

Quantitative importance of ciliates in the planktonic biomass of lake ecosystems

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Abstract

No previous study of plankton in lakes has estimated the relative contribution of ciliated protozoa to the biomass of the total plankton community, including phytoplankton. In a series of south-central Ontario lakes, ciliates comprise on the order of 5 to 10% of the total planktonic biomass of these relatively oligotrophic lakes and exist there in densities of 20–40 ml⁻¹. Therefore, ciliates constitute an important component of lake ecosystems that should not be ignored in limnological studies of zooplankton abundance and distribution.

Introduction

Ciliated protozoa increasingly are being realised to be important components of aquatic ecosystems, but there have been few studies of their relative importance or of their absolute contribution to overall biomass. Our ignorance about ciliates in nature mostly has been the result of inadequate sampling: nearly all zooplankton sampling methods rely on filtering, which destroys ciliates by lysing their soft cell bodies on netting. Furthermore, settled bulk column samples which have been stained and settled usually are not examined for ciliates. Here I report a comparative analysis of the relative biomass contribution of ciliates to the plankton of several freshwater lakes in Ontario, and I examine the temporal stability of ciliate biomass in one of these lakes.

In marine planktonic ecosystems, the potential (Johannes, 1965; Berk *et al.*, 1977) and estimated (Heinbokel, 1978; Heinbokel *et al.*, 1979) grazing impact of ciliates has been investigated, as has their importance in the microbenthos of marine sediments (Fenchel, 1967, 1969 & 1980). Laboratory studies have shown their ability to rapidly recycle

phosphorus in freshwater systems (Buechler & Dillon, 1974; Taylor & Lean, 1981). The potential importance of ciliates in food chains has been argued (Sorokin, 1972; Porter *et al.*, 1979; Crisman *et al.*, 1981) and tested in a small zooplankton community (Pace & Orcutt, 1981).

Previous studies of ciliates in freshwater lakes usually have been confined to a single lake (Nauwerck, 1963; Davis, 1973; Goulder, 1974; Rigler *et al.*, 1974; Mamaeva, 1976; Finlay, 1978 & 1981; Hecky *et al.*, 1978; Hecky & Kling, 1981; Bark, 1981; Pace & Orcutt, 1981; Pace, 1982), although a series of Florida lakes has been examined monthly for a year (Beaver & Crisman, 1982). All of these studies have used a taxonomic approach in classifying ciliates, and many have considered ciliates in isolation from other faunal components. In contrast, I have used a purely size-based approach for phytoplankton, ciliates, and other zooplankton, in order to focus on the allocation of biomass into different functional size categories of microplankton (Sprules & Holtby, 1979; Sprules & Knoechel, *in press*), rather than its allocation among species. For ciliates, the order Oligotrichida is the predominant taxonomic group represented in our planktonic samples (Corliss, 1979).

Table 1. Seasonally averaged biomass (in $\mu\text{g l}^{-1}$) and limnological data for a set of Ontario lakes in 1981.

Name	Location		Mean depth (m)	Maximum depth (m)	Surface area (km ²)	Secchi depth (m)	Total (P) ($\mu\text{g l}^{-1}$)	Epilimnetic Chlorophyll A ($\mu\text{g l}^{-1}$)	pH	Conductivity (mS m ⁻¹)	Dissolved Oxygen (mg l ⁻¹)
	Lat. (° N)	Long. (° W)									
White	44 50'	78 29'	3.72	10.4	1.75	4.4	14	1.4	7.73	16.9	8.2
Blue Chalk	45 12'	78 56'	9.37	21.9	0.50	8.4	9	0.7	6.59	4.3	10.2
Crosson	45 05'	79 02'	8.15	23.5	0.59	3.6	17	1.3	5.35	4.0	9.0
Mountain	45 59'	78 43'	13.43	31.4	3.19	7.0	7	1.0	7.08	6.8	11.2
Plastic	45 11'	78 50'	8.10	16.8	0.33	6.3	14	0.9	5.54	3.8	9.4
Three Mile	45 10'	79 27'	3.48	11.0	9.29	3.7	16	1.1	6.82	10.1	13.7
King	45 53'	79 30'	2.56	5.8	0.29	3.4	28	1.4	5.17	4.2	9.7
Ruth	46 01'	79 31'	5.72	14.6	1.97	5.6	14	1.7	6.28	5.0	10.3
Young	44 43'	79 10'	4.33	10.4	0.93	4.5	19	1.4	8.40	23.5	9.5

Table 1. (continued)

Name	Ciliate numbers (ml ⁻¹)	Ciliate biomass density	0–10 μm phyto-plankton	> 10 μm phyto-plankton	Filament phyto-plankton	Herb. zoo-plankton	Carn. zoo-plankton	Ciliates as % of total
White	37.4	140.6	346.5	307.4	305.1	312.8	175.6	8.9
Blue Chalk	28.4	39.9	217.0	151.7	131.9	388.0	354.9	3.1
Crosson	17.1	26.9	320.0	212.4	51.6	226.8	91.2	2.9
Mountain	28.8	36.1	204.3	234.6	194.8	99.5	222.2	3.6
Plastic	17.8	76.7	203.6	273.1	48.5	297.6	60.5	8.0
Three Mile	20.1	30.7	288.2	418.2	415.2	245.1	160.6	2.0
King	15.0	47.2	274.3	331.2	57.6	667.0	145.9	3.1
Ruth	19.2	70.8	251.1	308.6	43.9	237.4	85.9	7.1
Young	27.9	89.2	325.5	439.2	108.6	696.4	435.7	4.3

Materials and methods

Nine lakes (Table 1) were sampled as part of a larger, cooperative project (by the Lake Ecosystem Working Group of the University of Toronto) at approximate fortnightly intervals during the ice-free period of 1981. The lakes were sampled at their deepest points, and separate water chemistry, zooplankton, and phytoplankton samples were taken concurrently, as outlined elsewhere (Sprules & Knoechel, in press).

Zooplankton samples were collected by a metered conical tow net with mesh size 110 μm hauled from near bottom to the surface and preserved in an aqueous 4% formalin – 4% sucrose solution. Individual specimens in sample aliquots were measured in counting chambers using an electronic calipers on projected images. Biomass estimates for zooplankton (by W. G. Sprules) were obtained using an empirical relationship between wet weight and length (Hillbricht-Ilkowska & Patalas, 1967) for

each of 10 functional size categories (5 each for herbivores and carnivores).

Both phytoplankton and ciliate samples were taken from the same pooled sample of two hauls of an 8 M weighted plastic tube (9 mm diameter), separated midway into two equal length compartments; samples of the two depth ranges were kept separately. Phytoplankton samples were fixed in Lugol's iodine solution, settled onto microscope slides with a special chamber (Knoechel & Kalf, 1976), and measured under phase microscopy. Volumes were calculated from geometric formulae and converted to biomass estimates (by R. Knoechel) for each of 5 spherical and 2 filamentous size categories²⁴ by assuming neutral buoyancy. In Table 1, the three smallest (0–10 μm) and the two largest (10–30 μm and >30 μm) spherical categories have been combined.

Ciliate samples of 120 ml volume were fixed in Lugol's iodine solution (final concentration 0.5%) and stored at 10 °C in the dark. Subsamples were

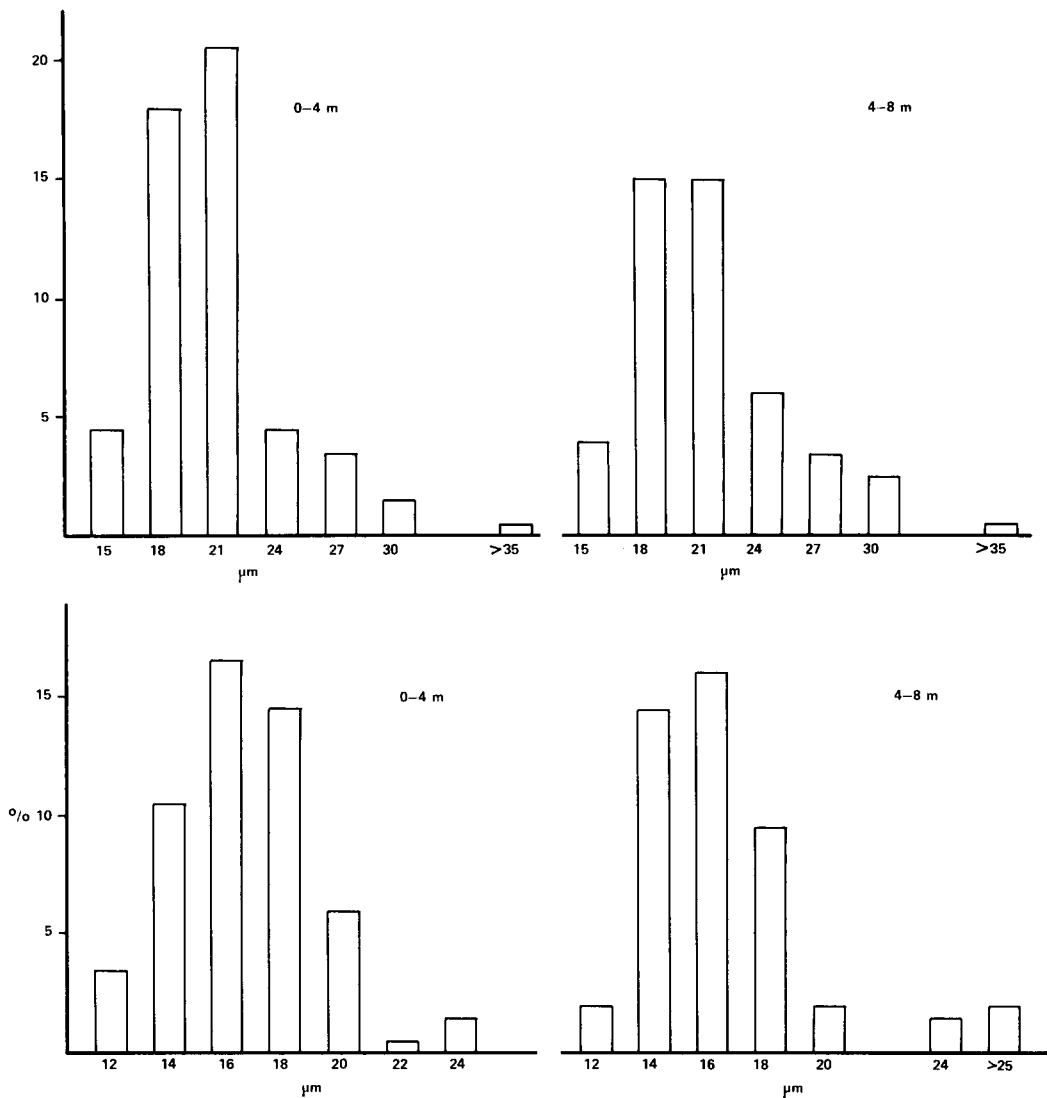


Fig. 1. Percentage histograms across all lakes of ciliate dimensions: (a) length (b) width.

settled overnight in 50 ml Utermohl chambers (Nauwerck, 1963) and examined by a single observer in uniform transects under phase microscopy with a Zeiss inverted microscope at 500X total magnification. Individual ciliates were measured for length and maximum cell body breadth, excluding feeding organelles. Volumes were estimated by assuming a prolate spheroid shape, and these were converted to biomass by using a conservative conversion factor of $0.416 \text{ pg } \mu\text{m}^{-3}$, which recently has been determined directly for the ciliate *Tetrahymena* (Gates *et al.*, 1982).

Results

Figure 1 presents percentage histograms for the total ciliate data. Ciliate densities and sizes at both the 0-4 m and 4-8 m depths were comparable. Figure 2 illustrates temporal trends over two sampling seasons for one lake. These results are typical of the other lakes which were sampled, in that there are few correlations among phytoplankton, zooplankton, and ciliate biomass values, either within size classes or overall. In this set of temperate lakes, the different compartments appear to show independ-

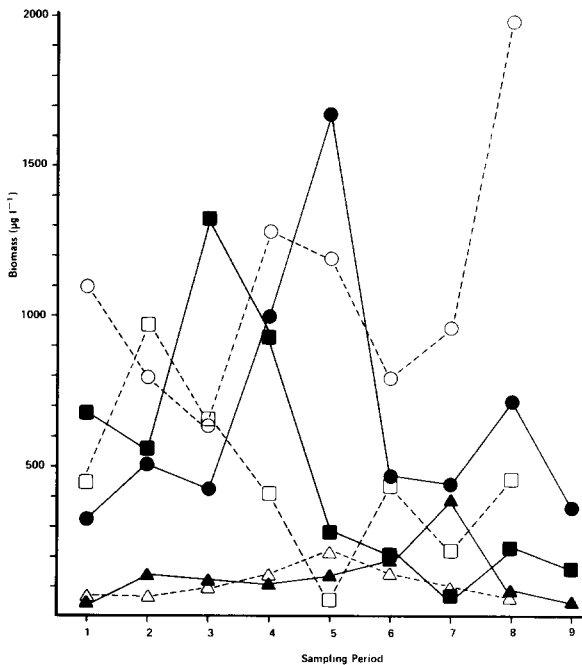


Fig. 2. Biomass fluctuations over two sampling seasons for White Lake. Solid lines and closed symbols are for the 1981 season (9 fortnightly samples, from early May to late August); dashed lines and open symbols are for the 1980 season (8 fortnightly samples, from late April to late August). Circles denote total 'edible' phytoplankton biomass (nannoplankton $< 30 \mu\text{m}$ diameter); triangles, mean ciliate biomass (0–8 m depth); squares, total zooplankton biomass.

ent abundance patterns. Detailed analyses of depth and temporal patterns for all the lakes are presented elsewhere (Gates, in press).

Figure 3 gives the ciliate data for the same lake over all sampling periods. Data previous to 1981 were obtained from fortuitously preserved phytoplankton samples which had been stored in the dark and which were settled and processed as outlined above. Only in the last two years of sampling were separate depth samples kept. The contribution of ciliates to total planktonic biomass over the four years sampled, 1978–1981, was 2.5, 2.5, 4.0, and 8.7%, respectively. Ciliate numerical densities were lower in 1979, and the mean volume of individual ciliates in the samples was significantly lower in 1978 and significantly larger in 1981. The late bloom of ciliates in 1981 was accompanied by an increase of testate amoebae as well, but, as shown in Fig. 2, did not accompany or directly follow peaks in other plankton compartments.

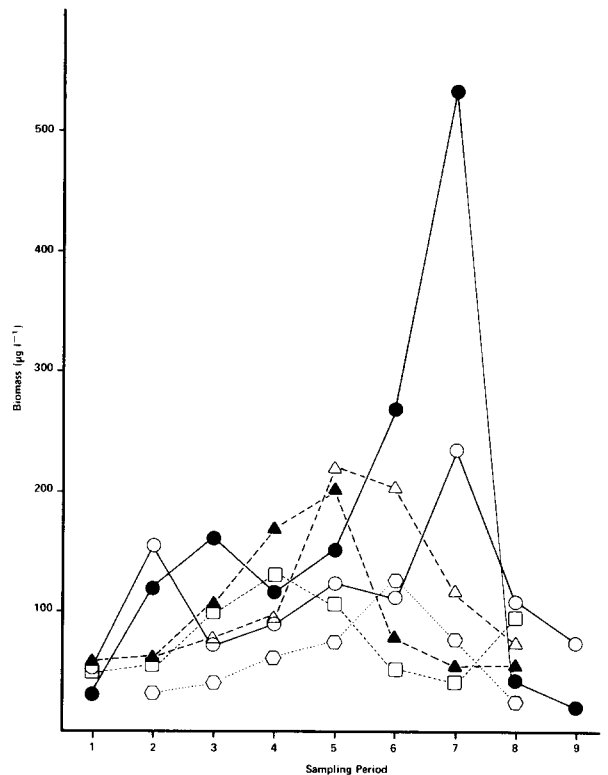


Fig. 3. Ciliate biomass fluctuations over 4 sampling seasons for White Lake. Circles denote 1981; triangles, 1980; squares, 1979; hexagons, 1978. Solid symbols for 1980 & 1981 represent the 0–4 m depth interval, while open symbols for those years represent 4–8 m samples; in previous years, no 4–8 m samples were taken.

Values for the seasonally averaged numerical and biomass densities of ciliates, and of the biomass densities for phytoplankton and zooplankton, are given in Table 1 for 1981. It is clear that there are no consistent trends across lakes with respect to the relative allocation of average biomass to the different compartments, although ciliates do constitute an appreciable amount of the total planktonic biomass. Indeed, because filamentous and other largely 'inedible' ($> 30 \mu\text{m}$) net phytoplankton (Sprules & Knoechel, in press) are included in the total, ciliates contribute an even greater percentage to the edible planktonic biomass.

Discussion

There are few comparable numerical and biomass density values for ciliates in the literature. For oligotrophic Lake Tanganyika, a ciliate abundance

of 8.8 ml^{-1} and a total protozoan biomass density of $184 \mu\text{g l}^{-1}$ has been reported (Hecky *et al.*, 1978; Hecky & Kling, 1981), while for an oligotrophic reservoir in the Soviet Union, densities of only 1.9 ml^{-1} were found (Mamaeva, 1976), and one oligotrophic Newfoundland lake (Davis, 1973) attained a maximum density for small ciliates of 5.2 ml^{-1} . Numerical densities of $9\text{--}19 \text{ ml}^{-1}$ and biomass densities of $52\text{--}83 \mu\text{g l}^{-1}$ were found in Jack Lake, another oligotrophic Ontario lake (Taylor & Lean, 1981). In the extremely oligotrophic and polar Char Lake, the average ciliate density over one year was 2.4 ml^{-1} , and the size range ($12.5\text{--}30 \mu\text{m}$) was comparable (Rigler *et al.*, 1974). Larger densities ($18\text{--}42 \text{ ml}^{-1}$) have been found in a Soviet mesotrophic lake (Sorokin & Pareljeva, 1972) and in the discrete ciliate populations of a small eutrophic lake in the English Lake District (Bark, 1981). In the large inland oligotrophic sea of Lake Ontario, planktonic ciliate densities in the epilimnion of the middle of the lake are of the order of $8\text{--}10 \text{ ml}^{-1}$ and biomass densities range from 35 to $60 \mu\text{g l}^{-1}$ (W. D. Taylor, unpubl.).

The numerical abundance found in the Ontario lakes agrees with the range of $8\text{--}60 \text{ ml}^{-1}$ found for a set of Florida lakes spanning a range of trophic levels, although none of the former set reached values in excess of 100 ml^{-1} found in certain hypereutrophic Florida lakes (Beaver & Crisman, 1982). The size range of ciliates was also comparable, although more larger ciliates were found in the Florida series. My estimate of average biomass density ($62.0 \mu\text{g l}^{-1}$, calculated from table 1) is less than the mean value of $124 \mu\text{g l}^{-1}$ reported for the oligotrophic subset of Florida lakes (Beaver & Crisman, 1982); however, this difference is partly due to different methods of estimation.

The prolate spheroid approximation to the shape of ciliates, used above, is the most commonly used method of converting linear cell measurements to volume estimates, but it produces an overestimate of the true cell volume for the pyriform genus *Tetrahymena* (Roberts, 1980; Gates *et al.*, 1982). However, for most of the ciliates found in plankton, such an estimate is more reasonable, because of their less elongate and more rotund shapes, and because the lateral extent of the large feeding organelles is ignored in measuring cell widths.

Most previous workers have assumed a specific gravity of 1.0, or greater (Sorokin & Pareljeva,

1972; Beaver & Crisman, 1982), for ciliates, and they have used this in estimating wet weight from volume (Schonborn, 1977) or from a regression of volume on cell length (Fenchel, 1967). I have used a directly measured value for wet weight (Gates *et al.*, 1982) of $0.416 \pm 0.071 \text{ pg } \mu\text{m}^{-3}$, which is based on the assumption of a prolate spheroid shape for *Tetrahymena*. However, a more accurate value is $0.787 \pm 0.166 \text{ pg } \mu\text{m}^{-3}$, based on electronic sizing of the cells (Gates *et al.*, 1982). This is still an underestimate since it is based on axenically grown cells: bacterized *Tetrahymena* cultures have average wet weights (Gates *et al.*, 1982) in excess of $1.1 \text{ pg } \mu\text{m}^{-3}$.

Therefore, the estimates of biomass given above are very conservative. True ciliate biomass densities in nature are probably larger, although confirmation will require direct measurements of ciliate weights from live field samples. Even though ciliates constitute a numerically small fraction of the total biomass in lakes, their heterotrophic role in consuming bacteria, which themselves release little phosphorus into oligotrophic lakes (Jonannes, 1965; Buechler & Dillon, 1974), means that small ciliates constituting only 1% of the aggregate biomass can account for nearly 50% of the total dissolved phosphorus in the lake (Buechler & Dillon, 1974; Taylor & Lean, 1981). My estimates of ciliate biomass imply, therefore, that ciliates comprise a quantitatively important component of lake ecosystems.

Summary

Phytoplankton, zooplankton, and ciliated protozoa were sampled from 9 Ontario lakes fortnightly during the ice-free period of 1981. Biomass estimates were made for these three plankton categories. The results indicate that the ciliates, which occurred in average densities of $20\text{--}40 \text{ ml}^{-1}$, constituted 5–10% of the total planktonic biomass.

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