

Biomass, Size Structure, and Composition of Phototrophic and Heterotrophic Nanoflagellate Communities in Lakes Huron and Michigan¹

Hunter J. Carrick^{2,3} and Gary L. Fahnenstiel²

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

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The abundance and biomass of surface (5 m) and deep (20–45 m) nanoflagellate communities in Lakes Huron and Michigan were determined during 1987. Abundances (10^2 – 10^3 cells·mL⁻¹) were comparable between lakes and similar to those reported from other oligotrophic environments. Community composition was skewed towards the small end of the size spectrum due to the prevalence of small chryomonads. In general, heterotrophic flagellates (Hnano) were more abundant than phototrophic flagellates (Pnano), while standing stocks of Pnano carbon (average 24.7 $\mu\text{g C}\cdot\text{L}^{-1}$) were greater than Hnano carbon (9.6 $\mu\text{g C}\cdot\text{L}^{-1}$) on nearly all sample dates. The abundance of nanoflagellates in both Lakes Huron and Michigan peaked in July, perhaps indicating increased growth at higher temperatures and/or a response to higher abundance of prey. Nanoflagellate communities in deep waters during thermal stratification were more abundant (50–70% higher carbon) than surface communities and were dominated by Pnano. High carbon standing stocks of deep communities did not correspond with high prey abundances. Thus, deep communities seem to be influenced by factors (e.g., light and nutrients) that maintain deep phytoplankton communities in the upper Great Lakes. While Hnano are quantitatively important in Lakes Huron and Michigan, representing nearly 20% of phytoplankton biomass, their trophic role is largely unknown.

L'abondance et la biomasse de la communauté de nanoflagellés de surface (5 m) et d'eaux profondes (20–45 m) des lacs Huron et Michigan ont été déterminées au cours de 1987. Les abondances (10^2 à 10^3 cellules·mL⁻¹) étaient comparables pour les deux lacs et semblables aux abondances observées dans d'autres milieux oligotrophes. La composition de la communauté était biaisée vers les petites tailles à cause de la présence majoritaire de petites chrysofycées. En général, les flagellés hétérotrophes (Hnano) étaient plus nombreux que les flagellés phototrophes (Pnano) et les stocks de carbone dérivés des Pnano (en moyenne 24,7 $\mu\text{g C}\cdot\text{L}^{-1}$) étaient supérieurs à ceux dérivés des Hnano (9,6 $\mu\text{g C}\cdot\text{L}^{-1}$), presque toutes les fois où des échantillonnages ont été réalisés. L'abondance de nanoflagellés dans les lacs Huron et Michigan était à son maximum en juillet, à cause peut-être des températures plus élevées et/ou d'une plus grande abondance de proies. Les communautés de nanoflagellés étaient plus abondantes dans les eaux profondes (50 à 70 % de plus de carbone) qu'en surface et étaient constituées surtout par des Pnano. Les stocks élevés de carbone des communautés des eaux profondes ne correspondaient pas à une abondance élevée de proies. Les communautés des eaux profondes semblent donc être touchées par d'autres facteurs (par exemple lumière et éléments nutritifs) qui expliquent la présence de communautés de phytoplancton en profondeur dans le secteur supérieur des Grands Lacs. Bien que les Hnano soient nombreux dans les lacs Huron et Michigan, représentant près de 20 % de la biomasse de phytoplancton, le rôle trophique qu'ils jouent est très peu connu.

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Picoplankton (organisms less than 2.0 μm in length) are important contributors to total productivity of aquatic ecosystems and are a significant and common feature of many marine systems (e.g., Li et al. 1983; Fuhrman et al. 1985; Cole et al. 1988) and oligotrophic lakes (Fahnenstiel 1980; Cole et al. 1984; Riemann and Sondergaard 1984; Stockner and Antia 1986). This recently discovered source of productivity has caused a reevaluation of existing concepts of trophic structure

within aquatic habitats (e.g., Azam et al. 1983). In the Upper Great Lakes as well as in marine systems, much of the primary production (annual average > 50%) can be attributed to organisms, primarily cyanobacteria, which pass a through 3- μm screen (Fahnenstiel et al. 1986; Fahnenstiel, unpubl. data). In addition, heterotrophic picoplankton, primarily bacteria, are responsible for a large portion of carbon flux (Scavia et al. 1986b; Scavia and Laird 1987) and nutrient recycling (Gardner et al. 1986, 1987).

However, the importance of heterotrophic nanoplankton (Hnano, flagellates and ciliates 2–20 μm in diameter) in aquatic ecosystems was not realized until recently (Sherr and Sherr 1984). Determinations of Hnano abundance, carbon standing

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²Center for Great Lakes and Aquatic Sciences, The University of Michigan, Ann Arbor, MI 48109, USA.

³School of Natural Resources, The University of Michigan, Ann Arbor, MI 48109, USA.

stock, and seasonal dynamics (e.g., Sorokin 1977; Beers et al. 1982; Sherr et al. 1984; Davis et al. 1985) indicate that these organisms are abundant components of marine plankton and have high metabolic rates (Fenchel 1982a; Sieburth 1984). Furthermore, marine Hnana significantly graze on picoplankton (Fenchel 1982b; for review see McManus and Fuhrman 1988b), control the flux of carbon within the microbial food web (Newell and Linley 1984; Pomeroy 1980), recycle nutrients (Goldman et al. 1985; Anderson et al. 1986), decompose particulate organics (Sherr et al. 1982), and appear to represent the dominant link between the microbial food web and higher trophic levels (Pace et al. 1984; Porter et al. 1985; Sherr et al. 1986, 1987).

Conversely, there are few measurements of heterotrophic nanoplankton abundance and distribution in freshwaters (Pick and Caron 1987). Although much information exists concerning the relative importance and abundance of phototrophic nanoplankton in the Laurentian Great Lakes (Vollenweider et al. 1974; Munawar and Munawar 1975, 1981, 1982; Munawar et al. 1978; Fahnenstiel and Scavia 1987a), Hnana biomass has only recently been estimated in Lake Ontario (Pick and Caron 1987), where they represent nearly 20% of total phytoplankton biomass (compared with phytoplankton biomass in Gray 1987). Here we report the abundance, size structure, and composition of phototrophic (Pnana) and heterotrophic (Hnana) nanoflagellate communities from an offshore station in both Lakes Huron and Michigan in 1987. We have restricted our analysis to nanoflagellates, because they are the dominant component of nanoplankton in the Upper Great Lakes (Munawar and Munawar 1981) and are potential grazers on picoplankton (Caron et al. 1985; Fahnenstiel et al. 1986; Scavia et al. 1986b).

Materials and Methods

Sampling was conducted in 1987 at single offshore stations in Lake Huron (43° 56' N, 82° 21' W; max. depth = 70 m) and Lake Michigan (43° 1' 11" N, 86° 36' 48" W; max. depth = 100 m) and on one occasion in 1986 (8 December) from the Lake Michigan station. The biological, chemical, and physical conditions at both stations are representative of offshore conditions (Makarewicz 1985, 1987), with ambient concentrations of total phosphorus being 5 and 8 $\mu\text{g}\cdot\text{L}^{-1}$ in Lakes Huron and Michigan, respectively (Schelske et al. 1986). In both lakes, phytoplankton standing stocks are low, typically less than 50 $\mu\text{g C}\cdot\text{L}^{-1}$, and chlorophyll-*a* concentrations range from 0.3 to 3.0 $\text{mg}\cdot\text{m}^{-3}$ (Fahnenstiel et al. 1989). Also, bacterial abundances range from 0.5×10^6 to 1.0×10^6 $\text{cells}\cdot\text{mL}^{-1}$, while autotrophic picoplankton span from 1.0×10^4 to greater than 10×10^4 (Scavia et al. 1986b; G. L. Fahnenstiel, NOAA, 1986–89 unpubl. data).

Monthly samples (December 1986–November 1987) from both lakes were collected from the surface when the water column was isothermal, and from both the surface (5 m) and deep (20–45 m) regions during thermal stratification, using opaque Niskin (5 L) sampling bottles. Subsamples were transferred into 250-mL amber bottles and preserved with glutaraldehyde (0.20 M final conc.) buffered with sodium cacodylate (0.1 M final conc.). Water column temperature profiles were measured with an electronic bathythermograph, and chlorophyll-*a* concentrations were determined fluorometrically (Strickland and Parsons 1972).

Samples were stored cold (5°C) prior to preparation for epifluorescence microscopy, which was performed within 24 h

after sampling following the method of Caron (1983). Once prepared, slides were immediately stored at -20°C , and were counted within one month to minimize the fading of autofluorescence (Caron 1983). Flagellate biomass and composition were estimated by enumerating 400–500 individuals from each prepared slide ($< 5\%$ counting error assuming Poisson statistics), using a Leitz Laborlux Microscope (mag = 1250 \times) equipped for autofluorescence (450–490 nm excitation and > 515 nm emission), and primulin analysis (320–380 nm excitation and > 420 nm emission). The length and breadth of individual organisms counted were determined. In addition, we observed trophic status (pigmented = phototrophic and non-pigmented = heterotrophic), the arrangement of external structures (i.e., flagella), and body shape. Cell volumes were calculated for each taxon assuming approximate geometric configurations; volume estimates for Pnana were subsequently converted to carbon based on Strathman (1966) conversion factors while Hnana cell volumes were converted to carbon using the conversion factor (cell volume $\times 0.15$ $\text{g C}\cdot\text{mL}^{-1}$) of Laws et al. (1984).

Results

Seasonal Abundance and Biomass

The abundance ($\text{cells}\cdot\text{mL}^{-1}$) of surface Hnana communities exhibited strong seasonality in both Lakes Huron and Michigan, while Pnana numbers showed little seasonal variation (Fig. 1A and 1C). In Lake Huron, Hnana abundances were greater than Pnana on all dates sampled, varying from 0.7×10^3 to 1.5×10^3 $\text{cells}\cdot\text{mL}^{-1}$ in the spring to over 5.0×10^3 $\text{cells}\cdot\text{mL}^{-1}$ during the summer. Pnana abundance ranged from 0.4×10^3 to 1.2×10^3 $\text{cells}\cdot\text{mL}^{-1}$ during isothermal periods (winter through spring) to more than 1.2×10^3 – 1.6×10^3 $\text{cells}\cdot\text{mL}^{-1}$ following thermal stratification. In Lake Michigan, the abundance of Hnana was also greater than that of Pnana for almost all dates sampled, as spring standing stocks were low (0.6×10^3 – 1.2×10^3 $\text{cells}\cdot\text{mL}^{-1}$), and increased more than two-fold during the summer (2.4×10^3 – 5.0×10^3 $\text{cells}\cdot\text{mL}^{-1}$). Pnana winter–spring standing stocks were 0.3×10^3 – 0.8×10^3 $\text{cells}\cdot\text{mL}^{-1}$ and only increased to between 1.4×10^3 – 1.9×10^3 $\text{cells}\cdot\text{mL}^{-1}$ during stratification.

Although Hnana had higher cell abundances than Pnana, Hnana carbon was lower than Pnana carbon on nearly all sampling dates and comprised 25.1 and 31.0% of total nanoflagellate carbon in Lakes Huron and Michigan, respectively (Fig. 1B and 1D). Nanoflagellate carbon in Lake Huron demonstrated little seasonality, with values for Hnana ranging from 2–8 $\mu\text{g C}\cdot\text{L}^{-1}$ to 9–13 $\mu\text{g C}\cdot\text{L}^{-1}$ in the spring and summer, respectively, while Pnana carbon varied from 13–16 $\mu\text{g C}\cdot\text{L}^{-1}$ in the spring to 23–38 $\mu\text{g C}\cdot\text{L}^{-1}$ following stratification. Nanoflagellate biomass showed more pronounced seasonality in Lake Michigan. Hnana carbon ranged from 2–6 $\mu\text{g C}\cdot\text{L}^{-1}$ in the spring to 8–24 $\mu\text{g C}\cdot\text{L}^{-1}$ during the summer, while spring Pnana carbon increased from 7–19 $\mu\text{g C}\cdot\text{L}^{-1}$ to 10–56 $\mu\text{g C}\cdot\text{L}^{-1}$ during stratification.

The abundance ($\text{cells}\cdot\text{mL}^{-1}$) of deep communities of Pnana and Hnana in both lakes increased between two- and three-fold during mid-stratification (July) compared with standing stocks estimated during early- (June) and late- (Oct.–Nov.) stratification (Table 1). Although the abundance of Lake Huron Pnana and Hnana were comparable, Pnana carbon was three- to four-fold higher than Hnana carbon. Similarly, Lake

TABLE 1. Abundance (cells·mL⁻¹) and carbon content (μg C·L⁻¹) of autotrophic and heterotrophic nanoflagellate communities from the deep (20–45 mm) region in Lakes Huron and Michigan during the stratified period. The ratio of Pnano:Hnano carbon is also presented.

Lake	Date	Pnano		Hnano		Carbon Ratio
		Abundance	Carbon	Abundance	Carbon	
Huron	10 June	1741	39.30	2515	18.83	2.09
	29 July	6090	86.50	5475	22.72	3.81
	15 Oct.	746	31.42	1466	7.64	4.11
Michigan	22 June	973	24.39	1682	8.38	2.91
	21 July	2972	33.38	4101	23.02	1.45
	20 Aug.	979	10.12	5197	23.71	0.42
	18 Sept.	221	5.92	947	3.67	1.61
	2 Nov.	443	12.80	1666	7.07	1.81

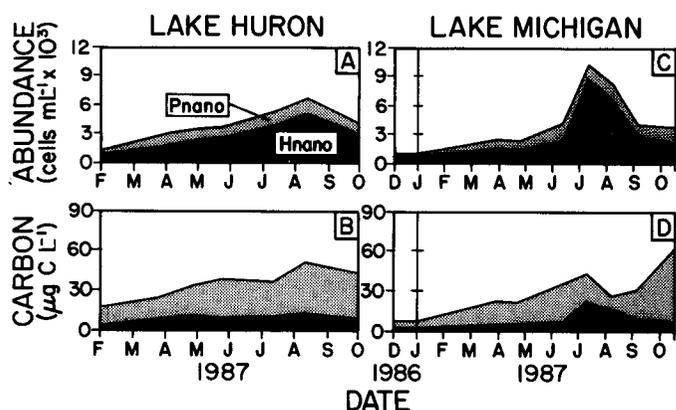


FIG. 1. Monthly estimates of surface (5 m) nanoflagellate abundance (A and C) and carbon content (B and D) for phototrophic (Pnano) and heterotrophic (Hnano) communities in Lake Huron (Feb.–Oct. 1987) and Lake Michigan (Dec. 1986–Nov. 1987).

Michigan Pnano carbon was 1.5 to nearly three times higher than Hnano carbon, with the exception of one date when the Pnano:Hnano carbon ratio was less than one (20 August), even though the abundance of Hnano was higher than that of Pnano on all dates sampled.

Size Structure

Seasonal frequency distributions of nanoflagellate size (ESD) for all sampling dates were skewed towards the small size classes (2–4 μm) with no major shifts between size classes (Fig. 2A–2H). The average ESD ± one standard deviation for surface communities was 3.06 ± 0.26 μm for Lake Huron and 3.26 ± 0.39 μm for Lake Michigan. The size structure of deep nanoflagellate communities from both lakes (Fig. 3A–3F) was also skewed towards the small end of the ESD size spectrum and showed a small degree of seasonal variation among the sampling dates (Lake Huron 3.34 ± 0.06; Lake Michigan 3.16 ± 0.20). Moreover, Hnano in general were smaller than Pnano in both surface and deep communities; a greater percentage of Hnano had ESDs which were in the 2–7 μm range, while most Pnano had ESDs greater than 7 μm (Fig. 4).

Community Composition

In both lakes, surface Pnano biomass was dominated by cryptomonads (i.e., *Rhodomonas minuta* Skuja, *Rhodomonas lens* Pasch. Ruttner, *Cryptomonas erosa* Ehr., and *Cryptomonas* sp.) throughout most of the year, with chrysomonads

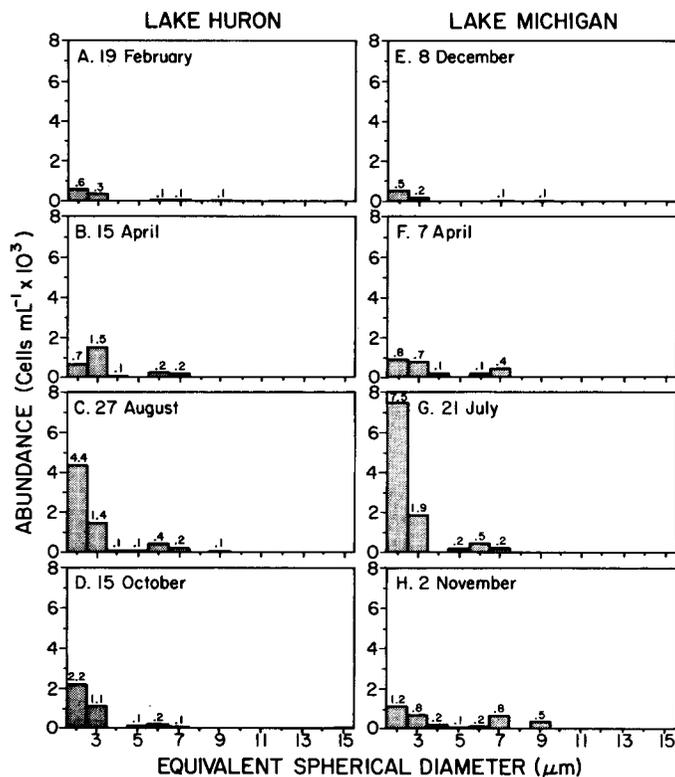


FIG. 2. Typical size (equivalent spherical diameter, μm) frequency distributions for surface (5 m) nanoflagellate communities in Lakes Huron (A–D) and Michigan (E–H).

and other small flagellates (*Dinobryon divergens* Imhof., *Chrysochomulina parva* Lackey, *Ochromonas* spp., and unidentified flagellates) becoming more important following stratification. In Lake Huron, the biomass of chrysomonads and small flagellates gradually increased during the year, whereas a chrysomonad peak in Lake Michigan occurred between 22 June and 21 July, followed by a pronounced increase in cryptomonad biomass on 2 November.

Hnano community composition was also similar between lakes and was composed primarily of colorless cryptomonads and chrysomonads. In Lake Huron, Hnano composition showed little seasonality. Hnano biomass contained on average 35.0% cryptomonads (*Katablepharis ovalis* Skuja, *Cryptaulax conoidea* Skuja, and *Chroomonas* sp.) and 36.2% chrysomonads (e.g., *Ochromonas* spp., *Chromulina* sp., *Monas* sp., and small unidentified flagellates), while other zooflagellates (mainly

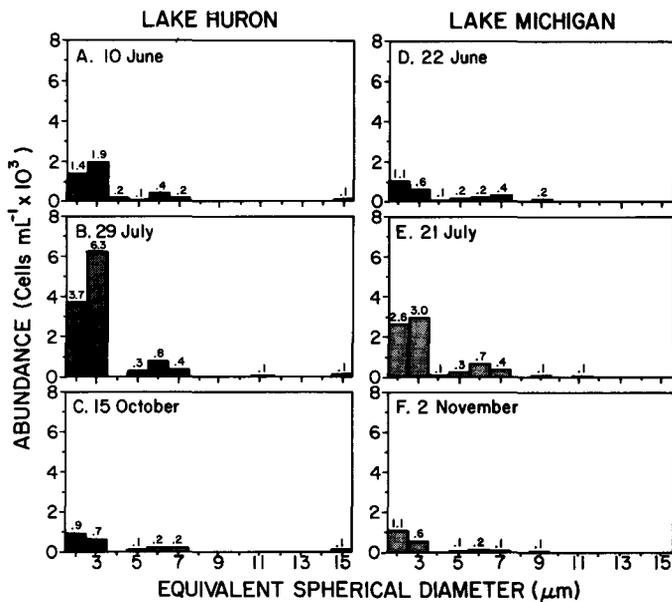


FIG. 3. Typical size (equivalent spherical diameter, μm) frequency distributions for deep (20–45 m) nanoflagellate communities in Lakes Huron (A–C) and Michigan (D–F).

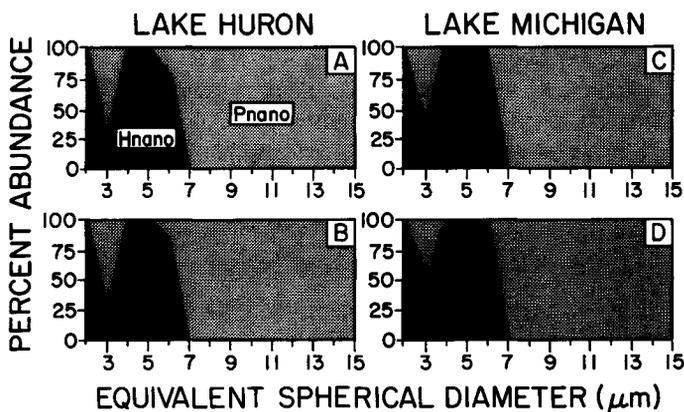


FIG. 4. Percent abundance ($\text{cells}\cdot\text{mL}^{-1}$) as a function of size (based upon equivalent spherical diameter, μm) for surface (A and B) and deep (C and D) heterotrophic (Hnano) and phototrophic (Pnano) nanoflagellate communities in Lakes Huron and Michigan. Percent abundances were averaged over all sampling dates and the standard deviations for estimates in any one size class were less than 24%.

choanoflagellates such as *Monosiga* sp. and *Diploeca* sp.) were subdominant. Similarly in Lake Michigan, cryptomonad populations constituted most of the Hnano biomass (37.2%) and varied little with season, while chrysomonads (35.2%) and other zooflagellates (17.7%) increased after 21 July (mid-stratification) and were responsible for much of the seasonality in Hnano biomass.

The composition of deep-water Pnano communities was similar to that in the surface waters with some exception. Cryptomonads dominated these assemblages; however, increases in Pnano carbon during mid-stratification in both lakes were primarily attributed to the increased biomass of chrysomonads (e.g., *Chrysochromulina parva* Lackey) and dinoflagellates (*Gymnodinium varians* Maskell and *Gymnodinium* sp.), which comprised 46.8 and 6.0%, respectively, of Pnano carbon. Moreover, the community structure of deep Hnano was also similar in both lakes, where cryptomonads, chrysomonads, and

other zooflagellates were co-dominant during early- and late-stratification periods, although communities shifted towards cryptomonad and chrysomonad dominance during mid-stratification.

Discussion

In general, the abundance (overall average \pm SD, $4.44 \pm 2.28 \times 10^3 \text{ cells}\cdot\text{mL}^{-1}$) and biomass ($34.2 \pm 14.2 \mu\text{g C}\cdot\text{L}^{-1}$) of surface nanoflagellate communities were comparable between Lakes Huron and Michigan, and they were also similar to those reported from other oligotrophic environments. These values agree with nanoflagellate standing stocks in Georgia coastal waters (Sherr et al. 1984), open oceans (Davis and Sieburth 1982), the North Atlantic (Davis et al. 1985), and the North Sea (Fenchel 1982b).

Hnano were more numerous than Pnano in both lakes in nearly all the samples analyzed (average Pnano:Hnano Lake Huron = 0.53, Lake Michigan = 0.59). Other workers have also observed higher or similar abundances ($\text{cells}\cdot\text{mL}^{-1}$) of Hnano compared to Pnano in marine systems, with Pnano:Hnano ratios being equal to or less than 1.0 (Caron 1983; Davis and Sieburth 1982; Davis et al. 1985; Sherr et al. 1984). This was not observed in the only other study of a Laurentian Great Lake, in which Pick and Caron (1987) found higher concentrations of Pnano compared with Hnano in Lake Ontario. While Pick and Caron's biomass estimates for Hnano (taken from their Fig. 4, midlake station 403) were comparable to ours (0.083 and $0.063 \text{ g}\cdot\text{m}^{-3}$, respectively), their biomass estimates for Pnano were two-fold higher than those presented here (0.33 and $0.15 \text{ g}\cdot\text{m}^{-3}$, respectively). The prevalence of non-flagellated Pnano (cocoid green algae and diatoms) seems to account for the greater abundance of Pnano measured in Lake Ontario (Pick and Caron 1987). These forms were not as abundant in our samples and hence were not included in our estimates. Such differences in nanoplankton community composition may reflect the more eutrophic nature of Lake Ontario relative to Lakes Huron and Michigan (Schelske et al. 1986).

Conversely, we found that Pnano carbon in the surface waters of both Lakes Huron and Michigan were consistently greater than Hnano carbon (average carbon Pnano:Hnano Lake Huron = 3.31, Lake Michigan = 2.61). This result is not surprising given that Pnano, despite their lower abundance, are larger than Hnano (see Fig. 4). The skewed size structure of nanoflagellates in these lakes can also be attributed to the abundance of colorless chrysomonads, 2–4 μm in equivalent spherical diameter, which represent nearly 70% of nanoflagellate abundance. This feature has been commonly observed in oligotrophic marine and freshwater systems (Sherr and Sherr 1983; Rassoulzadegan and Sheldon 1986; Anderson 1987). The majority of these taxa probably belong to the genera *Ochromonas* and *Chromulina* based upon body shape and flagellation. However, the identity of these flagellates is difficult to ascertain and requires confirmation with transmission electron microscopy (Estep et al. 1986).

Seasonal Variation in Nanoflagellate Biomass

The surface abundance of nanoflagellates peaked during mid-stratification in Lake Michigan and to a lesser extent in Lake Huron, primarily because of a dramatic increase in the abundance of small chrysomonads. This is similar to seasonal variation in nanoplankton communities previously observed in

other temperate aquatic systems (Fenchel 1986) and in the Great Lakes (Munawar et al. 1978; Pick and Caron 1987). Positive correlations between nanoflagellate abundance and temperature for both Lakes Huron and Michigan ($r=0.90$, $P=0.006$; $r=0.84$, $P=0.009$, respectively) may reflect higher nanoflagellate growth rates at higher temperature, as some marine nanoflagellates demonstrate increased growth (Caron et al. 1986) and metabolism (Sherr et al. 1988) at higher temperatures.

The seasonal increase in Lake Michigan nanoflagellate abundance observed here coincides with increases in populations of potential prey. The abundance, growth rates, and carbon production of Lake Michigan bacteria (Scavia and Laird 1987) and autotrophic picoplankton (G. L. Fahnenstiel, NOAA, 1987 unpubl. data) are also maximal during mid-stratification. Moreover, Hnano abundance in Lake Michigan was strongly correlated ($r=0.92$, $P=0.001$) with bacterial abundance (H. J. Carrick, NOAA, 1987 unpubl. data), perhaps suggesting a predator-prey relationship, in that small flagellates have been implicated as the major consumers of bacteria in Lake Michigan (Scavia et al. 1986b; Scavia and Laird 1987). This relationship was not observed in Lake Huron, probably due to the relatively small degree of seasonal variation in concentrations in Hnano (this study) and bacteria (H. J. Carrick, NOAA, 1987 unpubl. data).

The subtle seasonal variation in Lake Huron nanoflagellate abundance is intermediate to that occurring in Lake Superior, which shows little to no seasonal variation (Munawar et al. 1978; Fahnenstiel and Glime 1983; Fahnenstiel et al. 1986), and in Lake Michigan, which demonstrates more pronounced flagellate seasonality (Fahnenstiel and Scavia 1987a; this study). This trend is reflected in the variation in phytoplankton standing stocks (measured as chlorophyll-*a*) in the three lakes; values for offshore Lake Huron stocks ($1.4\text{--}2.2\text{ mg}\cdot\text{m}^{-3}$) lie between the values determined for Lake Superior (ca. $1.0\text{ mg}\cdot\text{m}^{-3}$ little variation) and Lake Michigan ($0.3\text{--}5.3\text{ mg}\cdot\text{m}^{-3}$) (Vollenweider et al. 1974). Also, seasonal variation in parameters like total phosphorus concentrations and silica utilization in Lake Huron are intermediate to those measured in Lakes Superior and Michigan (Schelske et al. 1986). This is not surprising given that Lake Huron receives a mix of water from both lakes Michigan and Superior (Schelske 1985) and appears to have an intermediate trophic status among the three upper Great Lakes (Schelske et al. 1983, 1986).

Vertical Variation: Comparison of Surface and Deep Communities

Vertical heterogeneity in nanoflagellate communities has been observed in some marine habitats (Townsend and Cam-

men 1985; Kimor et al. 1987; Eppley et al. 1988), whereas little vertical structure was observed in Lake Ontario (Pick and Caron 1987). Based upon our results, the average biomass of deep nanoflagellate communities were 73 and 56% higher than that of surface communities in Lakes Huron and Michigan, respectively (Table 4), and were dominated by phototrophic flagellates (average carbon Pnano:Hnano = 2.37, SD = 1.26). The development of this subsurface nanoflagellate community was greatest during mid-stratification, while decreases in the deep:surface carbon ratio after July were related to increasing mixing depth and the eventual mixing of the subsurface community (Table 2). This progression was also evidenced by the diminishing ratio of deep:surface chlorophyll-*a* estimates (values < 1.5), indicating a decline of the deep-water phytoplankton community in each lake (Fahnenstiel and Scavia 1987b). The vertical distribution of nanoflagellates observed here is similar to that determined for phytoplankton in Lake Michigan (Fahnenstiel and Scavia 1987b) and Lake Superior (Fahnenstiel and Glime 1983), and for autotrophic picoplankton in lakes Huron and Michigan (G. L. Fahnenstiel, NOAA, 1987 unpubl. data). However, there does not appear to be a concomitant increase in bacteria at this depth in the water column (Scavia and Laird 1987) for Lake Michigan. Thus, it seems more likely that deep nanoflagellate communities are influenced more by factors such as light and nutrients, which regulate subsurface phytoplankton in Lake Michigan (Fahnenstiel et al. 1984). The lower light penetration in Lake Ontario (1% light at 11.5 m, Cuhel and Lean 1987) compared with that in Lakes Huron and Michigan (20–30 m, G. L. Fahnenstiel, NOAA, 1987 unpubl. data; Scavia et al. 1986a, respectively) might account for the lack of vertical heterogeneity in nanoflagellates in Lake Ontario compared with the results presented here.

Trophic Role of Nanoflagellates in the Upper Great Lakes

Hnano are quantitatively important in both Lakes Huron and Michigan, representing nearly 20% of phytoplankton carbon (compared with G. L. Fahnenstiel, NOAA, 1987 unpubl. data), which is similar to that observed for Lake Ontario communities (Pick and Caron 1987). However, the role of nanoflagellates in the upper Great Lakes food web is unclear. Given the present information, we can estimate Hnano clearance rates, assuming a constant clearance of 1×10^5 cell volumes·flagellate⁻¹·h⁻¹ (Fenchel 1982a). Thus, surface Hnano (average biovolume $23.6\ \mu\text{m}^3$) in both lakes (average abundance 2.9×10^3 cells·mL⁻¹) clear on average $2.4\ \text{nL}\cdot\text{flagellate}^{-1}\cdot\text{h}^{-1}$, which is similar to rates determined elsewhere for species of equivalent size (Fenchel 1982a; Sherr et al. 1983). This clearance rate accounts for

TABLE 2. Comparisons of total nanoflagellate carbon ($\mu\text{g C}\cdot\text{L}^{-1}$) and chlorophyll-*a* concentration ($\text{mg}\cdot\text{m}^{-3}$) between surface (5 m) and deep (20–45 m) communities in Lakes Huron and Michigan for several dates during the stratified period.

Lake	Date	Surface Carbon	Deep Carbon	Carbon Deep:Surface	Chlorophyll Deep:Surface
Huron	10 June	38.85	53.13	1.37	1.93
	29 July	37.05	109.20	2.95	11.03
	15 Oct.	44.51	39.06	0.88	0.69
Michigan	22 June	30.68	32.77	1.07	4.19
	21 July	21.20	56.40	2.65	2.36
	20 Aug.	10.28	33.83	3.29	1.47
	18 Sept.	22.88	9.59	0.42	—
	2 Nov.	56.39	19.87	0.35	0.34

20% of bacterial loss rates previously determined in Lake Michigan which has been attributed to micrograzers (Scavia and Laird 1987; Scavia and Fahnenstiel 1988). This estimate is low compared to most other studies (e.g., Fenchel 1982a; Landry et al. 1984), although some investigations have observed similar rates of bacterial grazing by Hnano (McManus and Fuhrman 1988a). However, it should be noted that small naked flagellates can undergo nearly 50% size reduction following preservation with glutaraldehyde, as well as other standard fixatives (Borsheim and Bratbak 1987; Bloem et al. 1988). Hnano shrinkage was not investigated here nor was 50% size reduction accounted in our biomass estimates, and subsequent clearance rates. Thus, doubling Hnano clearance to account for size reduction following preservation, Hnano can account for nearly 40% of bacterial losses. Moreover, if we assume that Pnano are active bacterial grazers in Lake Michigan as reported elsewhere (Bird and Kalff 1986, 1987; Porter 1988) and include them in our calculation (Pnano clearance rate $12.6 \text{ nL} \cdot \text{flagellate}^{-1} \cdot \text{h}^{-1}$), approximately 50% of bacterial losses in Lake Michigan can be attributed to nanoflagellate grazing. This suggests that other pelagic microzooplankton (i.e., ciliates and rotifers) in addition to heterotrophic nanoflagellates, are active in controlling bacterial populations in Lake Michigan. For instance, ciliated protozoa can be significant bacterivores in both marine (Sherr and Sherr 1987; Sherr et al. 1987) and freshwater (Simek et al. 1988) systems. In addition, Hnano in the Great Lakes might utilize other nutritional resources, as they have been shown to be important grazers of autotrophic picoplankton (Campbell and Carpenter 1986) and other algae (Goldman and Caron 1985; Suttle et al. 1986), and are equipped to use dissolved organic matter as an additional nutritional source (Sherr 1988). Although the contribution of nanoflagellate biomass to upper Great Lakes plankton is now evident, their role in the Great Lakes food web is not presently understood and merits further study.

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