

PLANKTONIC PROTOZOA IN LAKES HURON AND MICHIGAN: SEASONAL ABUNDANCE AND COMPOSITION OF CILIATES AND DINOFLAGELLATES

Hunter J. Carrick^{1,2} and Gary L. Fahnenstiel²
Great Lakes Environmental Research Laboratory
National Oceanic and Atmospheric Administration
2205 Commonwealth Blvd.
Ann Arbor, Michigan 48105

ABSTRACT. The abundance and biomass of surface (5 m) and deep (30-45 m) ciliate and dinoflagellate protozoa in the offshore waters of Lakes Huron and Michigan were determined from December 1986 to November 1987. Protozoan (ciliates and dinoflagellates) abundance (4 to 15 cells·mL⁻¹) and biomass (13-140 µg·L⁻¹, wet wt.) were comparable between lakes and similar to those reported from other oligotrophic environments. On average, ciliates comprised the majority of protozoan abundance (80%) and biomass (73%). The mean size (ESD) of these communities was small (20.6 µm) due to the numerical dominance of small choreotrichs, oligotrichs, and species of *Gymnodinium*. Total biomass in both lakes peaked during late June-July and again during the October-November period. These seasonal changes in biomass were accompanied by species replacements: tintinnids, strobilids, oligotrichs, and *Gymnodinium* species were abundant in the spring isothermal period, shifting to oligotrich dominance during summer stratification (May-July); a more diverse assemblage followed during late stratification (October-November) in which haptorids, prorodontids, and *Peridinium* species became more important. Deep and surface communities were comparable in terms of abundance and biomass, although deep community biomass decreased as stratification intensified. Because the biomass of ciliates alone represents approximately 30% of crustacean zooplankton biomass, protozoa may be more important grazers than once thought.

INDEX WORDS: Protozoa, ciliates, dinoflagellates, Lake Huron, Lake Michigan, grazing.

INTRODUCTION

Flagellated and ciliated protozoa (most < 200 µm in size) represent a most diverse group of organisms, with high metabolic rates and a great range in form and function (Fenchel 1987). A re-evaluation of the existing conception of trophic structure within aquatic habitats has been prompted by the discovery that picoplankton (organisms < 2 µm in size) and nanoplankton (organisms < 20 µm in size) contribute significantly to ecosystem metabolism (e.g., Pomeroy 1974, Stockner and Antia 1986). Protozoa appear to be the dominant consumers of pico- and nano-plankton production and are ubiquitous in many aquatic systems (Azam *et al.* 1983, Sherr and Sherr 1984). Given that protozoa are the dominant link between the microbial food web and higher

trophic levels, i.e., metazoans (Pace *et al.* 1984; Porter *et al.* 1985; Sherr *et al.* 1986, 1987), determination of the structure and function of these communities is needed in order to evaluate the fate of pico- and nanoplankton productivity.

At present there appears to be a gap in our knowledge of Great Lakes zooplankton. Comparatively, population dynamics (Stemberger and Evans 1984, Evans 1986, Johannsson 1987), feeding ecology (Bowers and Vanderploeg 1982; Vanderploeg *et al.* 1984), and trophic interactions (Taylor 1984, Scavia and Fahnenstiel 1987, Lehman 1988) of the larger macrozooplankton (primarily rotifers and crustacean zooplankton > 200 µm in size) have been well documented, while information on the smaller, pelagic ciliated and flagellated protozoa is scarce. Only very recently have flagellated protozoan biomass and distribution in the Great Lakes been measured (Pick and Caron 1987, Carrick and Fahnenstiel 1989), and still fewer measurements of ciliated

¹School of Natural Resources, The University of Michigan, Ann Arbor, MI 48109

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

protozoan abundance and distribution exist (Taylor and Heynen 1987). Further, protozoa may play a pivotal role in the Great Lakes food web, because of high picoplankton abundance (Caron *et al.* 1985, Pick and Caron 1987) and production (Fahnenstiel *et al.* 1986; Gardner *et al.* 1986, 1987; Scavia *et al.* 1986; Scavia and Laird 1987).

As a continuation of previous work on freshwater protozoa in which we determined the abundance and seasonality of small (<20 μm in size) flagellated protozoa (Carrick and Fahnenstiel 1989), here we present information on the abundance and composition of ciliate and the larger dinoflagellate protozoa at a single offshore station in both Lakes Huron and Michigan from December 1986 to November 1987.

METHODS

Sampling was conducted at single offshore stations in Lake Huron (42° 56' N, 82° 21' W; max. depth = 70 m) and Lake Michigan (43° 1' 11" N, 86° 36' 48" W; max depth = 100 m); however, a second station in northern Lake Huron (45° 25' N, 82° 55' W; max. depth = 80 m) was sampled in May and July. Approximately monthly samples (December 1986–November 1987) from both lakes were collected using opaque Niskin (5 L) sampling bottles from the surface when the water column was isothermal, and from both the surface (5 m) and deep (30–45 m) regions during thermal stratification, defined by early (surface water temp. <15°C) and late (surface water temp. >15°C) stratification periods (Fahnenstiel and Scavia 1987a). Sub-samples were transferred into 500-mL amber bottles and preserved with Lugol's acid iodine (1% final conc., Taylor and Heynen 1987). Water column temperature profiles were measured with an electronic bathythermograph, and chlorophyll concentrations were determined fluorometrically (Strickland and Parsons 1972).

Ciliate biomass and community composition were determined using the \ddot{U} termohl technique (\ddot{U} termohl 1958). Briefly, aliquots (25-mL to 50-mL) were settled onto coverslips, and the entire area of the coverslip was systematically scanned with an inverted microscope (mag = 200 \times) to avoid counting biases induced by edge-effects (Sandgren and Robinson 1984). Each individual encountered was identified to the level of genus by consulting several references (Kudo 1966, Corliss 1979, Lee *et al.* 1985); conspecific taxa were delineated by size. However, overall protozoan system-

atics used here conforms to that proposed by Lee *et al.* (1985). Cell volumes were estimated by determining the average cell dimensions from ten randomly chosen individuals of each taxon in each sample (mag = 400 \times). The average dimensions were then applied to the geometric configuration which best approximated the shape of each taxon (e.g., spheres, prolate spheres, and cylinders for some tintinnid species). Cell volumes were subsequently converted to biomass (wet weight) assuming a specific weight of 1.0 $\text{g}\cdot\text{mL}^{-1}$, while the equivalent spherical diameter (ESD, μm) of each taxon was calculated from its cell volume.

RESULTS

Abundance and Biomass

Overall, surface ciliate and dinoflagellate communities were similar between lakes. Ciliates ranged in abundance from 2 to 14 $\text{cells}\cdot\text{mL}^{-1}$, while biomass varied from 9.9 to 87.3 $\mu\text{g}\cdot\text{L}^{-1}$ (Fig. 1). Generally, ciliate abundance and biomass in both lakes were lowest in the winter (December and February), increased during early thermal stratification (May–June), and increased again during late stratification (October–November); however, in Lake Huron this second peak in abundance during October to November was of a greater magnitude than that occurring in Lake Michigan. Dinoflagellates were less abundant (0.4 to 7.4 $\text{cells}\cdot\text{mL}^{-1}$) than ciliates and constituted less biomass (3.4 to 68.0 $\mu\text{g}\cdot\text{L}^{-1}$), yet also had low abundances in the winter which increased during early (May–June) and late (July–September) stratification.

The abundance and biomass of deep communities were comparable with surface communities, except during early- to mid-stratification in Lake Michigan (Fig. 2). The greater abundance of deep communities was attributable to the development of a subsurface dinoflagellate community in Lake Michigan during June and July (surface to deep biomass ratio = 5.53 and 3.13, respectively) and to a lesser extent in July in Lake Huron (biomass ratio = 1.45). Unlike the dinoflagellates, ciliates reached their highest abundance in the surface waters of both lakes and did not seem to contribute significantly to the subsurface protozoan community in either lake.

Size Structure

While the average size of surface ciliate and dinoflagellate communities (based on cell abundance)

SURFACE PROTOZOA

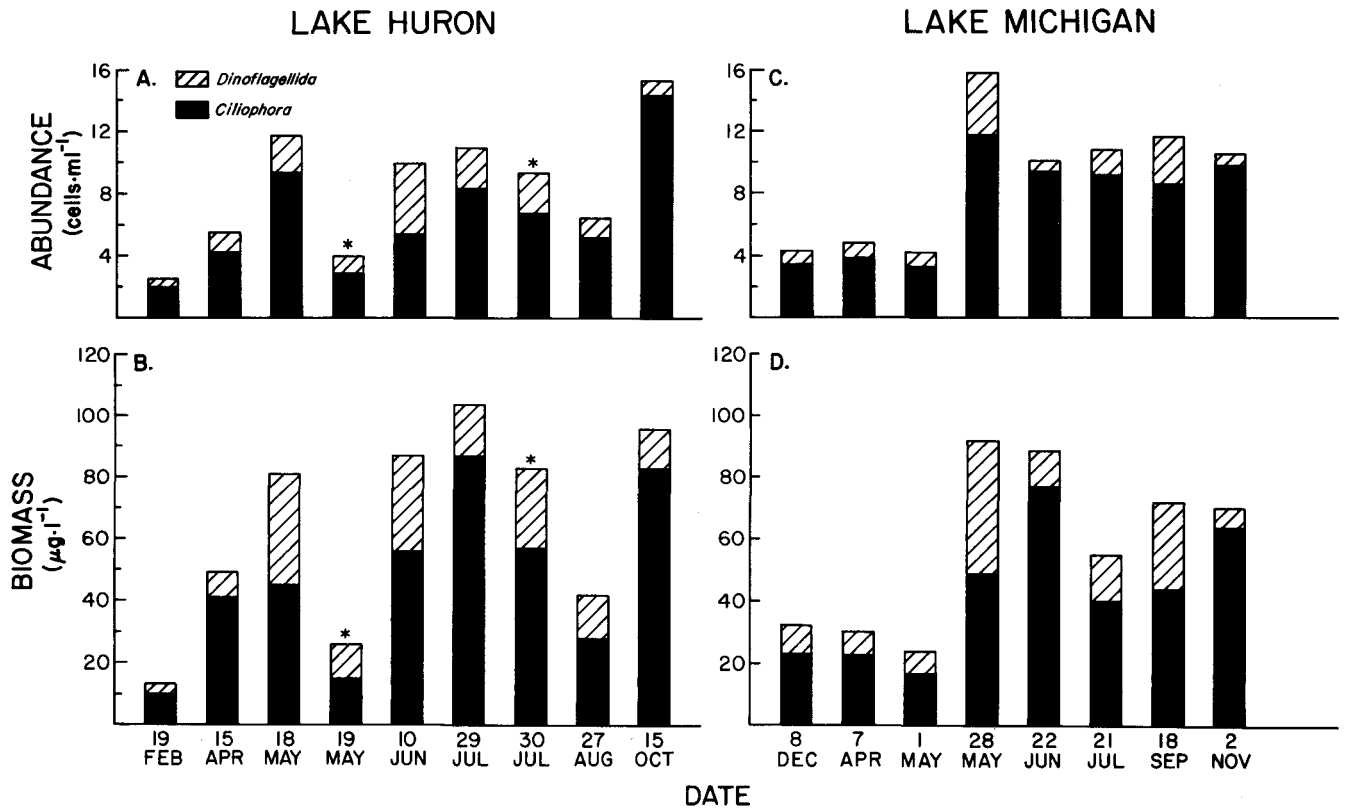


FIG. 1. Distribution of ciliate and dinoflagellate abundance (A and C) and wet weight biomass (B and D) in the surface waters (5 m) of Lake Huron (February–October 1987) and Lake Michigan (December 1986–November 1987). Stars indicate samples collected from northern Lake Huron.

did not show much temporal or spatial variation (overall average = $20.6 \pm 2.7 \mu\text{m}$), the distribution of individuals among size classes did change through time. Modal values for size frequency histograms (based upon percent cell abundance) were skewed toward the small classes (12–27 μm) due to the prevalence of small choreotrichs (*Strobilidium* species) and prorodontids (*Urotricha* sp. and *Balanion* sp.) which occurred in nearly all samples (Fig. 3). In the winter samples, individuals were more evenly distributed across size classes (Figs. 3A and 3E), compared with the bimodal size distribution which occurred during the spring and summer periods (Figs. 3B, 3C, 3F, and 3G). By late-stratification in both lakes, most individuals were ca. 20 μm in size (Figs. 3D and 3H). These patterns were consistent for deep communities in both lakes as well (Fig. 4).

Community Composition

Based upon the 35 taxa encountered, surface communities in both lakes were dominated by choreotrichs and oligotrichs (Tables 1 and 2). Winter and spring samples were dominated by choreotrichs (*Strobilidium* and *Tintinnidium*), oligotrichs (mainly *Strombidium* and *Halteria*), sessilids (e.g., *Vorticella* and *Vaginacola*), and dinoflagellates belonging to the family Gymnodiniidae (*Gymnodinium helveticum* and *Gymnodinium* sp.). This assemblage persisted throughout the spring; however, by the onset of thermal stratification (June), oligotrichs (mainly *Strombidium viride*) increased in abundance and accounted for more than half of community biomass in both lakes. In addition, prorodontids (*Urotricha* sp. and *Balanion* sp.), haptorids (*Askenasia* sp. and *Mesodinium* sp.),

DEEP PROTOZOA

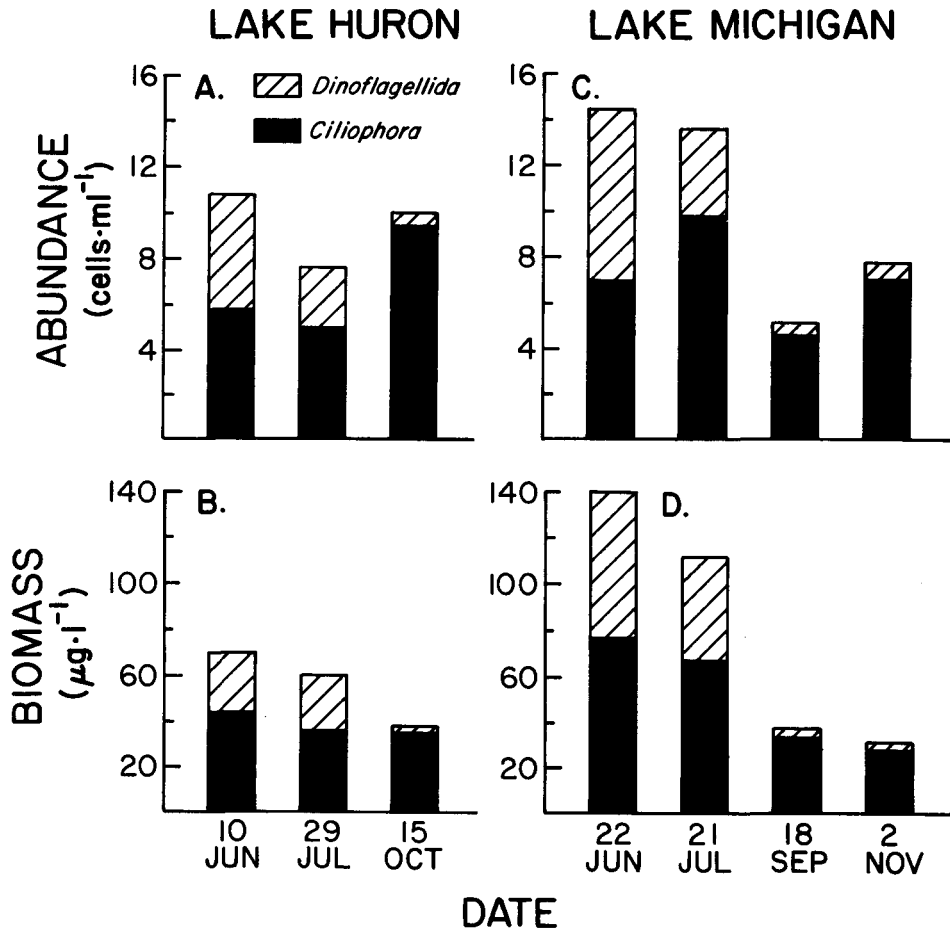


FIG. 2. Distribution of ciliate and dinoflagellate abundance (A and C) and wet weight biomass (B and D) in the deep region (30–45 m) of Lake Huron (June–October 1987) and Lake Michigan (June–November 1987).

and dinoflagellates belonging to the family peridiniidae (*Peridinium* sp. and *Ceratium hirudinella*) became increasingly abundant following stratification. During late stratification (particularly in Lake Michigan), the fauna resembled that occurring in the previous spring.

Deep communities in both lakes were similar in terms of composition (Table 3). During early stratification (June), the assemblage was reminiscent of the surface spring assemblage, dominated by oligotrichs (mainly *Strombidium viride*), tintinnids (*Codonella* and *Tintinnidium* sp.), and the dinoflagellate *Gymnodinium helveticum*. During mid- to late-stratification, haptorids (primarily

Mesodinium sp.) and prorodontids (*Urotricha pelagica* and *Urotricha* sp.) became very abundant, while an unknown ciliate (probably *Stokesia vernalis*) accounted for greater than 30% of ciliate and dinoflagellate biomass combined.

DISCUSSION

Abundance of Great Lakes Ciliates and Dinoflagellates

The abundance and biomass of surface ciliophora were comparable between Lakes Huron and Michigan (overall average 7.0 ± 3.5 cells·mL⁻¹ and 45.4

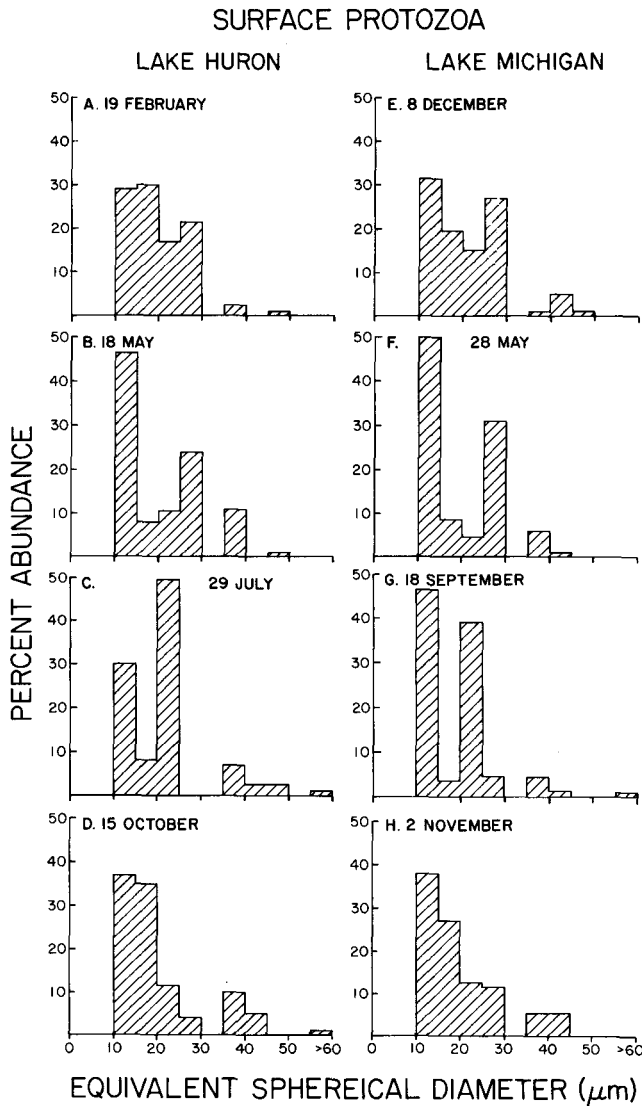


FIG. 3. Typical size (equivalent spherical diameter, μm) frequency distributions for surface (5 m) ciliate and dinoflagellate communities in Lakes Huron (A-D) and Michigan (E-H).

$\pm 24.1 \mu\text{g}\cdot\text{L}^{-1}$), and similar to values for oligotrophic Ontario lakes (Gates and Lewg 1984) and oligotrophic marine environments (Sorokin 1981, Sherr and Sherr 1984, Montagnes *et al.* 1988). In addition, our estimates of ciliate biomass fall within the range determined for three oligotrophic Québec lakes (44.1 to 50.2 $\mu\text{g}\cdot\text{L}^{-1}$, after conversion assuming specific gravity of 1.0 $\text{pg}\cdot\mu\text{m}^{-3}$ [Pace 1986]), whose total phosphorus (3.37–6.5 $\mu\text{g}\cdot\text{L}^{-1}$) and chlorophyll (1.3–2.0 $\mu\text{g}\cdot\text{L}^{-1}$) values are similar

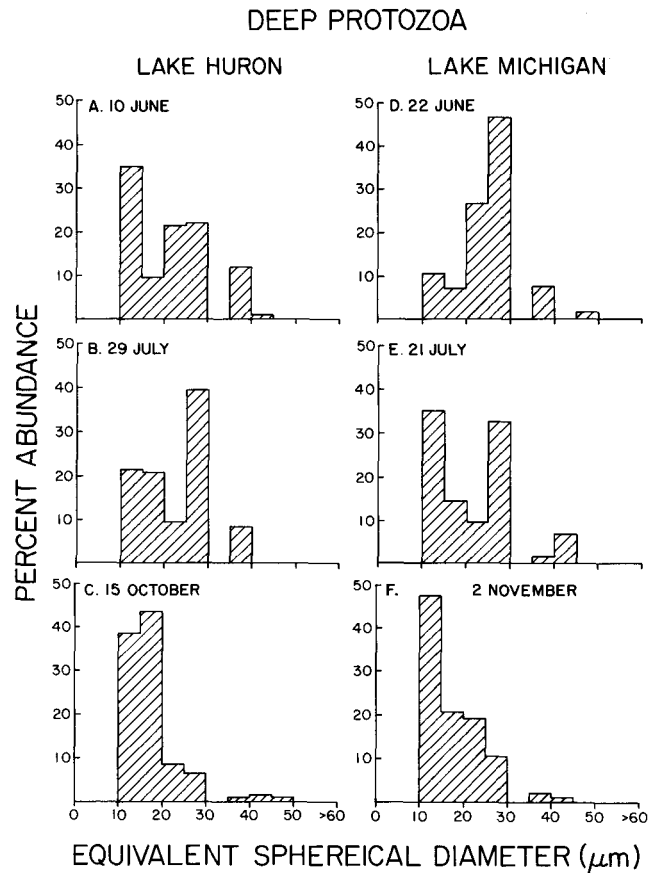


FIG. 4. Typical size (equivalent spherical diameter, μm) frequency distributions for deep (30–45 m) ciliate and dinoflagellate communities in Lakes Huron (A–C) and Michigan (D–F).

to those in Lakes Huron and Michigan. Also, the abundance and biomass values reported here appear to be at the low end of the spectrum for oligotrophic Florida lakes (Beaver and Crisman 1982, Beaver *et al.* 1988).

In comparison to the only other Laurentian Great Lake studied, the annual average of ciliate abundance and biomass in Lakes Huron and Michigan were 30% ca. lower than measurements by Taylor and Heynen (1987) for Lake Ontario (12.8 ± 9.3 and 68.6 ± 48.7 , respectively). This difference probably reflects the higher trophic status of Lake Ontario compared to Lakes Huron and Michigan (Schelske *et al.* 1986), given the positive relationship which has been shown between ciliate abundance and biomass with lake trophic status (Beaver and Crisman 1989).

Dinoflagellates were also similar between Lakes

TABLE 1. Percent composition (biomass, $\mu\text{g}\cdot\text{L}^{-1}$, wet wgt.) among several orders of ciliate and dinoflagellate protozoa sampled on several dates (lower value is the associated water temperature) from the surface waters (5 m) of Lake Huron.

Order	Date (day/month) Temperature ($^{\circ}\text{C}$)								
	19/2	15/4	18/5	19/5	10/6	29/7	30/7	27/8	15/10
Order	1.5	3.3	5.1	3.0	10.5	21.2	21.0	20.0	12.6
Phylum Ciliophora									
Choreotrichida									
Strobilidiina ¹	10.5	8.4	8.6	9.1	6.4	12.8	4.4	13.4	9.7
Tintinnina ¹	15.7	19.8	10.8	9.4	0.4	2.4	1.3	4.0	3.2
Haptorida	7.2	3.5	4.4	3.4	3.0	24.2	3.6	2.5	17.8
Oligotrichida	16.5	30.6	42.3	17.2	52.0	31.0	33.4	27.9	36.4
Prorodontida	1.3	2.1	1.4	2.6	1.5	7.0	3.7	8.6	6.1
Scuticociliatida	0	0	0	0.3	0	0.2	0.2	0.6	0.1
Sessilida	10.4	9.1	2.5	1.9	0.7	0	0.4	0.4	2.0
Unknowns	13.7	9.7	2.4	14.1	0.7	6.4	20.9	8.8	11.0
Phylum Sarcomastigophora									
Dinoflagellida									
Gymnodiniidae ²	24.7	15.7	27.7	41.4	32.9	0.5	1.3	0.6	3.5
Peridiniidae ²	0.9	1.0	0	0.5	2.5	15.5	30.8	33.2	10.3

¹Suborder level of taxonomy

²Family level of taxonomy

TABLE 2. Percent composition (biomass, $\mu\text{g}\cdot\text{L}^{-1}$, wet wgt.) among several orders of ciliate and dinoflagellate protozoa on several dates (lower value is the associated water temperature) from the surface waters (5 m) of Lake Michigan.

Order	Date (day/month) Temperature ($^{\circ}\text{C}$)							
	8/12 ¹	7/4	1/5	28/5	22/6	21/7	18/9	2/11
Order	2.0	3.0	3.8	10.0	19.0	21.8	19.7	10.8
Phylum Ciliophora								
Choreotrichida								
Strobilidiina ²	8.9	15.1	15.6	10.2	5.0	18.2	6.2	18.9
Tintinnina ²	10.0	24.9	23.7	0.9	4.1	0	4.4	5.6
Haptorida	4.0	7.8	3.1	0.1	1.0	7.0	9.3	7.8
Oligotrichida	7.3	13.4	19.9	35.9	64.7	31.5	17.6	18.8
Prorodontida	1.5	1.8	2.3	1.6	5.1	4.4	19.2	5.7
Scuticociliatida	0	0.5	0	0	0	3.0	0	0.3
Sessilida	2.3	1.8	2.2	0.4	0.6	3.1	1.0	3.9
Unknowns	37.2	10.3	2.1	3.7	5.8	6.2	3.4	31.3
Phylum Sarcomastigophora								
Dinoflagellida								
Gymnodiniidae ³	27.3	20.3	27.0	46.7	2.5	2.6	2.8	3.7
Peridiniidae ³	1.6	4.2	4.1	0.7	11.3	24.0	36.2	4.1

¹Sampled in 1986

²Suborder level of taxonomy

³Family level of taxonomy

TABLE 3. Percent composition (biomass, $\mu\text{g}\cdot\text{L}^{-1}$, wet wgt.) among several orders of ciliate and dinoflagellate protozoa sampled on several dates (lower value is the associated water temperature, $^{\circ}\text{C}$) following thermal stratification from the deep region (30–45 m) of Lake Huron and Lake Michigan.

Order	Lake Huron			Lake Michigan			
	10/6 5.0	29/7 5.0	15/10 6.1	22/6 6.3	21/7 11.6	18/9 6.6	2/11 10.1
Phylum Ciliophora							
Choreotrichida							
Strobilidiina ¹	9.5	4.7	6.0	0.6	9.1	16.4	26.9
Tintinnina ¹	7.5	9.3	3.1	12.1	8.8	2.0	8.6
Haptorida	3.0	6.8	28.9	5.0	2.2	15.6	8.9
Oligotrichida	38.9	32.2	10.6	21.6	4.6	1.2	7.0
Prorodontida	3.2	1.0	10.5	5.8	3.0	6.1	15.5
Scuticociliatida	0	0	0	0	0	0.3	0
Sessilida	2.7	1.5	9.0	0	0.5	2.3	10.8
Unknowns	2.3	3.9	26.0	7.2	30.8	44.5	11.5
Phylum Sarcomastigophora							
Dinoflagellida							
Gymnodiniidae ²	27.5	39.9	2.8	40.5	34.0	8.3	7.6
Peridiniidae ²	5.6	0.9	3.3	7.2	7.2	3.4	3.2

¹Suborder level of taxonomy

²Family level of taxonomy

Huron and Michigan (average abundance 1.7 ± 1.3 cells $\cdot\text{mL}^{-1}$ and biomass 16.2 ± 10.7 $\mu\text{g}\cdot\text{L}^{-1}$), and constituted 20% and 27% of total ciliate and dinoflagellate abundance and biomass, respectively. These biomass estimates agree well with a previous investigation, in which offshore Lake Huron phytoplankton were enumerated (May to November average = 16.2 $\mu\text{g}\cdot\text{L}^{-1}$, Munawar and Munawar 1975).

Variability in Ciliate and Dinoflagellate Communities

The biomodal peak in ciliate and dinoflagellate abundance observed here is similar to the seasonal pattern determined for Lake Ontario ciliates (Taylor and Heynen 1987) and Lake Huron dinoflagellates (Munawar and Munawar 1975). It is plausible that grazing losses may contribute to the observed seasonality, because peak abundances occur before and after the seasonal (June to early August) increase in crustacean zooplankton commonly observed in Lake Michigan (Dorazio *et al.* 1987, Scavia and Fahnenstiel 1987).

Samples from northern and southern Lake Huron show some degree of spatial variation in ciliate and dinoflagellate abundance; May samples from the northern station yielded lower standing

stocks (see Fig. 1). We believe lower densities at the northern Lake Huron station are likely a function of differing water temperature between stations (3.0°C at the northern station and 5.0°C at the southern station). Further, abundances in May at the northern Lake Huron station are similar to those at the southern station under comparable temperature regimes (10 April), while both stations in July had similar abundances when water temperatures were the same (21°C).

In addition to predation, seasonal changes in community composition may also be related to changes in the available prey (Pace 1982). Similar to observations by Pace (1982) in Lake Oglethorpe, ciliate communities here were dominated by oligotrichs, tintinnids, and sessilids prior to thermal stratification (surface water temperature $<4^{\circ}\text{C}$, see Tables 1 and 2). It seems plausible that this assemblage is feeding on abundant phytoplankton (primarily diatoms) resulting from the characteristic spring bloom (Fahnenstiel and Scavia 1987b). Following stratification (surface water temperature $>6^{\circ}\text{C}$), the prey available to grazers consists of smaller phytoflagellates (Fahnenstiel and Scavia 1987b; G. L. Fahnenstiel, NOAA, 1987 unpubl. data) and autotrophic (G. L. Fahnenstiel, NOAA, 1987 unpubl. data) and heterotrophic picoplankton

(Scavia *et al.* 1986). At this time, smaller oligotrichs, haptorids, and prorodontids became more abundant and may feed on organisms in the pico- to nanoplankton size range (Fenchel 1987, Sherr and Sherr 1987). Further, common summer species such as *Halteria* and *Urotrichia* have been shown to feed effectively on phytoflagellates (Skogstad *et al.* 1987).

The abundance and composition of deep communities also varied as stratification progressed. During early stratification (June), deep communities were similar in composition and biomass to spring surface communities (see Table 3). Thus, deep communities (as well as the spring assemblage) appear to be dominated by taxa able to handle larger algal prey (i.e., diatoms), which commonly occurs during spring mixis and at the base of the euphotic zone following stratification (Fahnenstiel and Scavia 1987b, c). For instance, *Gymnodinium helveticum* accounted for 30–40% of ciliate and dinoflagellate biomass in this region and was observed in this study (H. J. Carrick, NOAA, personal observation) to ingest large planktonic diatoms (e.g., *Stephanodiscus niagare*). Ingestion of diatoms by *G. helveticum* has also been observed in previous studies (Nauwerck 1963, Frey and Stoermer 1980). During mid- to late-stratification (July–November), biomass of deep communities decreased and composition became similar to the surface community, presumably due to increased mixing depth and water exchange with the epilimnion.

Lastly, several chlorophyll-bearing ciliates (e.g., *Stokesia vernalis* and *Strombidium* species) were abundant in our samples, and thus appear to be mixotrophic. These species occurred in both surface and deep samples. Whether the distribution of these taxa is restricted to the euphotic zone as observed elsewhere (Pace 1982, Taylor and Heynen 1987, Stoecker *et al.* 1989) and are actively photosynthetic was not determined here and requires further study.

Importance of Protozoa in the Great Lakes

The results presented here show that ciliates and dinoflagellates in Lakes Huron and Michigan are a numerically important component of the plankton. Taken alone, average ciliate biomass from May through September (average = $50.0 \mu\text{g}\cdot\text{L}^{-1}$, wet wt.) constitutes a substantial fraction (ca. 30% assuming 0.279 wet/dry conversion of Gates 1984)

of crustacean zooplankton ($49.4 \mu\text{g}\cdot\text{L}^{-1}$ dry wt, G. A. Laird and D. Scavia, NOAA, 1987 unpubl. data) biomass sampled during the same period in Lake Michigan. This agrees with the findings of Taylor and Heynen (1987), who showed that ciliate biomass was of the same order of magnitude as crustacean zooplankton standing stocks in Lake Ontario. Based upon ciliate biomass and their high metabolic rates (Taylor 1984), Taylor and Heynen (1987) concluded that ciliates (and possibly rotifers) were the major grazers at their offshore Lake Ontario site. This may hold true for communities in Lakes Huron and Michigan as well. When heterotrophic flagellate biomass (May–September Lake Michigan average = $25.5 \mu\text{g}\cdot\text{L}^{-1}$ dry wt., Carrick and Fahnenstiel 1989) is combined with estimates of ciliate biomass from this study, then heterotrophic ciliated and flagellated protozoa alone constitute greater than 80% of crustacean zooplankton biomass. This suggests that protozoa in the upper Great Lakes may account for a significant portion of community metabolism and grazing of microbial production compared with crustacean zooplankton. Furthermore, this estimate of protozoan biomass is probably conservative, in that (1) it does not take into account pigmented flagellates which might also be important grazers (Bird and Kalff 1986, 1987; Borass *et al.* 1988; Porter 1988) and (2) size reduction following preservation (at times nearly 50% in some taxa), which can occur in both flagellated (Borsheim and Bratbak 1987, Bloem *et al.* 1988) and ciliated (Choi and Stoecker 1989) protozoa was not accounted for here.

Ciliates and dinoflagellates are grazed by crustacean zooplankton in both marine (Berk *et al.* 1977, Robertson 1983, Stoecker and Sanders 1985) and freshwater systems (Porter *et al.* 1979), which can limit these communities (Smetacek 1981) and act as a trophic transfer of microbial production (Sherr *et al.* 1987). Given the negative association between protozoa and crustacean zooplankton observed in the Great Lakes (this study), it seems reasonable that ciliates and dinoflagellates are an important trophic link to metazoans. Furthermore, the great range in size and composition of protozoa, like that observed in the Great Lakes, suggests that these organisms fill a diversity of niches in the food web (Fenchel 1987). Because of their pivotal position in the food web and poorly understood feeding ecology, more work is required to evaluate the role of protozoa in freshwater systems.

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