Seasonal dynamics of rotifer and crustacean zooplankton populations in a eutrophic, monomictic lake with a note on rotifer sampling techniques*

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Abstract

The abundances, biomass, and seasonal succession of rotifer and crustacean zooplankton were examined in a man-made, eutrophic lake, Lake Oglethorpe, over a 13 month period. There was an inverse correlation between the abundance of rotifers and crustaceans. Rotifers were most abundant and dominated (>69%) the rotifer-crustacean biomass during summer months (June–September) while crustacean zooplankton dominated during the remainder of the year (>89%). Peak biomasses of crustaceans were observed in the fall (151 μg dry wt l^{-1} in October) and spring (89.66 μg dry wt l^{-1} in May). Mean annual biomass levels were 46.99 μg dry wt l^{-1} for crustaceans and 19.26 μg dry wt l^{-1} for rotifers. *Trichocerca rousseleti, Polyarthra* sp., *Keratella cochlearis* and *Kellicottia bostoniensis* were the most abundant rotifers in the lake. *Diaptomus siciloides* and *Daphnia parvula* were the most abundant crustaceans. Lake Oglethorpe is distinct in having an unusually high abundance of rotifers (range 217–7980 l^{-1}). These high densities can be attributed not only to the eutrophic conditions of the lake but also to the detailed sampling methods employed in this study.

Introduction

Limnologists have been examining and describing patterns of seasonal succession of zooplankton species since the turn of the century (Hutchinson, 1967). Historically, a majority of this work has been conducted in dimictic temperate lake systems and typically has not considered the dynamics of both rotifer and crustacean zooplankton simultaneously. The purpose of this study was to describe the annual population dynamics of both rotifer and crustacean zooplankton in Lake Oglethorpe, a cold monomictic lake located in northeast Georgia, U.S.A. The relative importance of rotifer and crustacean species are presented and compared to other limnetic systems. The accuracy of rotifer sampling techniques are also evaluated. The seasonal dynamics of protozoan zooplankton species and their relative importance in the zooplankton community of Lake Oglethorpe have been published elsewhere (Pace & Orcutt, 1981; Pace, 1982).

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Study site

The watershed of Lake Oglethorpe consists of a combination of woodlands, agricultural fields and residential yards. The lake is eutrophic, (range of total phosphorus = 16–1078 μg l^{-1}) but primary production rates are moderate (100–200 g C m^{-2} a^{-1}), probably due to high turbidity (Pace & Orcutt, 1981; Pace, 1982). Temperatures in Lake Oglethorpe ranged from 4 ° to 30 °C over the annual cycle of 1979 (Orcutt, 1982). A period of mixis occurred from November to March. The lake began to stratify in March and remained stratified from April through October. An anaerobic hypolimnion developed at the onset of lake stratification and persisted from May to December with the anoxic layer reaching a maximum shallow water depth of 3.5 m in midsummer. The lake contains six species of fish known to be planktivorous for at least part if not all of their life history: *Lepomis cyanellus*, *Lepomis macrochirus*, *Lepomis auritus*, *Pomoxis nigromaculatus*, *Notemigonus crysoleucus* and *Micropterus salmoides* (Carlander, 1977).

Methods

Rotifers and crustacean zooplankton were sampled monthly from December 1978 through December 1979 in Lake Oglethorpe. All samples were taken at the same 8 m deep central lake station. Zooplankton were sampled by four different methods to insure that the most accurate sampling techniques were used for the quantification of various sizes of zooplankton. All crustacean zooplankton except copepod nauplii were collected by both vertical net tows using a 0.5-m diameter conical net (64-μm mesh) and a Juday trap (64-μm mesh net). Vertical net hauls were taken from a 6-m depth to the surface, pulled at a rate of 1 m s^{-1}. Crustacean zooplankton were quantified from two (replicate) vertical profiles taken with a Juday trap. Each vertical profile consisted of a series of Juday trap samples taken at 1-m intervals from the surface to the bottom. Body-length measurements used to calculate biomass estimates were made on animals collected by vertical net hauls. All crustacean zooplankton samples were preserved by adding the sample to sucrose formalin to make a 4% solution and counted in a modified Bogorov chamber with a dissecting microscope (30×).

Whole water samples were taken to quantify rotifers and copepod nauplii with a 5-l Van Dorn bottle at 1-m intervals from the surface through 7-m. Approximately 230 cm^3 were preserved with 10 cm^3 saturated solution of $HgCl_2$ and stained with a drop of 0.04% bromophenol blue (Pace & Orcutt, 1981). Small rotifers were counted in whole water samples at 250× magnification with an inverted microscope by scanning an entire settling chamber (5–25 cm^3 depending on concentrations of algae and detritus). This prevented the omission of very small rotifers which potentially can pass through even small mesh sieves. Larger rotifers, and copepod nauplii which were not retained quantitatively by a 64-μm mesh net, were collected by gently filtering 0.5 to 2.0-l of whole water samples through a 26-μm sieve. The sieve was rinsed thoroughly and its contents preserved in $HgCl_2$. These samples were counted in settling chambers with an inverted microscope (100×).

Zooplankton biomasses were estimated from length-weight regressions (crustacean zooplankton), and volume estimates (rotifers and copepod nauplii). Rotifer and nauplii volumes were estimated by assuming that the organisms conformed to simple geometric shapes or combinations thereof (Ruttner-Kolisko, 1977). Dry-weight estimates were calculated by assuming a specific gravity of 1.0 and a dry weight to wet weight ratio of 10%, except for *Asplanchna* sp., in which a ratio of 4% was used (see Dumont *et al.*, 1975). Crustacean dry weights were calculated from the length-weight regressions of Pace & Orcutt (1981) and from monthly body length measurements according to Persson & Ekbohm (1980).

Results

Abundance and seasonal distribution of rotifers

There was a high degree of seasonal variability within and between groups of rotifer species (Fig. 1). Some species were present throughout the year such as *Keratella cochlearis* (Fig. 1a) and *Polyarthra* sp. (Fig. 1b). Maximum densities of *Keratella cochlearis* (647 l^{-1}) and *Polyarthra* sp. 2 776 l^{-1}) were found in September when these genera together comprised 43% of the total density and 71% of the total rotifer biomass. *Kellicottia bostoniensis* was also present throughout the year and was most abundant in October (365-l^{-1}; Fig. 1c). This species, however, maintained higher densities in the winter months and was rare during summer stratification (Fig. 1c).

A second suite of species consisted of those found primarily during winter mixis. These included *Asplanchna* sp. (Fig. 1d), *Conochilus unicornis*, and *Ascomorpha minima*. Similarly, a number of rotifers were abundant only during summer stratifica-

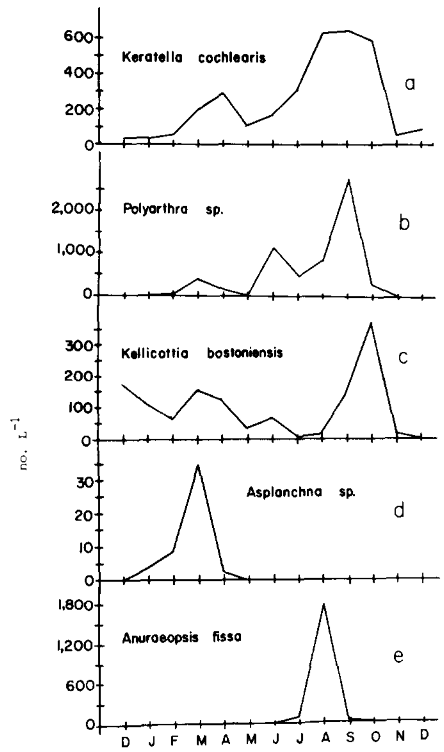

Fig. 1. Seasonal population dynamics of planktonic rotifers; *Keratella cochlearis, Polyarthra* sp., *Kellicottia bostoniensis, Asplanchna* sp., and *Anuraeopsis fissa* over the annual cycle of 1979.

tion and were absent during lake mixis (aestival species; Hutchinson, 1967). These included *Anuraeopsis fissa* (Fig. 1e), *Trichocerca rousseleti, Trichocerca cylindrica, Filina longiseta, Hexarthra* sp., and *Collotheca* sp. Several of these species such as *Anuraeopsis fissa* were found in the metalimnion in association with high concentrations of algae, bacteria, and detritus.

Rotifer sampling procedure

The relative capture efficiency of a 26-μm mesh sieve was considered for the quantitative sampling of four genera of rotifers. Population densities determined from sieved samples were compared with those quantified from whole water samples by a general linear regression procedure (Table 1). A slope of 1.0 indicates 100% capture efficiency for samples sieved through a 26-μm mesh and decreasing slopes indicate a reduction in capture efficiency.

Table 1. Mean body size dimensions and slopes (±SE) of linear regression analysis for population densities of rotifers determined from quantification of whole water samples vs. samples sieved through a 26 μm mesh funnel.

Species	Width × length μm	Slope	n	r^2
Keratella cochlearis	61 × 141	1.01 ± 0.16	35	0.55
Polyarthra sp.	60 × 94	0.92 ± 0.06	28	0.88
Anuraeopsis fissa	39 × 65	0.60 ± 0.09	12	0.79
Trichocerca rousseleti	29 × 72	0.33 ± 0.04	24	0.76

Regression analyses (Table 1) indicate capture efficiency not significantly different from 100% for the two larger of the four species examined, *Keratella cochlearis* (61 × 141 μm in size) and, *Polyarthra* sp. (60 × 94 μm in size), and substantial population losses of the two smaller species examined, *Anauraeopsis fissa* (60% capture efficiency; 39 × 65 μm in size) and *Trichocerca rousseleti* (33% capture efficiency; 29 × 72 μm in size).

Abundance and seasonal distribution of crustacean zooplankton

Seasonal population densities of crustacean zooplankton are presented in Fig. 2. The primary crustacean zooplankton and their respective maximum densities include; *Diaptomus siciloides* (30.24 copepidid and adults l^{-1}), *Daphnia parvula* (21.83 animals l^{-1}), *Ceriodaphnia lacustris* (20.73 animals l^{-1}), *Diaphanosoma brachyurum* (3.83 animals l^{-1}), two cyclopoid copepods (12.31 copepidid and adult animals l^{-1}) and *Bosmina longirostris* (0.14 animals l^{-1}). Crustacean zooplankton were most abundant in October (59.79 animals l^{-1}, excluding copepod nauplii) and least abundant in August (3.82 animals l^{-1}, excluding nauplii). *Diaptomus siciloides* and *Daphnia parvula* were the dominant crustaceans in Lake Oglethorpe and showed peak abundances in October at which time they accounted for approximately 84% of the total crustacean zooplankton biomass. Both populations maintained relatively high and constant densities throughout the winter and showed a decline in numbers throughout the summer. *Diaptomus siciloides* was the most abundant crustacean during all months except December (1978 only), and May and September 1979, accounting for 37.7 to 72.2% of the total crustacean density. *Daphnia parvula* (54.9%)

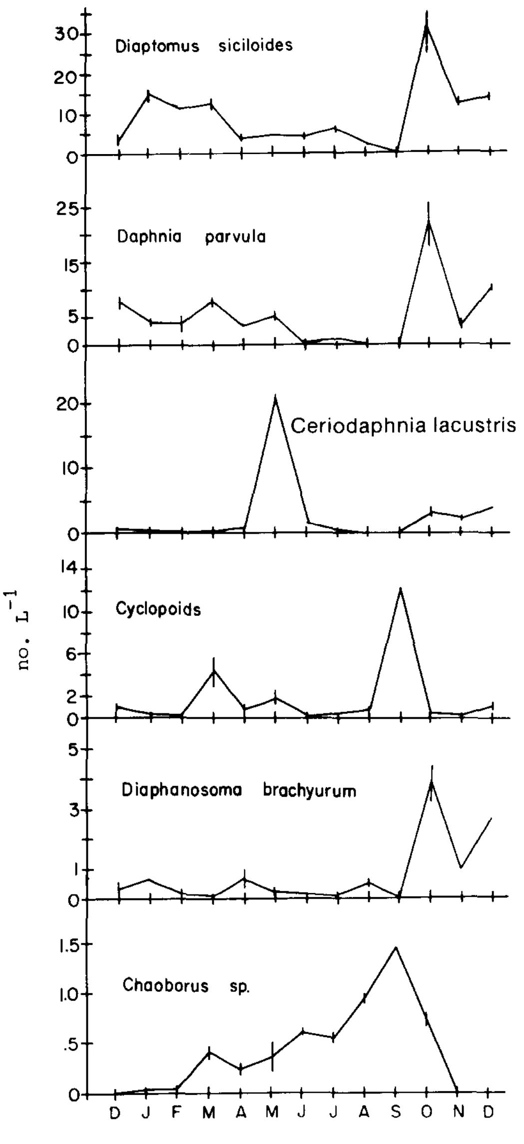

Fig. 2. Seasonal population dynamics of crustacean zooplankton; *Diaptomus siciloides, Daphnia parvula, Ceriodaphnia lacustris, Cyclopoid copepods, Diaphanosoma brachyurum*, and the midge larvae *Chaoborus* sp. over the annual cycle of 1979.

dominated in December, *Ceriodaphnia lacustris* (63.6%) in May, and cyclopoid copepods (96.2%) in September. *Diaphanosoma brachyurum* was also most abundant in October, but at a much lower density (3.83 animals l^{-1}) than *D. siciloides* and *D. parvula*. *Bosmina longirostris* was rare on all sampling dates and never accounted for more than 1.0% of the total crustacean density. Copepod nauplii densities, determined from whole water samples sieved through a 26-μm mesh filter, ranged from 22.00 animals l^{-1} in April to 186.7 animals l^{-1} in October (Table 2). Densities were relatively high from October through December (105.5–186.7 animals l^{-1}) and low (22.0–66.4 animals l^{-1}) all other months except February (138.2 individuals l^{-1}).

Chaoborus densities

The invertebrate predator, *Chaoborus* sp. was not found among the plankton during the winter (November through February; Fig. 2). It increased in number between February and September (maximum density = 1.48 animals l^{-1}) and showed declining populations in October.

Relative abundance and biomass of rotifer and crustacean zooplankton

Rotifer and crustacean zooplankton densities ranged from 217 to 7 980 animals l^{-1} and 3.82 to 59.79 animals l^{-1} (excluding copepod nauplii) respectively, over the thirteen month sampling period. Seasonal biomass estimates ranged from 2.87 to 60.55 μg dry wt l^{-1} for rotifers and from 5.36 to 151.55 μg dry wt l^{-1} for crustaceans (including copepod nauplii; Table 2). Rotifers always dominated numerically and maintained densities that were typically 10 to 100 times greater than those of the crustacean community. Rotifer densities were greater during the warmest months (June–September) ranging from about 2 000 to 8 000 animals l^{-1} and lower during the rest of the year (217 to 1 629 animals l^{-1}). Crustacean zooplankton showed the opposite trend and were less abundant from June to September (3.82 to 12.79 animals l^{-1}) and more abundant during cooler months of the year (10.85 to 59.79 animals l^{-1}). Crustacean zooplankton dominated in terms of biomass most of the year (October through May) at which time they accounted for 62 to 96% of the total rotifer–crustacean biomass. During June, July, and September rotifers accounted for a majority of the zooplankton biomass (65 to 85%) and in August the two groups were nearly equivalent in biomass. On an annual basis crustaceans dominated zooplankton standing stocks with a mean annual biomass of 46.99 μg dry wt l^{-1} as compared to rotifers which had a mean annual biomass of 19.26 μg dry wt l^{-1}.

Table 2. Monthly biomass estimates and densities of rotifers and crustaceans and the percent composition of each group relative to the rotifer-crustacean community biomass over the annual cycle of 1979.

	Rotifers $\mu g\ l^{-1}$	number l^{-1}	Crustaceans $\mu g\ l^{-1}$ (including nauplii)	no. l^{-1} (excluding nauplii)	Copepod nauplii number l^{-1}	% Biomass rotifers	% Biomass crustaceans
Dec.	2.87	255	38.32	13.22	171.00	0.07	0.93
Jan.	4.52	217	71.69	19.99	66.43	0.06	0.94
Feb.	13.17	1001	36.39	16.06	30.16	0.27	0.73
Mar.	31.39	1629	52.02	25.32	138.25	0.38	0.62
Apr.	17.83	942	24.79	10.85	49.75	0.42	0.58
May	3.61	837	89.66	32.57	22.00	0.04	0.96
June	29.82	2982	16.26	7.09	29.75	0.65	0.35
July	15.04	2031	16.19	8.49	32.25	0.48	0.52
Aug.	30.13	4611	5.36	3.82	24.00	0.85	0.15
Sept.	60.55	7980	16.27	12.79	37.75	0.79	0.21
Oct.	19.76	1359	151.55	59.79	186.75	0.12	0.88
Nov.	4.23	260	39.70	23.34	105.50	0.10	0.90
Dec.	17.42	722	84.91	32.32	123.00	0.17	0.83

Discussion

Planktonic rotifer communities have not been studied as thoroughly as crustacean zooplankton and few comparative studies of these two groups have been conducted. Thus, there is some controversy as to the relative importance of each of the two groups in limnetic systems. Nauwerck (1963) noted that rotifers always dominated crustacean zooplankton numerically in Lake Erken, although they seemed relatively unimportant in terms of biomass (Hutchinson, 1967). More recent work has emphasized the importance of planktonic rotifers in freshwater systems (Nauwerck, 1978; Makarewicz & Likens, 1979). Rotifers have been found to dominate crustacean zooplankton numerically by as much as 20:1 in north temperate Lake Ontario, suggesting they may occasionally attain biomass levels equivalent to that of crustaceans (Nauwerck, 1978). This was the case in Lake Oglethorpe where rotifers dominated numerically throughout the entire year (by as much as 110:1) and dominated in terms of biomass (>69%) during warm months (June through September).

A comparison of rotifer densities in Lake Oglethorpe (mean annual density = 1 900 rotifers l^{-1}; annual cycle range = 217–8 000 rotifers l^{-1}) with similar data from a variety of lakes located over a broad range of latitudes and trophic conditions (Table 3) indicates rotifer standing stocks in Lake Oglethorpe to be among the highest recorded in limnetic systems. For example, Stross *et al.* (1980)

Table 3. Summary of rotifer densities noted in a variety of lakes located over a broad range of latitudes and trophic conditions. Densities represent seasonal ranges or annual means.

Lake	Rotifer densities no. l^{-1}	Reference
Heimdalsvatn	50	Larsson, 1972*
Peipsi-Pihkva	2– 60	Habermann, 1974*
Vortsjarv	8– 114	Habermann, 1974*
Gossenkollesee	14– 41	Eppacher, 1968*
V. Finstertalersee	13– 240	Pechlaner *et al.*, 1972*
Mikolajskie	430– 1800	Spodniewska *et al.*, 1973*
		Bottrell *et al.*, 1976*
Neusiedlersee	11– 784	Zakovsek, 1961*
		Ruttner, pers. commun.*
		Herzig, 1979*
Attersee	2– 9	Muller, 1976*
Titisee	3– 88	Szymanski-Bucarey, 1974*
Piburger See	73– 297	Schaber, 1974, 1976*
Balaton	140	Zankai-Ponyi, 1972*
Lake Suwa	37– 156	Kurasawa *et al.*, 1952*
Lake George	302– 804	Burgis, 1969*
Lake Werowrap	200– 2100	Walker, 1973*
Valencia	132	de Infante, 1978
Vasikkalampi	40– 17700	Eloranta, 1982
Medical Wa.	0– 1051	Mires *et al.*, 1981
Florida ponds	25– 300	Fry & Osborne, 1980
Thonotosassa Fla.	5– 1000	Wyngaard *et al.*, 1982
Grasmere	4	Elliott, 1977
Subartic tundra ponds	rare	Stross, 1980
Lanao	32	Lewis, 1979
Ontario	10– 240	Nauwerck, 1978
Huron (mesotrophic area)	63– 400	Stemberger, 1979
Huron (eutrophic area)	583– 1317	Stemberger, 1979
Oglethorpe	217– 7980	Orcutt & Pace, this study

* From Herzig, 1979; Table 22.5.

found rotifers to be rare in subarctic tundra lakes and ponds, and Lewis (1979) noted a mean annual density of <32 rotifers l^{-1} in Lake Lanao, a tropical monomictic lake. Rotifers were also substantially more abundant in Lake Oglethorpe than in fourteen lakes considered by Herzig (1979; see Table 3 of this paper) which included northern European and mountainous lakes (60–240 rotifers l^{-1}), eutrophic European lakes (400–1 800 rotifers l^{-1}) and tropical lakes (100–1 500 rotifers l^{-1}). Our non-exhaustive survey of 25 lakes revealed only one lake, Vasikkalampi pond, Finland to show densities (40–17 700 rotifers l^{-1}) higher than those noted in Lake Oglethorpe.

The eutrophic condition of Lake Oglethorpe may in part explain its high rotifer densities. Eutrophic systems generally have higher rotifer densities than lakes of lesser trophic conditions (Stemberger, 1979; Herzig, 1979; Makarewicz & Likens, 1979; Mires *et al.*, 1981). However, rotifer densities in Lake Oglethorpe were higher than what has been noted in a number of other eutrophic lakes.

The higher densities found in this study are also due to the sampling methods used. Rotifers have most commonly been sampled with a 64–76-μm mesh net. The inadequacy of this relatively large mesh size for collecting small size rotifers has been documented (Likens & Gilbert, 1970; Ejsmont-Karabin, 1978). Unfortunately, the use of finer mesh netting often results in reduced sampling efficiency brought about by net clogging (Tranter & Heron, 1967; Smith *et al.*, 1968; Likens & Gilbert, 1970) a particularly difficult problem in eutrophic lakes. Sieving whole water samples through a relatively small mesh funnel (35–48-μm mesh, Likens & Gilbert, 1970; 10–20-μm mesh, Ejsmont-Karabin, 1978) is an improved technique for sampling rotifers since it (1) captures small rotifers typically missed by standard mesh size nets (64–76-μm), and (2) avoids the problem of reduced capture efficiency due to net clogging. In this study rotifers were quantified from both samples sieved through a 26-μm mesh funnel after collection, and counts of whole water samples in settling chambers. An evaluation of the efficiency at which a 26-μm mesh sieve captured four different species of rotifers indicated a decrease in capture efficiency for rotifers of decreasing size (see Table 1) and substantial losses of small sized rotifers (40% for *Anuraeopsis fissa* and 67% for *Trichocerca rousseliti*). Ejsmont-Karabin (1978) noted a similar trend. Rotifer losses of 27, 32, 43 and 54% were found when whole water samples were filtered through a 10, 20, 30 and 60-μm mesh sieve, respectively.

Contrary to these results, Likens & Gilbert (1970) found no statistical differences in rotifer densities quantified from whole water samples or samples sieved through a 35 or 48-μm mesh funnel, suggesting rotifers are accurately quantified when sieved through any mesh less than 48-μm in size. However, they compared densities of only two relatively large species, *Polyarthra vulgaris* and *Keratella cochearis* both of which were found to be efficiently retained (92 and 100% capture efficiencies) by a 26-μm mesh sieve in this study.

It appears that the quantification of rotifers from whole water samples as well as sieved samples in this study insured an accurate quantification of rotifer density. In part this may explain the relatively high rotifer densities we noted in Lake Oglethorpe. We suggest that, to insure an accurate quantitative assessment of small rotifers and an entire rotifer assemblage that typical sampling methods (see Likens & Gilbert, 1970; Ejsmont-Karabin, 1978) should be accompanied by whole water sample counts.

Rotifers in Lake Oglethorpe accounted for a substantial portion of the rotifer-crustacean community relative to other lakes. On average they constituted 95% of the total density and 39% of the total biomass. Although this comparison has seldom been made, data from Lake Lanao (Lewis, 1979) indicate that rotifers accounted for only 39% and <2% of the density and biomass of the rotifer-crustacean assemblage in that lake. In the north temperate lake, Mirror Lake, rotifers were found to account for 12.8 to 18.6% of the zooplankton biomass (Makarewicz & Likens, 1979). Schindler (1970) noted that rotifers accounted for 67% of the herbivorous zooplankton in a Canadian Shield lake. Mires *et al.* (1981) compared densities of crustaceans and rotifers in Medical Lake, Washington and found rotifers to account for 89.9 and 43.5% of zooplankton densities when the lake was eutrophic (1977) and mesotrophic (1980), respectively.

Although rotifers generally do not dominate zooplankton communities in terms of mean annual biomass, they may maintain higher production rates than crustacean zooplankton due to their shorter generation times and higher intrinsic rates of increase (Allan, 1976). In Mirror Lake, NH, rotifers account for approximately 40% of the annual secondary production but only 15% of the mean annual biomass (Makarewicz & Likens, 1979). Correspondingly, the greater abundance of rotifers in Lake Oglethorpe relative to crustaceans suggests that rotifers may dominate in terms of annual secondary production, energy flow and nutrient recycling in that lake, and certainly do so during warm months when rotifers dominate.

We interpret patterns of seasonal succession cautiously because of the infrequency in which sampling was done. However, there were several general relationships that were evident. There was a strong similarity in the rotifer assemblages found during mictic and stratified conditions in Lake Oglethorpe with those characterized as either cold or warm water forms, respectively, in temperate dimictic lakes (Hutchinson, 1967; Nauwerck, 1978). Similar to dimictic lakes, crustacean zooplankton in Lake Oglethorpe showed typical fall and spring population blooms although the fall rather than spring bloom sustained the higher densities. Crustaceans also maintained relatively high population densities throughout winter and extremely low densities during the summer, contrary to the case in dimictic lakes.

The inverse relationship between peak seasonal abundances of rotifer (June–September) and crustacean (October–May) zooplankton in Lake Oglethorpe might be explained by a number of mechanisms. Threlkeld (1979) presented several hypotheses to explain the midsummer decline of *Daphnia* populations in Wintergreen Lake, Michigan. These included, increased water temperature, changing of food conditions and increased activity by invertebrate and vertebrate predators. Continually declining densities of all crustacean zooplankton in Lake Oglethorpe and corresponding high rotifer densities throughout summer months may be explained by a similar set of parameters. Lake Oglethorpe goes through a seasonal shift in its phytoplankton community and bacterial densities such that summer conditions are typified by high densities of large filamentous blue-green algae (Porter, unpubl. data) and high bacterial densities (Porter & Feig, 1980), whereas smaller algae (greens, diatoms and cryptomonads) dominate during mixis when bacterial densities are considerably lower. This shift in food resources may partially explain the seasonal shift to smaller sized zooplankton during summer months (Gliwicz, 1977). Large filamentous algae typical of summer months are known to inhibit feeding by large crustacean zooplankton (Webster & Peters, 1978), whereas smaller zooplankton such as rotifers which generally feed on particles <20 μm in size (Allan, 1976) are uninhibited feeding between filaments (Webster & Peters, 1978), and probably benefit from seasonally high bacterial densities in summer.

This seasonal shift in the Lake Oglethorpe zooplankton community may also reflect increased selective predation on crustacean zooplankton during warm months. There is a distinct inverse relationship between summer crustacean densities and increasing densities of the invertebrate predator *Chaoborus*. In addition, the presence of various species of planktivorous fish in the lake also suggests strong selective predation on crustacean zooplankton (O'Brien, 1979) during warm months when these visual predators are probably most active.

In summary, results of this study indicate that rotifers are a significant component of the planktonic community in Lake Oglethorpe. Their importance changes seasonally and has probably often been under-estimated in other studies due to deficiencies in sampling techniques.

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