of colonial cyanobacteria to total picoplankton abundance increased

LAKE MICHIGAN

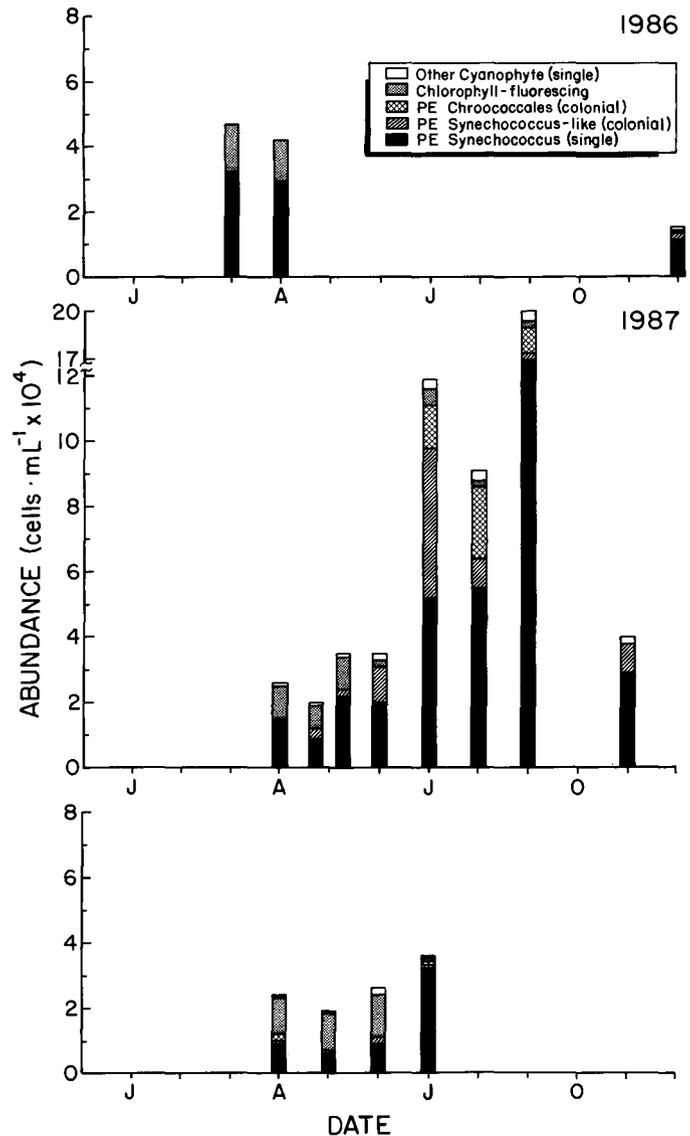


FIG. 2. Seasonal abundance and composition of phototrophic picoplankton from the surface-mixed layer at a single station in Lake Michigan. Picoplankton groups are as defined in Fig. 1.

dramatically from approximately 5% during the spring isothermal period to over 20% during thermal stratification. Most of the large increase in total picoplankton abundance during thermal stratification can be attributed to this increase in colonial forms (Fig. 1 and 2), particularly in Lake Huron. On average, colonial phycoerythrin-containing cyanobacteria contributed 21.1 and 13.6% of total picoplankton abundance in Lakes Michigan and Huron, respectively.

These colonial cyanobacteria were divided into two groups based on cell morphology. The first and most abundant group of colonial cyanobacteria (Table 2) was morphologically similar to the single *Synechococcus* group described above, differing only in the colonial mode of growth. This coccoid colonial *Synechococcus*-like group was separated because we were unable to produce any colonial aggregations in our culture of the single *Synechococcus* isolate under a variety of conditions, and the ecology of these two groups is probably different. The

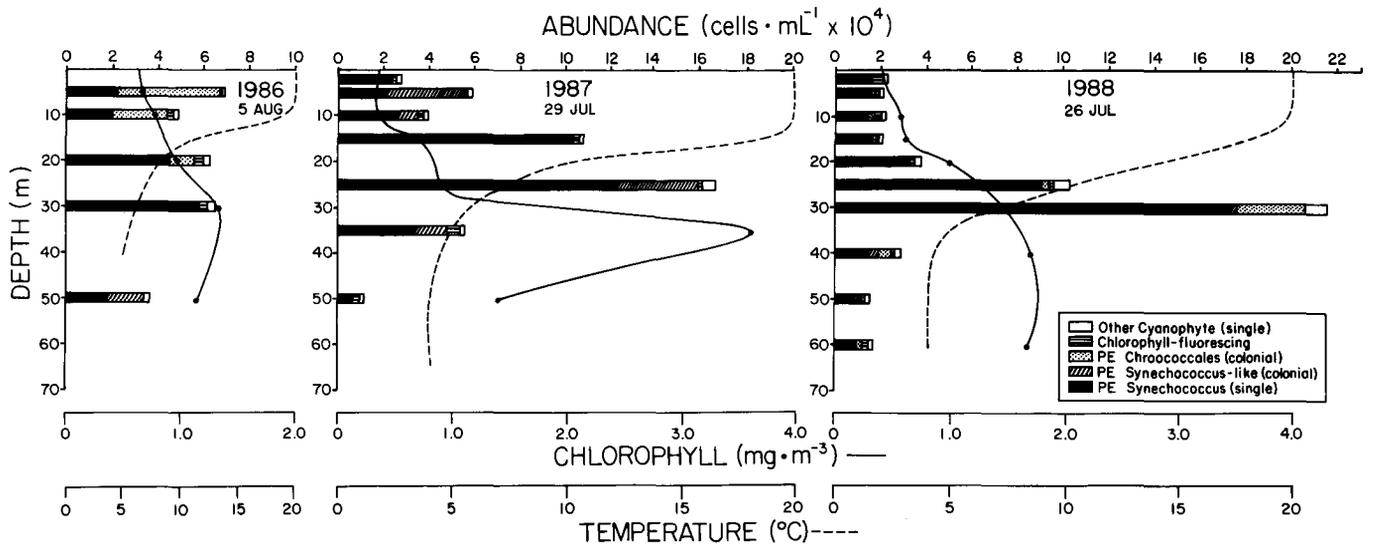


FIG. 3. Vertical distribution and composition of phototrophic picoplankton during thermal stratification at a station in southern Lake Huron (43°54'N, 82°21'W) on 5 August 1986, 29 July 1987, and 26 July 1988. The solid line represents chlorophyll concentration and the broken line represents temperature. Picoplankton groups are as defined in Fig. 1.

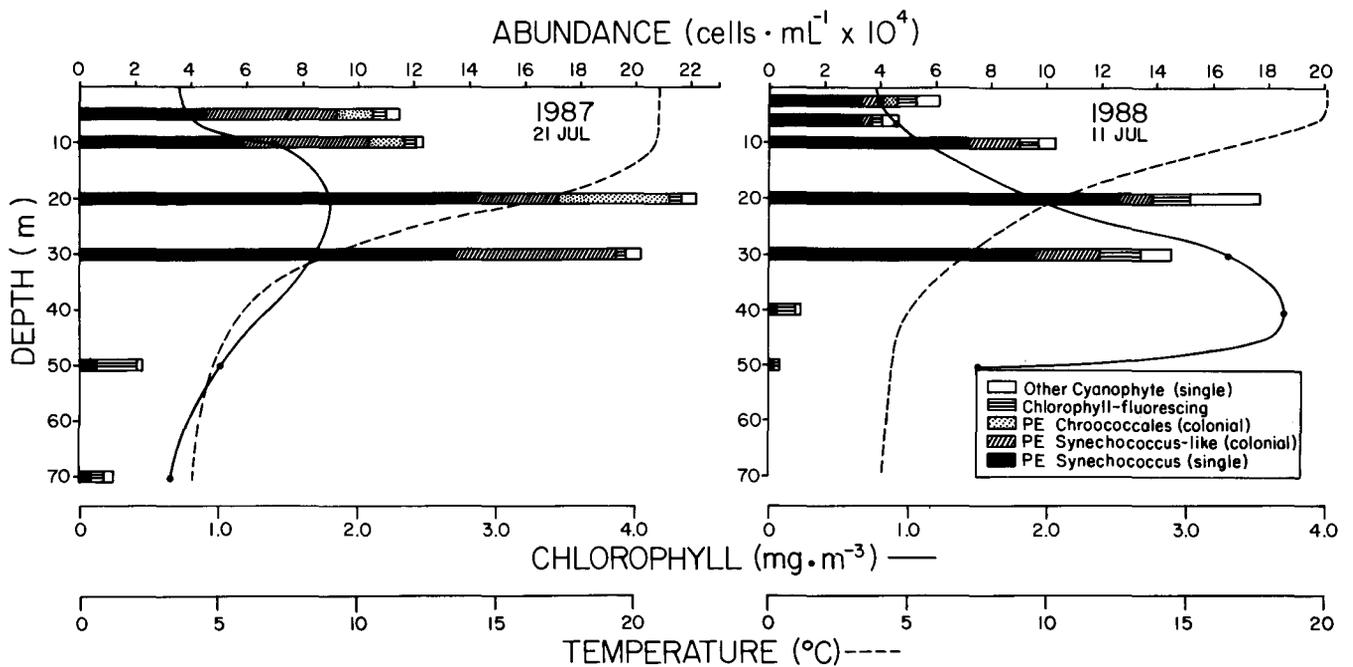


FIG. 4. Vertical distribution and composition of phototrophic picoplankton during thermal stratification at a station in southern Lake Michigan (43°1'N, 86°36'W) on 21 July 1987 and 11 July 1988. The solid line represents the chlorophyll concentration and the broken line represents temperature. Picoplankton groups are as defined in Fig. 1.

maximum abundance of this colonial type of cyanobacteria was 5.80×10^4 cells·mL⁻¹ in Lake Michigan and 4.48×10^4 cells·mL⁻¹ in Lake Huron. These cells contributed on average 15 and 7.7% of total picoplankton abundance in Lakes Michigan and Huron, respectively.

The second type of colonial cyanobacteria was a more diverse group of taxa which belonged to the order Chroococcales, but were distinct from the *Synechococcus*-like colonial form described above. The vast majority of these cells was similar to the old taxonomic genera of *Aphanothece* and *Microcystis* (Prescott 1964). Rod-shaped colonial cells were particularly

abundant in Lake Huron in 1986 (Fig. 1). As with the *Synechococcus*-like colonies, these colonial forms were most abundant during thermal stratification (Fig. 1 and 2). On average, only 5.9 and 6.1% of total picoplankton abundance in Lakes Huron and Michigan, respectively, was contributed by this group of phycoerythrin-containing Chroococcales cyanobacteria (Table 2).

A group of red-fluorescing cells contributed substantially to total picoplankton abundance. This red fluorescence was emitted at wavelengths >660 nm, and therefore, we assume that this fluorescence was due to chlorophyll *a* or a chlorophyll

TABLE 2. Percent composition of major picoplankton groups during the isothermally mixed and thermally stratified periods in Lakes Huron and Michigan. The regions of the water column are defined as surface-mixed layer (S), metalimnion (M), and hypolimnion (H).

Lake	Thermal period	Region	PE single <i>Syn.</i> ^a	PE colonial <i>Syn.</i> -like ^b	PE colonial <i>Chrooc.</i> ^c	Chl-fluor. ^d	Other ^e
Michigan	Isothermal	S	54.8	5.2	0.9	35.9	2.2
	Stratification	S	61.0	15.5	6.2	13.3	4.0
	Stratification	M	53.7	18.1	9.0	15.3	3.9
	Stratification	H	43.5	14.7	4.7	36.1	1.1
Mean			53.8	15.0	6.1	24.4	2.8
Huron	Isothermal	S	57.9	5.4	0.0	34.2	2.5
	Stratification	S	63.5	10.4	13.6	9.3	3.2
	Stratification	M	74.3	6.6	5.4	9.9	3.8
	Stratification	H	59.1	8.2	3.9	25.1	4.8
Mean			65.1	7.7	5.9	17.5	3.8
Grand mean both lakes			59.5	11.4	6.0	21.0	3.1

^aPhycocyanin-containing single *Synechococcus*.

^bPE colonial *Synechococcus*-like cells.

^cOther PE colonial Chroococcales.

^dChlorophyll-fluorescing cells.

^eOther cyanophytes.

TABLE 3. Mean dimensions and biovolume of dominant picoplankton.

Dominant picoplankton ^a	Mean biovolume (μm^3)	Mean dimensions (μm)
PE single <i>Synechococcus</i>	0.56	Diameter 1.0
PE colonial <i>Synechococcus</i> -like	0.70	Diameter 1.1
PE colonial Chroococcales	0.71	Length 1.6, width 0.9
Chlorophyll-fluorescing	0.96	Diameter 1.2

^aPicoplankton groups are as defined in Table 2.

a-like pigment (Chisholm et al. 1988). These small (1.2 μm) single chlorophyll-fluorescing cells constituted 24.4 and 17.5% of total picoplankton abundance in Lakes Michigan and Huron, respectively. Maximum abundance of these cells occurred during the isothermal mixing periods, with abundances of 1.68×10^4 cells·mL⁻¹ in Lake Michigan and 1.93×10^4 cells·mL⁻¹ in Lake Huron (Table 2). These cells were also relatively abundant in the hypolimnion during thermal stratification (Table 2); however, there was no pronounced abundance peak within the hypolimnion (Fig. 3 and 4).

Unclassified or other types of picoplankton constituted only a small percent of total picoplankton abundance (Fig. 1-4; Table 2). These cells were mostly single rod-shaped phycocyanin-containing cyanobacteria or phycocyanin-containing cyanobacteria.

Size and Biomass Estimates

As noted above, the picoplankton community was dominated by very small individuals ranging in mean size (longest dimension) from 1.0 to 1.6 μm (Table 3). We did not detect any consistent change in picoplankton size between lakes or across seasons. The mean and range of picoplankton carbon were similar in Lakes Huron and Michigan: mean 4.3 mg C·m⁻³ (0.8-16.8) in Lake Huron; mean 5.7 mg C·m⁻³ (0.4-18.0) in Lake

TABLE 4. Mean and range of picoplankton carbon expressed as percentage of total phototrophic carbon during the periods of isothermal mixing and thermal stratification.

Lake	Thermal period	Depth	Mean percent and range
Michigan	Isothermal	Surface	4.4 (1.4-12.7)
	Stratification	Surface	12.1 (2.8-30.0)
	Stratification	Metalimnion	20.0 (1.3-49.6)
	Stratification	Hypolimnion	4.6 (0.5-13.5)
Mean			11.5 (0.5-49.6)
Huron	Isothermal	Surface	11.1 (4.4-23.9)
	Stratification	Surface	11.0 (1.3-31.5)
	Stratification	Metalimnion	11.1 (3.7-23.4)
	Stratification	Hypolimnion	2.6 (1.4-4.8)
Mean			10.4 (1.3-31.5)
Grand mean both lakes			10.2

Michigan. Despite their small size, picoplankton contributed significantly to total pelagic phototrophic carbon, with an overall average of 10.2% (Table 4). The contribution of picoplankton carbon to phototrophic biomass was variable, ranging from a low of 1% during mixing periods to maximum values of over 30% during midstratification (Table 4). More seasonal variability in percent picoplankton carbon was apparent in Lake Michigan than in Lake Huron (Table 4). The maximum contribution of picoplankton to total phototrophic carbon was 50%, which was observed in Lake Michigan in August 1987.

Fractionated Primary Production

Phytoplankton primary production in both lakes was dominated by organisms passing a 10- μm screen (Fig. 5 and 6). For surface-mixing layer communities, the overall contributions to carbon fixation among the <1, <3, and <10- μm size fractions were 17, 40, and 70%, respectively (Table 5). The per-

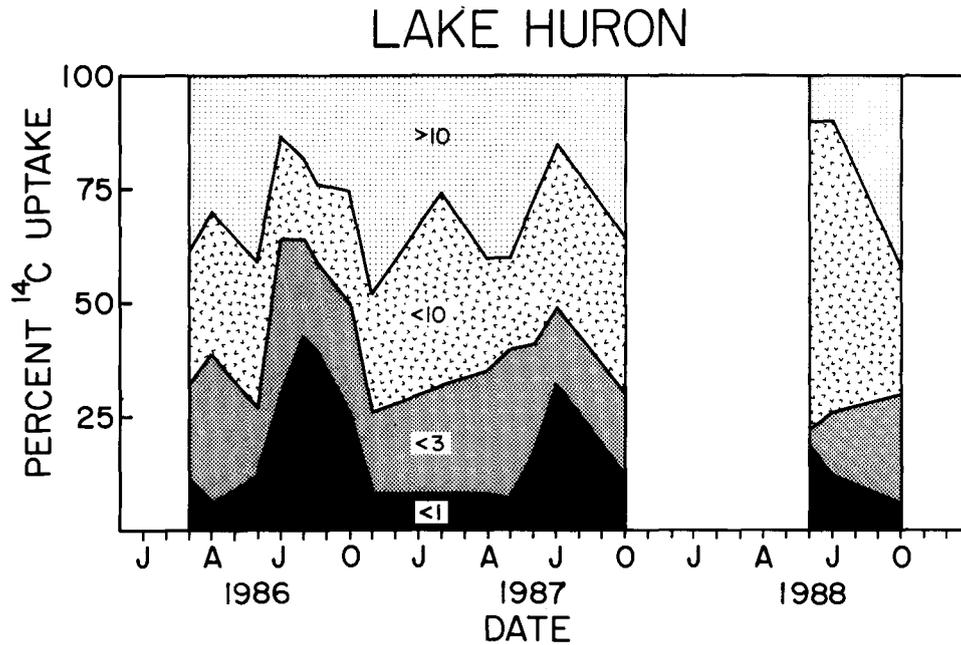


FIG. 5. Percent of primary production by the <1 , <3 , and <10 μm size classes for surface-mixed layer communities from a station in southern Lake Huron ($43^{\circ}54'N$, $82^{\circ}21'W$).

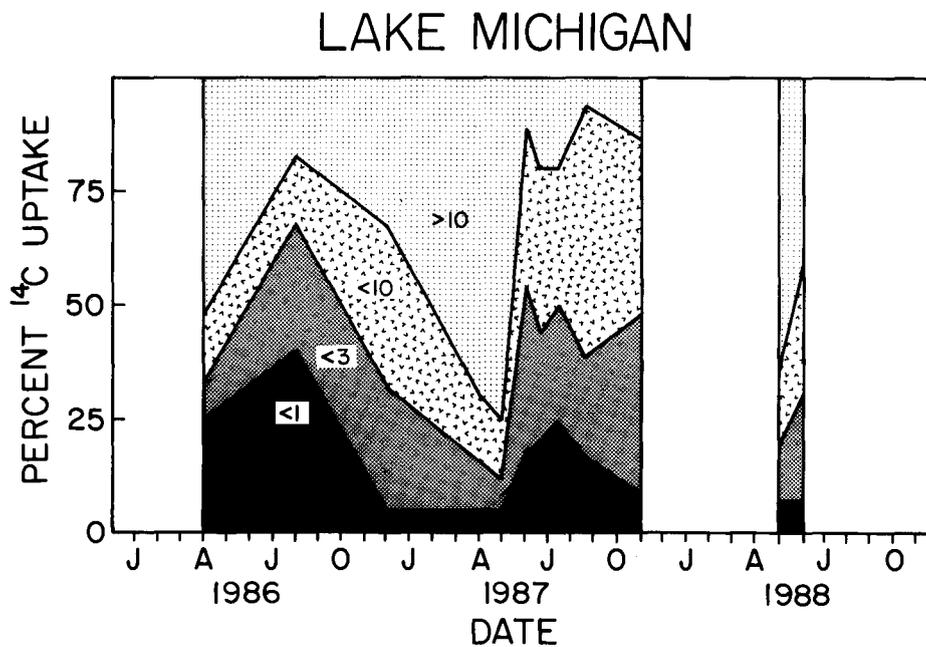


FIG. 6. Percent of primary production by the <1 , <3 , and <10 μm size classes for surface-mixed layer communities from a station in southern Lake Michigan ($43^{\circ}1'N$, $86^{\circ}36'W$).

cent of carbon fixation by each fraction showed a consistent seasonal pattern in each lake, with the greatest contribution of each fraction occurring during thermal stratification (Fig. 5 and 6). During the midstratification period, approximately 30, 50, and 80% of primary production was attributable to organisms passing 1-, 3-, and 10- μm screens, respectively (Table 5). Within the deep chlorophyll layer, the contributions of the <1 and <3 μm size fractions were similar to the surface communities.

Discussion

The phototrophic picoplankton communities of Lakes Michigan and Huron exhibit striking similarities to picoplankton communities in other freshwater and marine environments, but also exhibit notable differences. In many respects, especially composition and distribution, the picoplankton communities in these lakes are a cross between communities previously described from freshwater and oceanic environments, which is

TABLE 5. Mean percent carbon fixation by the <1, <3, and <10 μm size classes from the surface-mixed layer in Lakes Huron and Michigan (n = number of sampling dates).

Lake	Thermal period	<1 μm	<3 μm	<10 μm	n
Michigan	Isothermal	9.2	22.6	41.1	5
	Internal stratification	12.9	43.3	78.9	4
	Midstratification	25.8	52.3	86.6	4
Mean		15.4	38.1	67.5	13
Huron	Isothermal	7.9	36.0	61.9	7
	Internal stratification	13.2	35.5	70.1	8
	Midstratification	32.1	51.3	82.1	7
Mean		17.5	40.8	71.6	22
Grand mean both lakes		16.7	39.8	70.1	35

probably related to the deep oligotrophic nature of Lakes Huron and Michigan.

Like many other freshwater and marine picoplankton communities (Glover et al. 1985; Murphy and Haugen 1985; Fahnenstiel et al. 1986; Iturriaga and Mitchell 1986; Jochem 1988; Weisse 1988), single phycoerythrin-containing chroococcoid cyanobacteria of the genus *Synechococcus* dominated throughout the year. Maximum abundances of these cells were generally found within the metalimnion/upper hypolimnion during thermal stratification. These cells were morphologically similar to *Synechococcus* cells from Lake Superior (Fahnenstiel et al. 1986; G. Fahnenstiel, unpubl. data) and the type I group described by Johnson and Sieburth (1979) and Leppard et al. (1987). While single phycoerythrin-containing *Synechococcus* account for 60% of total phototrophic picoplankton in Lakes Huron and Michigan, other types of phototrophic picoplankton, particularly chlorophyll-fluorescing and colonial cyanobacteria, became abundant at certain times of the year. Previously described freshwater and marine communities did not exhibit this type of diversity.

Recent descriptions of freshwater picoplankton communities have failed to note abundant chlorophyll-fluorescing (red) cells of picoplankton size (0.5–2.0 μm). The phototrophic picoplankton community in Lake Constance was almost exclusively chroococcoid cyanobacteria (Weisse 1988), and phycoerythrin-containing cyanobacteria also dominated in Lakes Ontario and Biwa (Caron et al. 1985; Nagata 1986). During the summer in Lake Biwa, chlorophyll-fluorescing phytoflagellates of approximately 3–4 μm were noted, but these cells would not be included as picoplankton in most previous investigations. However, in Lakes Huron and Michigan, chlorophyll-fluorescing nonflagellated cells of approximately 1 μm become very abundant, and in some cases dominant, during isothermal mixing periods (Table 2; Fig. 1 and 2). Chlorophyll-fluorescing cells in this size range are abundant in many marine environments (Glover et al. 1985; Murphy and Haugen 1985; Chisholm et al. 1988; Jochem 1988; Li and Wood 1988). A shift in the picoplankton communities from cyanobacteria to chlorophyll-fluorescing reported for the Kiel bight of the western Baltic Sea (Jochem 1988) is similar to the one reported here. Chlorophyll-fluorescing cells are probably a more important constituent of freshwater picoplankton communities than has been previously reported.

Although red-fluorescing phototrophic picoplankton are abundant in the Great Lakes and in marine environments, these communities may be taxonomically very different. In the Great Lakes, the red-fluorescing community is dominated by *Chlo-*

rella-like eukaryotes, and prochlorophytes do not appear to be present (Fahnenstiel et al. 1991b). However, in the marine environment, prochlorophytes are extremely abundant, particularly in oceanic regions, and the community of red-fluorescing cells probably is composed of both eukaryotes and prochlorophytes (Johnson and Sieburth 1982; Chisholm et al. 1988).

The importance of colonial picoplankton also may differ between freshwater and marine environments. Previous descriptions of marine picoplankton communities have not included significant abundances of colonial cyanobacteria. Single cyanobacteria dominate the surface waters of most marine communities (Johnson and Sieburth 1979; Glover et al. 1985; Murphy and Haugen 1985; Iturriaga and Mitchell 1986). The role of colonial picoplankton is unclear; they may not have been counted as picoplankton. For example, Li et al. (1983) noted aggregates of cyanobacteria of up to 96 cells in the tropical ocean, but did not mention their overall contribution to picoplankton abundance.

Whether aggregate or colonial cells of 1–2 μm size are included as picoplankton is related to one's definition of picoplankton. Picoplankton can be defined either by the size of the organism (Sicko-Goad and Stoermer 1984; Stockner and Antia 1986) or by the ability to pass through a certain size screen (Smith et al. 1985; Joint 1986). Because of the variability and unpredictability in filter fractionation material (Runge and Ohman 1982; Stockner et al. 1990), we have chosen the former definition to describe our picoplankton communities and we also have differentiated between single and colonial forms.

Colonial or aggregate cyanobacteria commonly occur in freshwater environments (Wetzel 1983; Reynolds 1984). In Lakes Huron and Michigan, colonial cyanobacteria, some morphologically similar to the single *Synechococcus*, were very abundant during summer stratification; in certain cases, the abundance of colonial forms exceeded that of single *Synechococcus* (Fig. 1 and 2). The majority of colonial cells occurred in small aggregates of 9–16 cells, and their relationship to the single cells is unclear. Environmental conditions in the summer, e.g. increased grazing and nutrient deficiency, may induce colonial growth or simply select for colonial species. Since colonial cyanobacteria of picoplankton size are common during summer stratification and have been counted as picoplankton in the past (Caron et al. 1985), the relationship between single and colonial forms merits further work.

The vertical distribution of picoplankton during thermal stratification in Lakes Huron and Michigan is similar to that reported for picoplankton from the marine environment. Maximum abundance of picoplankton generally occurred within the lower metalimnion/upper hypolimnion at depths of 20–30 m which corresponds to the 0.6–6.0% isolumes. In many marine systems, the maximum abundance of picoplankton during stratification occurred near the depths of similar isolumes (Glover et al. 1985; Murphy and Haugen 1985; Waterbury et al. 1986) although there is some variability (Glover et al. 1988). However, the vertical distribution of picoplankton in Lakes Huron and Michigan differs from that reported for freshwater environments where the maximum abundances typically occurred within the epilimnion (Nagata 1986; Pick and Caron 1987; Weisse 1988). This difference in freshwater communities is likely related to the relationship between light penetration and mixing depth (Waterbury et al. 1986); there is greater light penetration into the metalimnion/hypolimnion in Lakes Huron and Michigan than in the other lakes studied. However, differential

nutrient availability with depth also may influence the vertical distribution of picoplankton (Shortreed and Stockner 1990).

One striking difference in the vertical distribution of picoplankton in Lakes Huron and Michigan as compared with oceanic environments is the absence of a deep peak of chlorophyll-fluorescing cells. In oceanic environments, chlorophyll-fluorescing cells become very abundant and sometimes are dominant below the 1% isolume (Glover et al. 1985; Murphy and Haugen 1985; Chisholm et al. 1988). Although red-fluorescing cells may be taxonomically different between the Great Lakes and the oceanic regions, the absence of a deep peak in the Great Lakes is probably related to spectral light penetration. In oceanic environments, more blue light is available at depth than in freshwater environments, and chlorophyll-fluorescing cells are better adapted for growth in blue light (Glover et al. 1986).

The density and seasonal pattern of occurrence of picoplankton in Lakes Huron and Michigan resembles that found in many temperate freshwater and marine environments. The range of picoplankton abundance in surface waters (10 000 to 220 000 cells·mL⁻¹) of Lakes Huron and Michigan is similar to values reported for freshwater and shelf and slope marine environments. (Caron et al. 1985; Joint 1986; Nagata 1986; Waterbury et al. 1986; Jochem 1988; Weisse 1988) but is on the high end of abundances reported from oceanic environments (Davis et al. 1985; Murphy and Haugen 1985). In temperate aquatic environments, maximum seasonal picoplankton abundance occurs during thermal stratification (Krempin and Sullivan 1981; Caron et al. 1985; Joint 1986; Jochem 1988). The same pattern was observed in Lakes Huron and Michigan, where maximum abundance was found during the July/October period. If, however, colonial forms were not included as picoplankton, much of this pronounced seasonality would disappear, particularly in Lake Huron. It is unclear if the pronounced seasonal peak noted by other investigators was due to colonial or single forms.

Despite their small size, picoplankton are important contributors to phototrophic biomass and primary production in Lakes Huron and Michigan. On average, picoplankton accounted for 10% of total phototrophic biomass, and on some occasions during the summer as much as 50%. This contribution to phototrophic biomass is higher than values reported from a Chesapeake Bay subestuary (Ray et al. 1989), Lake Constance (Weisse 1988), and southern California coastal waters (Krempin and Sullivan 1981), but is in the range of values for Lake Ontario (Pick and Caron 1987), the Kiel Bight (Jochem 1988), the Baltic Sea (Larsson and Hagstrom 1982), and Lake Biwa (Nagata 1986).

Our size-fractionated ¹⁴C uptake experiments demonstrated the importance of phototrophic organisms that pass through 1- and 3- μ m screens (Fig. 5 and 6). However, because not all phototrophic organisms are precisely fractionated (Runge and Ohman 1982; Waterbury et al. 1986) and because larger phototrophs may be damaged and broken during filtration procedures (Bloem and Gilissen 1985; Goldman and Dennett 1985), the relationship between production in a specific size fraction and picoplankton production is not always clear.

To evaluate the use of size fractionation experiments for estimating picoplankton production, we compared direct estimates of phototrophic picoplankton production determined with track autoradiography and microscopic counts on several occasions with production in the <1 and <3 μ m size fractions (G. Fahnenstiel, unpubl. data). On average, production by phototrophic picoplankton was similar to production in the <1

μ m size fraction. Based on these comparisons and the results of this study, phototrophic picoplankton contribute an average of 17% of primary production in Lakes Huron and Michigan, but their contribution likely exceeds 40% during the period of thermal stratification.

In summary, phototrophic picoplankton are very abundant and significant contributors to phototrophic biomass and primary production in Lakes Huron and Michigan. Because of their importance, particularly during summer stratification, many of our ideas and models of food web structure and carbon flow in the Great Lakes need to be reevaluated. Budgets and analyses of community chlorophyll and carbon that include typical phytoplankton rate processes such as sedimentation, grazing, and growth must recognize the difference between larger, more traditional phytoplankton and picoplankton; otherwise, predictions on the control of phytoplankton community structure may be in error (Lehman 1988; Scavia et al. 1988). Furthermore, our results, combined with the results of Scavia et al. (1986) and Scavia and Laird (1987) on the importance of heterotrophic picoplankton, suggest that heterotrophic and phototrophic picoplankton are responsible for the majority of planktonic community metabolism during summer stratification in the upper Great Lakes. A similar central role of heterotrophic and phototrophic picoplankton has been suggested for the oceans (Pomeroy 1980; Fenchel 1988).

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