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The relative importance of protozoans, rotifers, and crustaceans in a freshwater zooplankton community¹

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Abstract

A complete analysis of the macro- and microzooplankton of a warm monomictic lake indicates that Protozoa dominate the community numerically. During winter mixis, ciliates are found at densities of $1-8 \times 10^3 \cdot \text{liter}^{-1}$ and constitute up to 32% of the zooplankton community biomass. With summer stratification crustaceans decline, while both the relative and absolute abundance of protozoans and rotifers increase. Densities of protozoans are highest ($1-2 \times 10^5 \cdot \text{liter}^{-1}$) in the metalimnion where scuticociliates bloom in zones of intense bacterial activity. During the period of these blooms (July–October), Protozoa account for 15–62% of the zooplankton biomass. This suggests that Protozoa make a significant contribution to rates of grazing, nutrient regeneration, and secondary productivity and should not be overlooked in zooplankton community studies.

Protozoa are rarely included in studies of freshwater zooplankton communities. This is primarily because cladocerans, copepods, and rotifers are considered to be most important in terms of density, biomass, production, grazing, and nutrient regeneration (Hutchinson 1967; Haney 1973; Hrbáček 1977; Porter 1977; Makarewicz and Likens 1979). The Protozoa also require methods of sampling not normally included in zooplankton studies. They are not quantitatively sampled by standard macrozooplankton nets with mesh openings of $64 \mu\text{m}$ or larger or by the $35\text{-}\mu\text{m}$ -mesh nets recommended for rotifers (*see* Likens and Gilbert 1970). As a consequence, information about planktonic Protozoa is fragmentary and incomplete. Previous quantitative studies have considered Protozoa over only brief intervals of the year (Sorokin and Paveljeva 1972), at a few depths (Bamforth 1958; Wilbert 1969), without regard to species composition (Rigler et al. 1974), or exclusive of the total zooplankton community (Bamforth 1958; Hecky et al. 1978). We report results from an annual study of a macro- and microzoo-

plankton association which shows that Protozoa (here used to refer to ciliates and amoebae) dominate numerically and are present at standing stocks comparable to the Crustacea and Rotifera. We describe methods of sampling and preservation for microzooplankton, including protozoans and small rotifers, and provide accurate biomass determinations for crustacean zooplankton.

The zooplankton community of Lake Oglethorpe, a 30-ha manmade lake ($z_{\text{max}} = 8.5 \text{ m}$), was sampled over 13 months. The site was chosen for its convenience and because we felt it was typical of the small lakes in the southeast used primarily for recreational fishing. Lake Oglethorpe is a warm monomictic lake with a winter mixis period from November to March followed by the development of stratification in spring. During summer the hypolimnion becomes anaerobic and remains so until turnover in October or November. The surface temperature ranged from 4° to 28°C , the bottom temperature from 3° to 13°C during 1979. Lake Oglethorpe is a eutrophic system based on chemical parameters (J. Meyer pers. comm.) and algal and bacterial densities (Porter and Feig 1980). Primary productivity, however, is below that normally found in eutrophic situations, due primarily to high turbidity (T. Jacobsen pers. comm.).

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with the fieldwork; K. Porter provided advice and encouragement. M. B. Csutor shared her unpublished method for preserving Protozoa. The criticisms of an anonymous reviewer, K. Porter, and J. Gerritsen improved earlier versions of this paper.

Methods

Zooplankton were sampled in three ways. Whole water samples were taken for protozoans and small rotifers with a 5-liter Van Dorn bottle. About 230 ml was preserved with 10 ml of a saturated solution of HgCl_2 and stained with a drop of 0.04% bromophenol blue (M. B. Csutor pers. comm.). Larger protozoans (*Epi-stylis*, *Vorticella*-aggregations, *Rhabdostyla*, and *Diffflugia*), rotifers, and copepod nauplii were sampled by gently filtering 0.5–2.0 liters of lake water through a 26- μm sieve; the sieve was thoroughly rinsed and its contents preserved in HgCl_2 . Macrozooplankton (cladocerans, cyclopoid and calanoid copepods, and ostracods) were sampled with a Juday trap (volume, 10.4 liters) with a 64- μm net and preserved with a sucrose Formalin solution (Haney and Hall 1973). Monthly samples were taken from an 8-m-deep central station at 1-m intervals from the surface to 7 m. We took 310 samples from 18 December 1978 to 14 December 1979.

Protozoans and small rotifers were counted in the whole water samples at 250 \times magnification with an inverted microscope by scanning an entire settling chamber. Generally a 25-ml chamber was used; however, at certain seasons and depths high concentrations of algae, detritus, or clays necessitated the use of a smaller chamber (5 or 10 ml). The filtered microzooplankton samples were poured into settling chambers (3–8 chambers depending on the density of animals and other particulate material), and larger protozoans, rotifers, and nauplii were counted with the inverted microscope (100 \times). Juday trap samples were counted with a dissecting microscope (30 \times) and a modified Bogorov chamber; two of these (2 and 3 m, December 1979) were

split before counting, and samples were not collected for the depths of 6 and 7 m in May because the trap was broken. Because of the time needed to count Protozoa (2–5 h per sample), we did not try to estimate the sampling or spatial variance of the zooplankton populations. Zooplankton were identified to genera or species, except for nauplii and some protozoans where similar forms were lumped together (i.e. small oligotrich ciliates consisting of several species <40 μm in maximum dimension).

We compared mercuric chloride with bromophenol blue (BPB) to other preservatives which had been used for counting protozoans. We preserved three aliquots of a whole water sample in either Lugol's iodide (1% final solution), Formalin (2%), or HgCl_2 + BPB, and we made four replicate counts for each preservative. Significantly fewer protozoans (*t*-test, $P < 0.05$) were counted in Formalin-preserved samples than in HgCl_2 . Some of the Protozoa were either destroyed or distorted beyond recognition by the Formalin. Specimens of *Mesodinium* sp. were rare in Formalin samples (6 observed in 4 counts) but common (35 in 4 counts of HgCl_2) in the other preservatives. Taylor et al. (1971) have noted that the marine ciliate *Mesodinium rubrum* disintegrates in Formalin. Mercuric chloride provides excellent preservation, and the stain makes the protozoans more visible, particularly when detrital or sediment loads are high. Lugol's is also an effective preservative, but the protozoans are stained the same color as other particulate matter, making them hard to discern at high particle concentrations.

A comparison of whole water counts with 26- μm -sieved samples indicated that the small rotifers *Ascomorpha* sp. (53 \times 40 μm) and *Trichocerca rouseleti* (81 \times 27 μm) were not quantitatively retained on the sieve. Several other investigators have noted that small rotifers pass directly through nets of even 10- μm mesh (Likens and Gilbert 1970; Bottrell et al. 1976). When sufficient numbers of these two small species were present in the settled whole water sample, we used

Table 1. Regressions of length vs. dry weight for major crustaceans in Lake Oglethorpe. Model: $\ln W = b \ln L + \ln a$, where W is weight (μg), L is length (mm), $\ln a$ is intercept estimator, b is slope estimator, r^2 is determination coefficient, and N is number of observations.

	$\ln a$	b	r^2	N
<i>Daphnia parvula</i>	1.44	1.80	0.80	44
<i>Ceriodaphnia reticulata</i>	2.83	3.15	0.90	23
<i>Diaptomus siciloides</i>	1.05	2.46	0.59	26
Cyclopoids	1.77	2.74	0.96	19

this value in preference to the count from the filtered sample.

We estimated the relative contribution of the major zooplankton groups (protozoans, rotifers, nauplii, and crustaceans—i.e. postnaupliar copepods and cladocerans) to community biomass by using their numerical abundance and measured volumes (microzooplankton) or dry weights (macrozooplankton). We estimated volumes of protozoans, rotifers, and nauplii by assuming that the organisms conformed to simple or combinations of simple shapes (Finlay 1977; Ruttner-Kolisko 1977; Taylor 1978). The appropriate measurements were made to the nearest $1.2 \mu\text{m}$ for protozoans and $3.1 \mu\text{m}$ for rotifers and nauplii on individuals ($n = 20$) preserved in HgCl_2 . Shrinkage caused by the preservative was minimal. For taxa present throughout the year, we calculated mean volumes for stratified ($n = 20$) and unstratified ($n = 20$) periods, because body sizes tended to be smaller at higher temperatures. We estimated dry weights from volumes by assuming a specific gravity of 1.0 and a dry weight to wet weight ratio of 10%, except for *Asplanchna* where a ratio of 4% was used (see Dumont et al. 1975).

Length-weight regressions were established for *Daphnia parvula*, *Ceriodaphnia reticulata*, *Diaptomus siciloides*, and cyclopoid copepods (two species) (Table 1). Living animals were isolated from plankton hauls or laboratory cultures, rinsed in distilled water, measured to the nearest 0.03 mm, dried at 60°C for 24 h, and weighed on a Cahn electrobalance (model 21). Some workers have stated

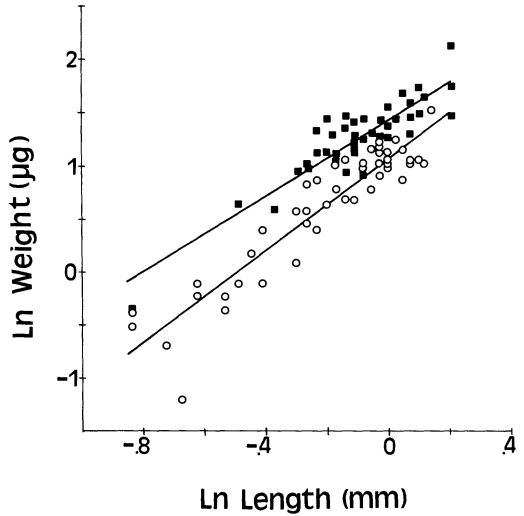


Fig. 1. Regressions of length vs. dry weight for Formalin-preserved (\circ) and fresh (\blacksquare) *Daphnia parvula*. Slopes of regressions are similar ($P > 0.5$), but elevation of Formalin regression ($\ln W = 2.16 \cdot \ln L + 1.08$, $r^2 = 0.86$, $n = 52$) is significantly lower ($P < 0.001$).

that animals preserved in Formalin are suitable for dry weight measurements (Dumont et al. 1975; Bottrell et al. 1976) while others have questioned this approach (Edmondson 1974). When we compared *D. parvula* preserved in sucrose-Formalin for 10 months to fresh animals (Fig. 1), our regressions had a similar slope (ANCOVA, $F = 0.153$, $P > 0.5$) but different elevations (ANCOVA, $F = 126.265$, $P < 0.001$). The dry weight of *D. parvula* was substantially underestimated by using Formalin-fixed animals, and consequently all regressions in Table 1 were established with unpreserved animals.

We estimated a mean weight for the field populations each month with the regression equations and a series of length measurements from monthly vertical net hauls (Persson and Ekbohm 1980). This mean weight coupled with the Juday trap densities was then used to calculate dry wt $\cdot \text{m}^{-2}$. For *Diaphanosoma brachyurum* we used a mean value of $2.45 \mu\text{g}$ dry wt $\cdot \text{animal}^{-1}$ ($n = 11$). A few rare organisms which never accounted for $>5\%$ of the total counts were excluded

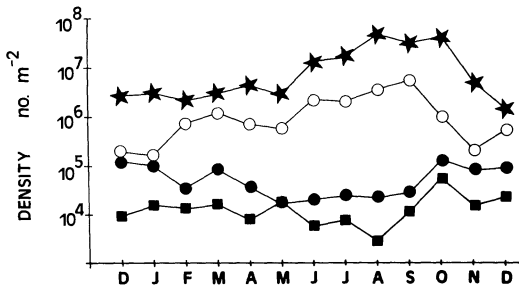


Fig. 2. Density per square meter of protozoans (★), rotifers (○), nauplii (●), and macrozooplankton (■) in Lake Oglethorpe, December 1978–December 1979.

ed from the biomass estimates; the biomass of eggs was also not considered.

Results

Throughout the year, protozoans were numerically the most abundant organisms in the zooplankton (10^6 – $10^7 \cdot m^{-2}$), usually an order of magnitude more numerous than the rotifers, which were also abundant (10^5 – $10^6 \cdot m^{-2}$). These two groups increased in absolute and relative abundance in June and remained at high densities until fall turnover in November (Fig. 2). Nauplii were abundant in winter, declined through spring, and reached a stable low level in summer before increasing again at fall turnover. Macrozooplankton reached highest densities in May (*C. reticulata*), October (*D. parvula* and *D. siciloides*), and December (*D. parvula* and *D. siciloides*).

In terms of biomass ($g \text{ dry wt} \cdot m^{-2}$), crustaceans (macrozooplankton and nauplii) were most important in the winter and spring plankton when protozoans constituted <20% (except January, 32%, and April, 42%: Fig. 3). During summer this pattern was reversed: macrozooplankton and nauplii declined in biomass while rotifers and protozoans increased. In August the last two groups accounted for 91% of the community biomass. As fall turnover approached there was an increase in macrozooplankton in October and, after another upsurge of protozoans in November, a return to winter biomass distributions.

The vertical distribution of protozoans was nearly uniform during winter mixis, although slightly higher densities in the upper waters (0–3 m) suggest that growth was most active in this zone (Fig. 4). With the development of stratification (March–May), there was a decline of protozoans in the hypolimnion and a concomitant increase in their densities in the warming epilimnion. A bloom of scuticociliates began in the meta- and hypolimnion in July and intensified in late summer and early fall. Densities of scuticociliates were highest just beneath the thermocline, which eroded as fall cooling began in September and October. This is indicated in Fig. 4 by the zones of high density in August (3–5 m) and October (6–7 m). During summer there was also an increase in the density and diversity of protozoans in the epilimnion. With turnover

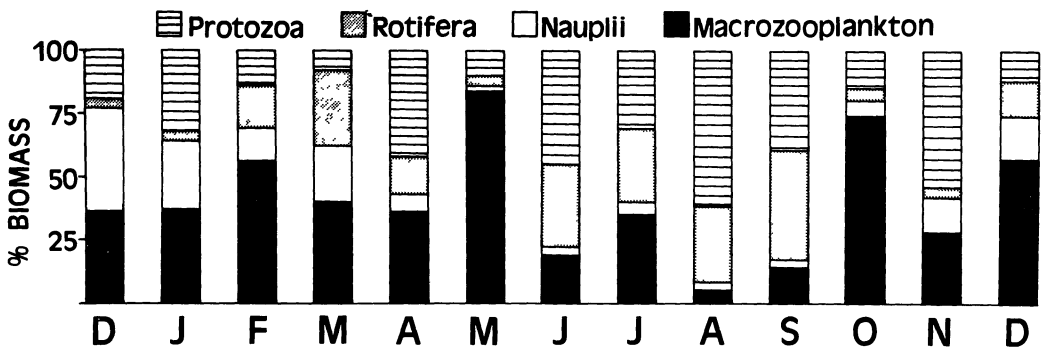


Fig. 3. Percentages of protozoans, rotifers, nauplii, and macrozooplankton in total community biomass for monthly samples, December 1978–December 1979.

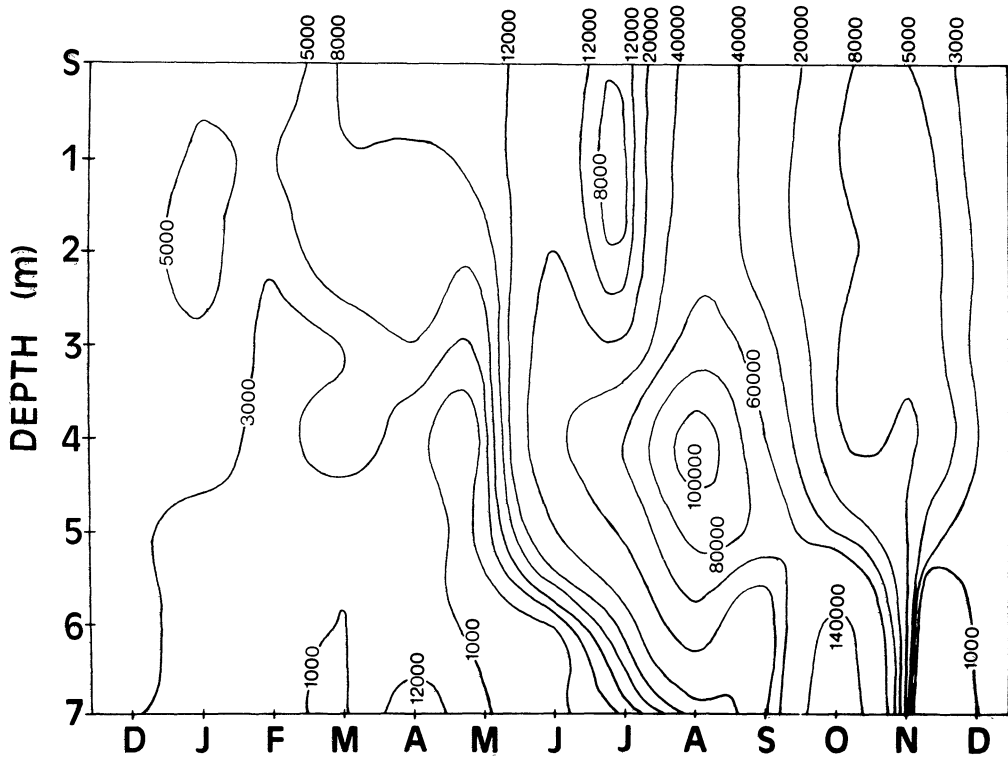


Fig. 4. Seasonal-depth distribution of Protozoa (No.·liter⁻¹) in Lake Oglethorpe over annual cycle, December 1978–December 1979.

there was a general decline of protozoans at all depths to winter concentrations.

In Table 2 species-specific depth distributions are shown for typical months in winter, spring, and late summer. Densities of the four most abundant protozoans are given, with the most important rotifer and crustacean for comparison. In the winter plankton, the freshwater tintinnid *Tintinnopsis* (= *Codonella*) *lacustris* was often the most abundant zooplankton. This widely distributed form is known to graze on small diatoms and chrysomonads (Bick 1972). Both the small oligotrichs and *Strombidium viride* are present in the plankton throughout the year, increasing to densities of 10^3 – 10^4 ·liter⁻¹ in May and August (Table 2). Some of the small oligotrichs and *S. viride* have symbiotic zoochlorellae (Kahl 1932; Bick 1972; Hecky et al. 1978), but the degree to which these organisms depend on autotrophic or heterotrophic nutrition is

unknown. We observed viable specimens beneath the euphotic zone. There was also no tendency for the small oligotrichs to be more abundant in the epilimnion during winter mixis when oxygen gradients were absent; however, these aerobic protozoans were constrained to the epilimnion after stratification (Table 2). The large peritrich *Rhabdostyla* sp. was the most important protozoan in terms of biomass in winter, reaching peak abundance in November.

In May *Mesodinium* sp. appeared in the plankton and maintained high densities (10^3 ·liter⁻¹) through October in the epilimnion. The testate amoeba *Diffugia* sp. was also an important component of the spring and summer plankton, reaching peak densities in May. By late summer the scuticociliates dominated the protozooplankton; they reached their highest densities in zones of high microheterotrophic activity and bacterial

Table 2. Density per liter of four most abundant protozoans and most abundant rotifer and crustacean for monthly samples in January, May, and August 1979. Maximum linear dimensions of protozoans are based on mean of 20 measurements of preserved specimens at 1,000×. Dash indicates no organisms recorded.

	Surface	1 m	2 m	3 m	4 m	5 m	6 m	7 m
January								
Protozoa								
<i>Strombidium viride</i> (44 μm)	1,840	1,400	320	800	160	240	80	40
Small oligotrichs (24 μm)	600	880	1,480	880	1,200	1,040	880	1,640
<i>Tintinnopsis lacustris</i> (63 μm)	1,720	2,720	3,720	2,400	2,120	680	760	360
<i>Rhabdostyla</i> sp. (123 μm)	265	207	140	159	140	143	140	245
Rotifer								
<i>Kellicottia bostoniensis</i>	89	70	123	92	89	97	120	213
Crustacean								
<i>Diaptomus siciloides</i>	26.4	38.4	11.8	12.8	10.5	9.2	10.4	9.3
May								
Protozoa								
<i>S. viride</i> (37 μm)	1,080	1,720	1,120	640	160	360	100	—
<i>Mesodinium</i> sp. (28 μm)	680	920	640	—	—	—	—	—
Small oligotrichs (22 μm)	3,280	4,400	2,320	2,480	1,080	1,240	—	100
<i>Diffugia</i> sp. (71 μm)	770	1,010	758	332	86	74	4	10
Rotifer								
<i>Trichocerca rouseleti</i>	1,480	1,440	1,640	200	240	240	—	—
Crustacean								
<i>Ceriodaphnia reticulata</i>	91.2	56.4	19.8	2.6	0.7	0.8	—	—
August								
Protozoa								
<i>S. viride</i> (37 μm)	2,200	2,200	2,000	2,200	1,600	—	200	—
Small oligotrichs (22 μm)	14,400	20,700	20,600	12,200	5,600	3,200	800	—
Scuticociliates (30 μm)	16,700	18,400	23,900	44,600	94,100	79,000	49,000	11,600
<i>Vorticella</i> sp. (23 μm)	800	2,000	2,300	800	100	—	—	—
Rotifer								
<i>Anuraeopsis fissa</i>	814	3,268	1,768	3,986	2,330	1,452	350	144
Crustacean								
<i>D. siciloides</i>	0.1	—	6.2	3.9	1.5	0.4	0.1	0.2

density (B. Hodson, A. Maccubin, K. Porter, Y. Feig pers. comm.). *Vorticella* sp. was found attached to chains of *Anabaena spiroides*; the alga provides a substrate for attachment and probably also an enriched food microenvironment.

For the months shown there was a ratio of about 10:1 between the densities of the most important protozoan and that of the most important rotifer. For the crustaceans this ratio was much higher, generally falling between 10² and 10³.

Discussion

The significance of these ratios with regard to secondary production, nutrient

recycling, and energy transfer is considerable, although speculative. Given the biomass of Protozoa in Lake Oglethorpe and the high growth rates of ciliates (Fenchel 1968; Finlay 1977; Heinbokel 1978a) relative to those of other zooplankton (Allan 1976), these organisms are likely to be the most important secondary producers in the lake. As for nutrient regeneration, high specific rates of phosphorus excretion are known for ciliates (Johannes 1965; Buechler and Dillon 1974). At these rates, the Protozoa in the epilimnion of Lake Oglethorpe are capable of turning over a quantity of phosphorus equal to the total pool (total

phosphorus = 15–30 $\mu\text{g P}\cdot\text{liter}^{-1}$) within a day during the warmer months (June–October). The planktonic Protozoa also represent a potential trophic link between microheterotrophic production and invertebrate predators (Porter et al. 1979). This phenomenon seems to be particularly important in Lake Oglethorpe during stratification. The scuticociliates graze on the active bacterial populations found along and beneath the thermocline (3–6 m). This zone of activity overlaps with the daytime holding depth of cladocerans and copepods, 3–4 m (J. Orcutt unpubl.), and crustaceans have been shown to feed on ciliates at these densities, 10–100 ciliates $\cdot\text{ml}^{-1}$ (McMahon and Rigler 1965; Tezuka 1974; Berk et al. 1977; Porter et al. 1979).

Observations indicate that many of the Protozoa graze on algal nanoplankton (i.e. *T. lacustris* and *S. viride*) (Bick 1972), but quantitative information on the feeding rates of these organisms is not available except for marine tintinnids: Heinbokel (1978b) measured filtering rates of 1–10 $\mu\text{l}\cdot\text{animal}^{-1}\cdot\text{h}^{-1}$ for natural assemblages. At these rates a concentration of 10³ Protozoa $\cdot\text{liter}^{-1}$ would filter 2–24% of the water per day. These and higher densities are found in the epilimnion of Lake Oglethorpe throughout the year, suggesting that protozoans may be important herbivores on the smaller algae in this system.

There is a shift in the biomass structure of the community during stratification from crustacean dominance to dominance by protozoans and rotifers. We suggest that this reflects both increased predation on crustaceans and changes in the size distribution and quality of zooplankton food resources. Densities of the predatory midge larvae *Chaoborus* increase during summer as macrozooplankton decline (J. Orcutt unpubl.). There is also an increase in both the lower (bacteria) and upper (filamentous blue-green algae) sizes of potential food resources (Porter and Feig 1980; Porter unpubl.). These conditions favor microzooplankton. We postulate that rotifers, and particularly protozoans, have a differential ability to

feed on planktonic bacteria which reach concentrations of 3×10^7 cells $\cdot\text{ml}^{-1}$ during summer (Porter and Feig 1980). The high concentration of filamentous and noxious blue-green algae ($>10^8\cdot\text{liter}^{-1}$; Porter unpubl.) inhibits feeding by larger zooplankters (Webster and Peters 1978), while microzooplankton would not be inhibited from feeding between the filaments (Webster and Peters 1978). The ability of some protozoans and rotifers to exploit the anaerobic hypolimnion, avoided by crustacean zooplankton, also accounts for the increased importance of microzooplankton during summer stratification.

The few studies available suggest that the densities of planktonic Protozoa in Lake Oglethorpe are not unusual. Rigler et al. (1974) noted densities of 10³–10⁴ ciliates $\cdot\text{liter}^{-1}$ in ultra-oligotrophic Char Lake; the estimated productivity of the ciliate fauna was second only to that of the dominant copepod, *Limnocalanus macrurus*. Hecky et al. (1978) found standing crops of Protozoa in Lake Tanganyika which on several occasions exceeded the standing crops of algae. Densities of 10³ ciliates $\cdot\text{liter}^{-1}$ were also found during all seasons in the epilimnion of Fuller Pond, a temperate mesotrophic kettle lake (Porter 1973). In Lake Erken, another mesotrophic lake, densities ranged from 10² to 10⁴ ciliates $\cdot\text{liter}^{-1}$, and ciliates accounted for up to 90% of the zooplankton community biomass during early spring algal blooms (Nauwerck 1963). Sorokin and Paveljeva (1972) observed densities of 10⁵ ciliates $\cdot\text{liter}^{-1}$ in Dalnee Lake, a eutrophic reservoir, at midwater depths during the declining phase of an algal bloom and the onset of intensive bacterial activity. The situation in eutrophic ponds is similar, with densities of 10³–10⁵ ciliates $\cdot\text{liter}^{-1}$ (Bamforth 1958; Wilbert 1969). Thus across a variety of lake types, the Protozoa are consistently an abundant component of the planktonic community. It also appears that protozoan abundance increases with increasing eutrophy. It is important to note that in all these studies protozoans were counted from whole water samples;

had nets been used, particularly nets of a large mesh size, most of the Protozoa would have been overlooked.

The position of particular protozoan species in the planktonic community depends on the degree to which a species is autotrophic. Protozoa deriving a preponderance of their nutrition from symbiotic zoochlorellae could be more appropriately considered phytoplankton. Certainly, this is the case for *M. rubrum*, a common and important primary producer in parts of the world ocean (Taylor et al. 1971; Hibberd 1977). In Lake Oglethorpe 5 of 22 taxa we found have been described as containing zoochlorellae (Bick 1972). Ciliates containing algal symbionts are also prominent in Lake Tanganyika (Hecky et al. 1978). There are, however, no studies of the facultative nature of the symbiosis or of the importance of symbionts when they occur. Most forms containing symbionts feed on particulate matter (Bick 1972). Although this problem requires further study, that does not diminish the conclusion that Protozoa are important components of the zooplankton; strictly heterotrophic forms such as *T. lacustris* and the scuticociliates are abundant throughout the year (Table 2).

Investigators of zooplankton communities have placed a heavy emphasis on Crustacea. Rotifers are significant components of planktonic systems spanning a range of trophic conditions (Makarewicz and Likens 1979). Protozoa are similarly important and perhaps dominant in many lakes, according to our results and those in the studies cited above. In order to understand patterns of energy flow, and factors determining community structure, we must expand our conception of planktonic systems to include these microconsumers.

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