Seasonal patterns of bacterivory by flagellates, ciliates, rotifers, and cladocerans in a freshwater planktonic community

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Abstract

Bacterivory in eutrophic Lake Oglethorpe, Georgia, was determined by direct observation of tracer particle uptake by all members of the planktonic community. Heterotrophic flagellates dominated grazing at all times, accounting for 49–81% of grazing on an areal basis and up to 98% of grazing at some depths. Pigmented (mixotrophic) flagellates were major grazers during winter and spring blooms, when they contributed up to 45% of community grazing on an areal basis and 79% at depths of maximum abundance. In late spring to early summer, rotifers and ciliates were responsible for as much as 25 and 30% of bacterivory at some depths, but averaged 3 and 11% over the year, respectively. Grazing impact of cladoceran crustaceans was generally < 1% of the total. Bacterivory by copepods was not detected. Total bacterial mortality due to grazing ranged from 11 to 162% of bacterial cell production estimated from the incorporation of [3H]thymidine.

Use of 0.57-µm microspheres as tracers gave similar estimates of ingestion to fluorescently labeled bacteria in this system. The use of 4% ice-cold glutaraldehyde mixed 1:1 with the water sample was found to be equally effective to an acrolein-tannic acid mixture for reducing egestion of particles by protists. We therefore consider our findings to be representative of bacterivory by the planktonic community in this eutrophic system.

The microbial loop is now recognized as a dynamic component of pelagic marine food webs (Pomeroy 1974; Azam et al. 1983; E. Sherr et al. 1986). In it, heterotrophic and autotrophic picoplankton and their protistan grazers recycle particulate and soluble nutrients released by the classical pelagic food chain of algae, crustacean zooplankton, and fish. In lakes, 50–100% of phytoplankton carbon production may pass through bacterioplankton (Simon 1987) and bacteria may constitute > 50% of the combined pico- and nanoplankton biomass (Carron et al. 1985). These figures suggest that the microbial loop is also active in freshwaters.

Grazing is believed to balance bacterioplankton production in both marine and freshwaters (e.g. Wright and Coffin 1984; Riemann 1985; Güde 1986; Sanders and Porter 1986; Scavia and Laird 1987). Heterotrophic flagellates tend to be the major bacterivores in marine systems (Fenchel 1982) and, by analogy, are assumed to be responsible for control of bacterial numbers in freshwaters (Riemann 1985; Scavia and Laird 1987; Güde 1986; Nagata 1988). In freshwaters, however, rotifers, cladocerans, and photosynthetic flagellates may also be significant consumers of bacteria (Starkweather 1980; Pace et al. 1983; Riemann 1985; Bird and Kalff 1986; Sanders and Porter 1988). When grazing and production do not balance, factors such as sedimentation, cell death, antibiotics, predatory bacteria, and viruses are proposed to be important sources of bacterial mortality (Pace 1988).

Due to the limited number of studies to date, the question remains whether bacterial production ultimately serves as a link or sink for higher trophic levels; that is, whether a significant proportion of bacterial carbon production is consumed in the mi-
In this study, we determine the relative grazing impact of protistan and metazoan members of the bacterivorous planktonic community in a eutrophic lake and compare grazing to bacterial production. We chose direct observation and enumeration of the uptake of bacteria-sized (0.57-μm) carboxylated polystyrene microspheres by individual members of the plankton as the method for in situ rate determinations because it allowed us to easily observe bacterivory at the individual and species level. We considered the isolation and identification of individual grazers a necessary improvement over grazer exclusion or label uptake methods that use size fractionation if pathways in the freshwater microbial loop were to be definitively traced. Fluorescent microspheres were chosen because they are highly visible inside consumers, do not decompose or fade, and are nonhazardous. Use of inert tracer particles and the egestion of tracer particles upon fixation may, however, introduce errors in tracer studies (Pace and Bailiff 1987; Sieracki et al. 1987; Nygaard et al. 1988). We, therefore, compare microspheres to fluorescently labeled freshwater bacteria (Sherr et al. 1987) as representative tracers of bacterivory in our system. Our routine method of fixation is the addition of sample to an equal volume of ice-cold 4% glutaraldehyde with storage on ice, a standard procedure for electron microscopy. This fixation method is compared with one using a more toxic mixture of acrolein, tannic acid, and glutaraldehyde suggested by Sieracki et al. (1987).

Methods

Field experiments—Lake Oglethorpe is a shallow (z_{max} ≈ 8 m) monomictic lake typical of small manmade lakes in the southeastern United States. Stratification and an anoxic hypolimnion develop in April and persist into October. The lake was drawn down 1 m during this study (March through July 1986) to control shore macrophytes. In situ grazing experiments were performed during winter mixis (19 February), onset of stratification (15 April), stratification (21 May and 25 June), and the beginning of autumn destratification (17 September) in 1986. For each depth, two whole-water samples were taken with an 8-liter Niskin bottle and combined. The length of the bottle (1 m) ensured that the entire water column was sampled to < 1 m from the bottom. In the initial experiment (February), 1-liter samples from each depth were poured into combusted, screw-top Erlenmeyer flasks, incubated with tracer particles, and subsampled for each grazer group. On subsequent experimental dates, to compensate for the two-orders-of-magnitude difference found between crustacean and protozoan abundances, we used five 1-liter replicate flasks to measure crustacean grazing and one 250-ml flask to determine protozoan and rotifer grazing at each depth.

Tracer amounts of 0.57-μm-diameter carboxylated fluorescent microspheres (Fluoresbrite, Polysciences, Inc.) were added to each flask to give a final concentration of ~5 × 10^5 ml⁻¹. Microspheres were sonicated immediately before addition. Microscopic observations showed that the microspheres remained dispersed as singlets throughout the short incubation period without coating them in bovine serum albumin as is required for seawater samples (Pace and Bailiff 1987).

Flasks from each depth were incubated for 15 min in the dark in styrofoam coolers containing water from that depth. This incubation period was chosen after a time series of up to 1 h showed that linear uptake of particles by all members of the grazing community was occurring at 15 min. Longer incubations reduced counting accuracy for some ciliates and rotifers due to high densities of ingested spheres. Furthermore, cladoceran gut passage times were exceeded by longer incubation times, resulting in underestimation of their ingestion rates due to defecation of the tracer particles. Finally, short incubations reduced the possibility that nonbacterivorous crustaceans and ciliates ate bacterivorous protozoans that had previously ingested beads.

Protozoan feeding was stopped by adding the total contents of the flasks to equal volumes of 4%, ice-cold, buffered glutaraldehyde. Crustacean grazing was ended by adding an ice-cold alcohol-Formalin mixture.
Lake community bacterivory

Distortion of crustacean body shape was reduced and evacuation of guts was not observed with this procedure. Samples were transported on ice and refrigerated before enumeration.

Enumeration techniques—An initial subsample taken from each flask was fixed immediately upon addition of microspheres to determine tracer and bacteria densities and to account for any background particles adhering to the exterior of cells. Background attachment was negligible for all species except Conochilus sp. This colonial rotifer was observed only in the April experiment at low densities. There was little difficulty in distinguishing ingested microspheres from those on the surface of cells or stuck to the gelatinous matrices of some species. This capability is one advantage over grazing experiments with radioactively labeled bacteria, where direct observation of individual plankters is not routine.

Differences in grazer size, abundance, and clearance rates required that ingested particles be enumerated differently for the various bacterivores. Microspheres ingested by ciliates, rotifers, and colonial flagellates were counted with epifluorescent and transmitted light on a Zeiss IM 35 inverted microscope. Subsamples of 50–100 ml were settled in 100-ml graduated cylinders. After 24 h, water was aspirated from the sample until 5 ml remained. About 2 h before enumeration, the residue was resuspended, rinsed into 10-ml settling chambers, and the fluorescent stain primulin (250 µg ml⁻¹ final concn) added. Generally, the entire bottom of the settling chamber was scanned at a magnification of 360× and all species were examined for particle ingestion at 360 or 800× depending on the number of ingested particles. Average ingestion and clearance rates were determined from 10–200 individuals of each species containing microspheres.

Nanoflagellates were examined on Nuclepore filters with epifluorescent microscopy after staining by a modification of Carron's (1983) primulin technique (Sanders and Porter 1986). Photosynthetic flagellates were distinguished from heterotrophs by their autofluorescence. Samples were stored on ice during transportation and staining; slides were made within 24 h of fixation and stored frozen until enumerated. This prevented loss of chlorophyll fluorescence, which was preserved for at least several months. For each depth, five transects were examined for each of three replicate slides at 1,000×. At any depth, grazing rates calculated for flagellates, ciliates, and rotifers generally had a standard error of <10% of the mean.

Preserved crustaceans were captured on 63-µm Nitex mesh, rinsed to remove microspheres stuck to carapaces, and observed with epifluorescent microscopy to determine which species ingested spheres. Only cladocerans ingested 0.57-µm microspheres. They were pooled for each replicate and sonicated to disrupt their guts and disperse the microspheres, which were counted either on filters or with flow cytometry (Gerritsen et al. 1987).

Tracer particles and fixatives—Since retention of particles ingested by protozoans may be affected by fixation, a comparison of particle retention was made between subsamples fixed by the ice-cold glutaraldehyde (2% final concn) technique used in our grazing experiments and with a mixture of acrolein, tannic acid, and glutaraldehyde (Sieracki et al. 1987). Subsurface lake water was incubated with 0.57-µm microspheres for 15 min on 25 February 1987, and subsamples were fixed concurrently with each preservative. Ingestion of microspheres was determined as previously described, and numbers of particles retained were compared by t-tests.

To test for possible biases in the measurement of ingestion rates due to selection against inert tracer particles, we compared clearance rates of 0.57-µm microspheres to fluorescently labeled, heat-killed bacteria (FW-1 clone, Sherr et al. 1987). The killed, fluorescent bacteria were rod-shaped and ~0.4 × 0.8–1.0 µm. Six replicate 200-ml samples of water from Lake Oglethorpe were incubated on 6 November 1986 with either 0.57-µm microspheres or fluorescent bacteria at final concentrations of 8.5 × 10⁵ ml⁻¹. Subsamples were fixed with cold glutaraldehyde immediately after addition of tracers and at 5, 10, 20, and 30 min after addition. Four flagellates and three ciliates
Table 1. Clearance rates (nl ind.\(^{-1}\) h\(^{-1}\)) of flagellates and ciliates determined from ingested microspheres after fixation in a mixture of acrolein, tannic acid, and gluteraldehyde or in ice-cold 2% gluteraldehyde. Temperature during the experiment—9°C; \(P\)—not significant, all cases.

<table>
<thead>
<tr>
<th>Morph type/species*</th>
<th>Acrolein mix</th>
<th>Glutaraldehyde</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Clearance n</td>
<td>Clearance n  t</td>
</tr>
<tr>
<td>Flagellates</td>
<td></td>
<td></td>
</tr>
<tr>
<td>HF No. 1 (4 × 4 (\mu)m)</td>
<td>0.031</td>
<td>0.034</td>
</tr>
<tr>
<td>HF No. 3 (2 × 2 (\mu)m)</td>
<td>0.033</td>
<td>0.032</td>
</tr>
<tr>
<td>HF No. 7 (2 × 4 (\mu)m)</td>
<td>0.296</td>
<td>0.299</td>
</tr>
<tr>
<td>Loricate HF (6 × 6 (\mu)m)</td>
<td>8.24</td>
<td>7.89</td>
</tr>
<tr>
<td>Colonial HF (4 × 5 (\mu)m)</td>
<td>4.74</td>
<td>5.57</td>
</tr>
<tr>
<td>MF No. 11 (4 × 7 (\mu)m)</td>
<td>0.022</td>
<td>0.015</td>
</tr>
<tr>
<td>Ciliates</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Halteria grandinella (25 (\mu)m)</td>
<td>82.9</td>
<td>77.8</td>
</tr>
<tr>
<td>Strobilidium sp. (15 × 21 (\mu)m)</td>
<td>89.7</td>
<td>80.3</td>
</tr>
</tbody>
</table>

* Average individual cell sizes in parentheses. HF—heterotrophic flagellate; MF—mixotrophic flagellate.

were abundant enough for statistical comparisons of uptake of the two particle types. Ingestion was determined by epifluorescent microscopy as previously described.

Production measurements—Bacterial production was determined for subsamples from each depth in May, June, and September with the method described by McDonough et al. (1986). Incorporation of [methyl-\(^{3}\)H]thymidine (50–90 Ci mmol\(^{-1}\); Amersham Corp.) into DNA was converted to bacterial cell production using a factor of 2 × 10\(^{11}\) cells mol\(^{-1}\) of thymidine incorporated (Fuhrman and Azam 1982).

Results

Fixative and tracer particle comparisons—Sieracki et al. (1987) found that some protists egested particles upon fixation with 1% glutaraldehyde, but not when a mixture of acrolein, tannic acid, and glutaraldehyde was used. We preferred to avoid the use of acrolein due to its extremely toxic and flammable nature—it has been used in military poison gas mixtures (Merck Index 1983). Sieracki et al. (1987) also showed that egestion decreased when samples were preserved with 1% glutaraldehyde vs. 0.25%. Since the acrolein mixture contained 2% glutaraldehyde, we suspected that the reduced egestion was due to increased glutaraldehyde concentration rather than the acrolein. We found no significant difference in particle retention by flagellates and ciliates fixed with the acrolein mixture and with the ice-cold 4%, buffered glutaraldehyde (2% final concn), which was routinely used in our experiments (Table 1). Furthermore, formation of a precipitate in the acrolein mixture made the smaller ciliates and flagellates difficult to enumerate. Although the same volume of water was processed for both treatments, the counts of individuals in the acrolein fixative were usually lower than in 2% cold glutaraldehyde (Table 1). Thus, an underestimate of abundance for many protozoans would result from standard use of the acrolein mixture. We therefore recommend the cold glutaraldehyde method of fixation used in our studies.

When clearance rates on 0.57-\(\mu\)m fluorescent microspheres were compared to those on fluorescein isothiocyanate labeled bacteria, there was no significant difference for three flagellate species or the ciliate *Vorticella microstoma* (Table 2). One colonial heterotrophic flagellate had a higher clearance rate on fluorescently labeled bacteria than on microspheres, while two oligotrichous ciliates ingested microspheres at significantly higher rates (Table 2). Therefore, no general pattern of selection was found for either tracer particle in this system. When total grazing impact was calculated, the two particles gave nearly identical community rates.

Bacterivore grazing rates and community composition—The major taxa of heterotrophic and mixotrophic flagellates, ciliates,
Table 2. Comparison of clearance rates (nl h\(^{-1}\)) for flagellates and ciliates when offered either 0.57-µm microspheres or fluorescently labeled bacteria at the same initial concentration (~9 \times 10^5 ml^{-1}). Temperature = 17°C. Community ingestion rate estimates were 6.86 \times 10^5 bacteria ml^{-1} d^{-1} for microspheres and 6.64 \times 10^5 for fluorescently labeled bacteria.

<table>
<thead>
<tr>
<th>Species</th>
<th>Microspheres</th>
<th>Fluorescent bacteria</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Clearance (n)</td>
<td>Clearance (n)</td>
</tr>
<tr>
<td>Flagellates</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Monas sp. 1</td>
<td>0.8</td>
<td>0.5</td>
</tr>
<tr>
<td>Monas sp. 2</td>
<td>0.6</td>
<td>0.7</td>
</tr>
<tr>
<td>Colonial heterotroph</td>
<td>3.9</td>
<td>6.4</td>
</tr>
<tr>
<td>Ochromonas sp.†</td>
<td>0.1</td>
<td>0.2</td>
</tr>
<tr>
<td>Ciliates</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Haltaria grandinella</td>
<td>126</td>
<td>72</td>
</tr>
<tr>
<td>Strombidium sp.</td>
<td>30</td>
<td>6</td>
</tr>
<tr>
<td>Vorticella microstoma</td>
<td>138</td>
<td>156</td>
</tr>
</tbody>
</table>

* \(t\)-tests performed on square-root-transformed data. † Mixotroph.

Heterotrophic flagellates showed shifts in species composition both seasonally and with depth. Although identification was limited to morphotypes based on cell size, shape, and flagellar characteristics, Monas species were generally the most abundant group (Bennett et al. in prep.). They ranged in size from 2 to 6 µm and had clearance rates ranging from 0.2 to 2.3 nl h\(^{-1}\). Chazanoflagellates (6-8 µm) had relatively high clearance rates but were present only in May and June (Table 3), reaching maximal abundance of 330 ml\(^{-1}\). Typically 80-95% of the nonpigmented flagellates had ingested microspheres during the feeding experiments. Bodo spp. were not common and rarely ingested spheres. They may be specialized as surface feeders, as Caron (1987) found for a marine bodonid. Total heterotrophic flagellate abundances during May and June ranged from 2 \times 10^3 to 4 \times 10^3 ml\(^{-1}\).

In February and April there were blooms of phagotrophic phytoflagellates, primarily the chrysophytes Dinobryon cylindricum, Dinobryon bavaricum, Ochromonas sp., and Chrysostephanosphaera globulifera. From May to September, Dinobryon, Ochromonas, and Chrysostephanosphaera were rare to absent, and the small, unidentified mixotrophs that succeeded them were neither as abundant nor as voracious (Bennett et al. in prep.). Per-cell grazing rates of the mixotrophs were in the same range as those of heterotrophic flagellates (Table 3).

Seasonal differences in ciliate abundances were similar to those found in previous years (Pace 1982). Common bacteriovorous ciliates included Halteria grandinella, Strombidium sp., Uronema spp., Cyclidium sp., Vorticella spp., Epistylis rotans, and Stokesia sp. (Table 3). On most dates, members of these species constituted 50-90% of the total ciliate population. However, in September when ciliates were most abundant (>2 \times 10^4 liter\(^{-1}\)), nonbacterivorous species accounted for 54-86% of the ciliate numbers, varying in dominance with depth. The herbivorous species observed are also listed in Table 3.

Bacterivorous rotifers, which included Gastropus sp., Hexarthra sp., Filinia longiseta, and Anuraeopsis fissa (Table 3), were abundant only in June and September. Kellicottia bostoniensis and Keratella spp. were present on all dates. Except for the June and September samples however, both the absolute number of ingested microspheres and the proportion of Kellicottia and Keratella...
Table 3. Major taxa found in the plankton of Lake Oglethorpe and the range of grazing rates from all depths in February, April, May, June, and September 1986. At any depth the grazing rate of a species generally had a standard error < 10% of the mean. Species grazing rates of cladocerans were not calculated because all species and sizes were lumped for enumeration of ingested spheres.

<table>
<thead>
<tr>
<th>Species</th>
<th>Bacterivorous</th>
<th>Months observed</th>
<th>Ingestion (bacteria ind. (^{-1}) h(^{-1}))</th>
<th>Clearance (ml ind. (^{-1}) h(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Flagellates</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Monas spp.</td>
<td>yes</td>
<td>All</td>
<td>3-23</td>
<td>0.4-3.0</td>
</tr>
<tr>
<td>Choanoflagellate</td>
<td>yes</td>
<td>M, J, S</td>
<td>8-42</td>
<td>0.9-5.5</td>
</tr>
<tr>
<td>Other heterotrophs</td>
<td>yes</td>
<td>All</td>
<td>5-36</td>
<td>0.6-3.8</td>
</tr>
<tr>
<td>Dinobryon bavaricum</td>
<td>yes*</td>
<td>F, A, J, S</td>
<td>8-38</td>
<td>2.8-15.2</td>
</tr>
<tr>
<td>Dinobryon cylindricum</td>
<td>yes*</td>
<td>All</td>
<td>6-12</td>
<td>1.9-6.2</td>
</tr>
<tr>
<td>Ochromonas sp.</td>
<td>yes*</td>
<td>All</td>
<td>2-53</td>
<td>0.2-6.1</td>
</tr>
<tr>
<td>Chrysostephanosphaera globulifera</td>
<td>yes</td>
<td>F, A</td>
<td>27-181†</td>
<td>2.3-44.4</td>
</tr>
<tr>
<td><strong>Ciliates</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Haleria grandinella</td>
<td>yes</td>
<td>All</td>
<td>67-1,276</td>
<td>17.0-222.0</td>
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<tr>
<td>Strombidium sp.</td>
<td>yes</td>
<td>All</td>
<td>34-331</td>
<td>8.8-42.8</td>
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<tr>
<td>Scuticociliate species</td>
<td>yes</td>
<td>A, M, I, S</td>
<td>90-500</td>
<td>15.4-73.8</td>
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<tr>
<td>Epistyliis plicatilis</td>
<td>yes</td>
<td>A, M</td>
<td>78-1,200</td>
<td>15.4-147.0</td>
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<tr>
<td>Vorticella microstoma</td>
<td>yes</td>
<td>All</td>
<td>60-235</td>
<td>15.2-27.1</td>
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<tr>
<td>Vorticella natans</td>
<td>yes</td>
<td>All</td>
<td>171-1,078</td>
<td>42.0-187.0</td>
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<td>Stokesia sp.</td>
<td>yes</td>
<td>J, S</td>
<td>161-598</td>
<td>17.3-87.3</td>
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<tr>
<td>Strombidium viride</td>
<td>no</td>
<td>All</td>
<td></td>
<td></td>
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<tr>
<td>Mesodinium spp.</td>
<td>no</td>
<td>All</td>
<td></td>
<td></td>
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<tr>
<td>Tintinnopsis lacustris</td>
<td>no</td>
<td>F, A</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tintinnidium florivile</td>
<td>no</td>
<td>F, A</td>
<td></td>
<td></td>
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<td>Paradileptus sp.</td>
<td>no</td>
<td>J, S</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lembudium magnum</td>
<td>no</td>
<td>J, S</td>
<td></td>
<td></td>
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<tr>
<td>Litonotus (Lionotus) spp.</td>
<td>no</td>
<td>J, S</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Condylostoma sp.?</td>
<td>no</td>
<td>J</td>
<td></td>
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<tr>
<td>Coleps sp.</td>
<td>no</td>
<td>M</td>
<td></td>
<td></td>
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<td>Didinium sp.</td>
<td>no</td>
<td>J, S</td>
<td></td>
<td></td>
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<tr>
<td>Unidentified oligotrichs</td>
<td>yes</td>
<td>F, M, J, S</td>
<td>190-629</td>
<td>2.2-55.0</td>
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<tr>
<td><strong>Rotifers</strong></td>
<td></td>
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<tr>
<td>Filinia longiseta</td>
<td>yes</td>
<td>F, A, J, S</td>
<td>537-2,130</td>
<td>66.0-297.3</td>
</tr>
<tr>
<td>Hexarthra sp.</td>
<td>yes</td>
<td>J, S</td>
<td>600-1,686</td>
<td>96.0-293.1</td>
</tr>
<tr>
<td>Gastropus sp.</td>
<td>yes</td>
<td>J, S</td>
<td>625-3,200</td>
<td>84.0-581.0</td>
</tr>
<tr>
<td>Anuraeopsis fissa</td>
<td>yes</td>
<td>J</td>
<td>55-183</td>
<td>10.9-28.8</td>
</tr>
<tr>
<td>Conochilus sp.</td>
<td>yes</td>
<td>A</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kellicottia bostoniensis</td>
<td>yes</td>
<td>F, A, M, J</td>
<td>22-327</td>
<td>3.8-51.4</td>
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<tr>
<td>Keratella spp.</td>
<td>yes</td>
<td>All</td>
<td>57-618</td>
<td>6.4-97.3</td>
</tr>
<tr>
<td>Polyarthra sp.</td>
<td>no</td>
<td>All</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trichocerca spp.</td>
<td>no</td>
<td>All</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Crustaceans</strong></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bosmina longirostris</td>
<td>yes</td>
<td>F</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ceriodaphnia lacustris</td>
<td>yes</td>
<td>A, M, J, S</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Daphnia parva</td>
<td>yes</td>
<td>All</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diaphanosoma brachyurum</td>
<td>yes</td>
<td>M, J, S</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Holopedium amazonicum</td>
<td>yes</td>
<td>J</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diaptomus mississippiensis</td>
<td>no</td>
<td>All</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tropocyclops prasinus mexicanus</td>
<td>no</td>
<td>A, M, J, S</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mesocyclops edax</td>
<td>no</td>
<td>F</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Copepod nauplii</td>
<td>no</td>
<td>All</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Mixotrophic.
† Rate for colony.

populations with ingested spheres were usually low. Polyarthra and Trichocerca spp. did not ingest microspheres.

All of the cladoceran species in the lake during this study ingested 0.57-μm microspheres. Rates for the individual species were not calculated, since all cladocerans from each replicate were pooled and sonicated.
Lake community bacterivory

Fig. 1. Relative grazing impact of planktonic bacterivores on bacteria-sized particles in Lake Oglethorpe during 1986. Mixotrophic and heterotrophic flagellates dominated grazing at all times (55-99%). Ciliates were responsible for as much as 30% of the bacterivory at some depths in spring and summer, while bacterivorous rotifers were abundant only in summer. Grazing impact of cladoceran crustaceans was generally <1%, with a maximum of 15% at the midday holding depth in February. Bacterivory by adult and naupliar copepods was not detected. Total grazing mortality ranged from 11 to 159% of bacterial cell production. The depth reported is at the top of the sampling bottle, which is 1 m long. Thus, the samples designated as 0 m are integrated from 0-1 m.

together for microsphere counts. The most abundant cladocerans were Daphnia parvula and Ceriodaphnia lacustris. Daphnia parvula had a maximum abundance of 33 liter\(^{-1}\) in May, while C. lacustris reached densities of up to 76 liter\(^{-1}\) in April. Bosmina longirostris was captured only in February and Holopedium amazonicum, which had not been observed in Lake Oglethorpe previously, was present in low numbers (<1 liter\(^{-1}\)) in June (Table 3). Diaphanosoma brachyurum was rare except at 4 m in June (16 liter\(^{-1}\)). The copepods Diaptomus mississippiensis, Tropocyclops prasinus mexicanus, and Mesocyclops edax and their nauplii were never seen to ingest microspheres.

Relative grazing impact—Flagellates accounted for 55-99% of the bacterivory by depth at all times (Fig. 1). Heterotrophic flagellates were the major grazers throughout the year, accounting for 15-96% of the total grazing impact by depth. In February and April, blooms of mixotrophic flagellates occurred and were responsible for up to 79% of the total bacterivory at 5 m in April (Fig. 1). Since mixotrophs had clearance rates similar to heterotrophic microflagellates (Sanders and Porter 1988), differences in grazing impact between heterotrophs and mixotrophs were due primarily to their relative abundances at the different depths. Mixotrophs were less abundant in June but increased in importance as bacterivores by September. Ciliate grazing was most intense in summer and was, in general, evenly distributed throughout the water column. Ciliates accounted for up 30% of the bacterivory in the epilimnion in June and averaged 11% throughout the year. Rotifers had a minor impact on bacteria, averaging 3% of the total ingestion, with a maximum of 25% in midwater in June (Fig. 1). Cladoceran grazing averaged <1% of total bacterivory, with maxima in February (15%) and June (8%) at midwater abundance peaks.

Heterotrophic flagellates dominated bacterivory at all times on an areal basis (Table 4). Grazing impact of the heterotrophic flagellate community ranged from 49 to 81% of integrated bacterivory and had a maximum in September. Mixotrophic flagellates accounted for between 2% (June) and 45% (February) of the total water-column grazing and had greatest impact in winter and spring (Table 4). Ciliates accounted for a minimum of 4% (February) and a maximum of 18% (June) of community bacterivory on an areal basis (Table 4). Ciliates ingested more than \(5 \times 10^6\) bacteria ml\(^{-1}\) d\(^{-1}\) averaged over depth in April, May, June, and September. Rotifer grazing was minor (0-2%) except for a contribution of 13% of community bacterivory in June. The cladocerans, primarily Daphnia and Ceriodaphnia, were responsible for <2% of water-column bacterivory at any time.
Table 4. Ingestion of bacteria (10^10 cells m^-2 d^-1) and percent impact for bacterivorous groups integrated for the whole water column. The higher total ingestion in February and September is due partially to changes in lake level (see text).

<table>
<thead>
<tr>
<th></th>
<th>February</th>
<th>April</th>
<th>May</th>
<th>June</th>
<th>September</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heterotrophic flagellates</td>
<td>168.49</td>
<td>118.64</td>
<td>161.71</td>
<td>154.66</td>
<td>374.81</td>
</tr>
<tr>
<td>Mixotrophic flagellates</td>
<td>155.45</td>
<td>47.25</td>
<td>33.15</td>
<td>4.2</td>
<td>40.9</td>
</tr>
<tr>
<td>Ciliates</td>
<td>12.4</td>
<td>18.10</td>
<td>31.14</td>
<td>42.18</td>
<td>36.8</td>
</tr>
<tr>
<td>Rotifers</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>30.13</td>
<td>9.2</td>
</tr>
<tr>
<td>Cladocerans</td>
<td>6.2</td>
<td>&lt;1.0</td>
<td>&lt;1.0</td>
<td>3.1</td>
<td>&lt;1.0</td>
</tr>
<tr>
<td>Total</td>
<td>341.178</td>
<td>183.233</td>
<td>225.233</td>
<td>233.459</td>
<td></td>
</tr>
</tbody>
</table>

The greatest number of bacteria ingested was 4.6 × 10^{12} bacteria m^-2 d^-1 in September when heterotrophic flagellates were most abundant (Table 4). On that date, nonpigmented flagellates alone ingested up to 20% of the standing stock and 77% of daily bacterial production at 2 m. Total bacterivory was nearly as great in February during the bloom of mixotrophic flagellates (Table 4). The lake level was dropped after the February sampling date, and the water-column depth from April through June was about 6 m. By September the lake was about 7 m deep again at the sampling station. Although this change in lake level increased the calculated total impact for February and September, grazing was lowest at the deepest depth (Table 5), so that the areal comparisons of grazing between dates are not greatly affected.

Bacterial production measured as incorporation of [3H]thymidine into DNA was determined for the field experiments during stratification in May, June, and September. Production ranged from 0.16 × 10^6 to 2.1 × 10^6 cells ml^-1 d^-1 (Table 5). Bacterial production and bacterivory tended to be lowest in the surface waters and greatest in, or just above, the metalimnion. This region of high bacterial abundance coincides with the thermocline and chemocline. From 11 to 162% of the estimated production was cropped by bacterivores daily. In May, >100% of production was predicted to be removed by grazing at all depths with measurable oxygen (Table 5). These high cropping rates may also have occurred in April. April grazing impacts ranged from 55 to 122% of production in April of the previous year. The ratio of grazing to production was lowest in June when water temperature and bacterial production were both high. On that date, abundances of bacterivorous flagellates and ciliates were the lowest recorded during the study. Consequently, rotifers and cladocerans had high relative grazing impacts at some depths (Fig. 1). Community grazing at depth removed up to 35% of the bacterial standing stock in February and 2–24% during spring, summer, and fall (Table 5). Standing stocks of bacteria were a half to a third as great on 19 February as on other dates.

Discussion

**Fluorescent microspheres as tracers**—After testing inhibitor and filtration methods in Lake Oglethorpe (Sanders and Porter 1986), we chose to use bacteria-sized fluorescent tracer particles in this seasonal field study of community bacterivory. The unique advantage of fluorescent particles is that they can be directly observed within individual plankters, thereby allowing the determination of relative and absolute grazing rates of bacterivorous groups. The method demonstrated that mixotrophic algae can have a major and previously unsuspected impact as bacterivores (Bird and Kalff 1986; Sanders and Porter 1988). In addition, community grazing can be calculated from species grazing rates coupled with their relative abundances.

This study and others (Table 2; Bird and Kalff 1986; Hoffman and Atlas 1987; Pace and Bailiff 1987; Sherr et al. 1987) found some protozoans preferred labeled bacteria to microspheres, while others did not. It is notable that two oligotrichous ciliates from Lake Oglethorpe, *Hulteria* and *Strombidi-
Table 5. Temperature, oxygen, and bacterial production and mortality due to grazing in Lake Oglethorpe during 1986.

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>Temp (°C)</th>
<th>Oxygen (ppm)</th>
<th>Production</th>
<th>Grazing</th>
<th>Grazing/production (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>(cells × 10^6 ml^-1)</td>
<td>(cells × 10^6 ml^-1 d^-1)</td>
<td>removed (% d^-1)</td>
</tr>
<tr>
<td>February</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>12.0</td>
<td>10.8</td>
<td>2.37</td>
<td>-</td>
<td>0.82</td>
</tr>
<tr>
<td>1</td>
<td>11.0</td>
<td>10.6</td>
<td>2.32</td>
<td>-</td>
<td>0.72</td>
</tr>
<tr>
<td>2</td>
<td>9.5</td>
<td>10.2</td>
<td>2.28</td>
<td>-</td>
<td>0.74</td>
</tr>
<tr>
<td>3</td>
<td>9.0</td>
<td>10.2</td>
<td>2.67</td>
<td>-</td>
<td>0.42</td>
</tr>
<tr>
<td>4</td>
<td>8.5</td>
<td>9.6</td>
<td>3.50</td>
<td>-</td>
<td>0.38</td>
</tr>
<tr>
<td>5</td>
<td>8.2</td>
<td>8.6</td>
<td>3.20</td>
<td>-</td>
<td>0.23</td>
</tr>
<tr>
<td>6</td>
<td>7.8</td>
<td>7.7</td>
<td>4.07</td>
<td>-</td>
<td>0.09</td>
</tr>
<tr>
<td>April</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>19.8</td>
<td>9.5</td>
<td>3.90</td>
<td>-</td>
<td>0.45</td>
</tr>
<tr>
<td>1</td>
<td>18.4</td>
<td>9.8</td>
<td>5.03</td>
<td>-</td>
<td>0.20</td>
</tr>
<tr>
<td>2</td>
<td>17.5</td>
<td>7.2</td>
<td>6.14</td>
<td>-</td>
<td>0.44</td>
</tr>
<tr>
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<td>4.0</td>
<td>8.70</td>
<td>-</td>
<td>0.22</td>
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<tr>
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<td>6.10</td>
<td>-</td>
<td>0.28</td>
</tr>
<tr>
<td>5</td>
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<td>1.0</td>
<td>7.22</td>
<td>-</td>
<td>0.24</td>
</tr>
<tr>
<td>May</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>24.0</td>
<td>9.2</td>
<td>4.30</td>
<td>0.16</td>
<td>0.18</td>
</tr>
<tr>
<td>1</td>
<td>23.9</td>
<td>9.4</td>
<td>5.26</td>
<td>0.39</td>
<td>0.63</td>
</tr>
<tr>
<td>2</td>
<td>23.7</td>
<td>9.2</td>
<td>4.44</td>
<td>0.34</td>
<td>0.35</td>
</tr>
<tr>
<td>3</td>
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<td>7.23</td>
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<td>0.39</td>
</tr>
<tr>
<td>4</td>
<td>16.0</td>
<td>&lt;0.3</td>
<td>7.01</td>
<td>0.35</td>
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<td>5</td>
<td>13.0</td>
<td>&lt;0.1</td>
<td>5.89</td>
<td>0.28</td>
<td>0.18</td>
</tr>
<tr>
<td>June</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>30.2</td>
<td>7.4</td>
<td>5.95</td>
<td>0.20</td>
<td>0.19</td>
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<td>2.06</td>
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</tr>
<tr>
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<td>27.2</td>
<td>6.0</td>
<td>6.65</td>
<td>1.52</td>
<td>0.37</td>
</tr>
<tr>
<td>4</td>
<td>21.0</td>
<td>0.6</td>
<td>5.68</td>
<td>0.61</td>
<td>0.38</td>
</tr>
<tr>
<td>5</td>
<td>16.8</td>
<td>&lt;0.1</td>
<td>6.21</td>
<td>0.48</td>
<td>0.76</td>
</tr>
<tr>
<td>September</td>
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</tr>
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<td>4.40</td>
<td>0.31</td>
<td>0.27</td>
</tr>
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<td>5.28</td>
<td>1.35</td>
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<tr>
<td>2</td>
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<td>7.7</td>
<td>5.64</td>
<td>1.50</td>
<td>1.33</td>
</tr>
<tr>
<td>3</td>
<td>24.2</td>
<td>1.0</td>
<td>6.26</td>
<td>1.59</td>
<td>0.51</td>
</tr>
<tr>
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<td>22.8</td>
<td>&lt;0.1</td>
<td>6.13</td>
<td>1.75</td>
<td>0.85</td>
</tr>
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<td>7.54</td>
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<td>0.73</td>
</tr>
<tr>
<td>6</td>
<td>17.0</td>
<td>&lt;0.1</td>
<td>7.13</td>
<td>0.44</td>
<td>0.43</td>
</tr>
</tbody>
</table>

* Grazing estimates for April ranged from 55 to 122% of production measured in April 1985.

*iuim, ingested microspheres at higher rates than fluoresceinlabeled bacteria (Table 2), while some estuarine oligotrichs ingested fluoresceinlabeled bacteria at higher rates than microspheres (Sherr et al. 1987). The marine ciliates Cyclidium and Uronema both grazed microspheres and bacteria at similar rates, while some marine heterotrophic flagellates apparently discriminated between bacteria and microspheres (Pace and Bailiff 1987; Sherr et al. 1987; Nygaard et al. 1988). The size difference of the cultured bacteria (0.8–1.0 μm) and the microspheres (~0.6 μm) used in these experiments may have been a factor affecting the relative grazing rates.

These data indicate that there is no perfect tracer particle for determining ingestion. Clearance rates determined for flagellates (0.1–20 nl ind.~1 h~1) and ciliates (2–220 nl ind.~1 h~1) using microspheres in Lake Oglethorpe were, however, within the range of those measured with a variety of methods in other systems (Bird and Kalff 1986; Fenichel 1982; Sherr et al. 1987). We chose fluorescent beads since they were readily avail-
able, inexpensive, brightly fluorescent (and thus easy to enumerate), and appeared to give reasonable estimates for ingestion of free-living bacterioplankton in this system. If there was discrimination against microspheres during any of our experiments in the lake, then our grazing estimates and total community impact estimates are conservative. Our conclusion that flagellates are the major bacterivores (see below) would be unaffected, since flagellates are more likely to be selective than ciliates (Nygaard et al. 1988).

**Bacterial production and bacterivory—**

Bacterial abundances in Lake Oglethorpe range from $2-8 \times 10^6$ ml$^{-1}$ and production ranges from $0.2-6.0 \times 10^6$ cells ml$^{-1}$ d$^{-1}$ (McDonough et al. 1986; Table 5). Both are in the range found in other freshwater systems (Güde 1986; Scavia and Laird 1987). In general, bacterial production and abundance in the lake are highest in the metalimnion and hypolimnion during summer stratification.

Grazing by the total bacterivorous community can crop $>100\%$ of bacterial production in spring (Table 5), when production is relatively low. This situation is also likely in winter, since cold temperature is correlated with reduced bacterial production (Simek 1986). In summer, production is higher and grazing accounts for less than daily production. On average, grazing accounted for $79\%$ and ranged from $11$ to $162\%$ of bacterial production. These results and our data from previous studies (Sanders and Porter 1986) are consistent with the paradigm of grazer control of bacterial abundance, but the ratio of grazing to bacterial production reported in Table 5 is not exact and should be interpreted with caution. Bacteria attached to particles account for $3-10\%$ of the total bacterial abundance in the lake (Pace et al. 1983; Sanders pers. obs.). Although attached bacteria are included in the productivity measurements, the microsphere method does not estimate grazing on attached particles. The relative activity of attached and free bacterioplankton is not known for Lake Oglethorpe.

The percentage of production removed by grazing also depends partly on the factor used to convert incorporation of $[^3H]$thymidine to cell production. Reported values for the factor vary by more than two orders of magnitude in different freshwater environments (Kirchman et al. 1982; Riemann 1985; Bell 1986; Sanders and Porter 1986). The factor may also vary seasonally (Scavia and Laird 1987), although not always (Lovell and Konopka 1985). Earlier studies in Lake Oglethorpe suggested that the factor used in the current investigation ($2 \times 10^{18}$ cells mol$^{-1}$) was 2-fold to 10-fold too low at some depths on at least two dates (McDonough et al. 1986; Sanders and Porter 1986). Given the uncertainty of the conversion factor, we opted to use the conservative value based on theoretical considerations (Fuhrman and Azam 1982). If production was underestimated, then grazing would account for a smaller portion of the bacterial mortality than indicated in Table 5. Studies of eutrophic Frederiksborg Slotsø (Riemann 1985), mesotrophic Lakes Constance (Güde 1986) and Biwa (Nagata 1988), and oligotrophic Lake Michigan (Scavia and Laird 1987), however, also support the conclusion that grazing is the major loss factor for bacterial populations, suggesting that it may be a general rule for lakes.

Bacterial production and total grazing pressure show a positive relationship in the few studies in which they were measured simultaneously (Fig. 2). This analysis includes data from both marine and freshwater systems, obtained by methods that vary among studies (Table 6). In a similar analysis of marine experiments, McManus and Fuhrman (1988) concluded that bacterial growth is often similar to grazing losses on time scales of 12–24 h. Grazing in these studies was also positively related to bacterial abundance (data not shown), but more of the variance in grazing was explained by bacterial production than by standing stock. Wright et al. (1987) also found production of bacteria to be correlated with grazing, but not with bacterial density in a temperate estuary.

There was relative constancy of the bacterial population densities over a range of bacterial production in Lake Oglethorpe (Fig. 3), which has also been observed in comparisons across systems (Hobbie 1979). This constancy may be due to the ability of
Table 6. Bacterioplankton production and grazing losses in planktonic assemblages.

<table>
<thead>
<tr>
<th>Production (10^6 cells ml^-1 h^-1)</th>
<th>Grazing</th>
<th>Grazing/production (%)</th>
<th>Methods (production, grazing)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Freshwater</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.12-0.56</td>
<td>0.06-0.51</td>
<td>42-121</td>
<td>[3H]tdr*, radioactive tracers</td>
<td>Riemann 1985</td>
</tr>
<tr>
<td>0.015-0.04†</td>
<td>0.01-0.03‡</td>
<td>50-147</td>
<td>[3H]tdr, decrease in [3H]DNA</td>
<td>Servais et al. 1985</td>
</tr>
<tr>
<td>0.003-0.30</td>
<td>0.05-0.32</td>
<td>§</td>
<td>[3H]tdr, size fractionation</td>
<td>Güde 1986</td>
</tr>
<tr>
<td>0.01-0.81</td>
<td>0.33</td>
<td>0-200</td>
<td>[3H]tdr, inhibitors</td>
<td>Sanders and Porter 1986</td>
</tr>
<tr>
<td>0.02-0.33†</td>
<td>0.04-0.12</td>
<td>51-&gt;100</td>
<td>[3H]tdr, inhibitors</td>
<td>Scavia and Laird 1987</td>
</tr>
<tr>
<td>0.11-0.25</td>
<td>0.06-0.29</td>
<td>23-122</td>
<td>Dilution, dilution</td>
<td>Tremaine and Mills 1987</td>
</tr>
<tr>
<td>0.01-0.02†</td>
<td>0.01-0.02</td>
<td>76-168</td>
<td>Size fract., size fract.</td>
<td>Nagata 1988</td>
</tr>
<tr>
<td>0.01-0.10</td>
<td>0.01-0.06</td>
<td>11-162</td>
<td>[3H]tdr, fluor. tracers</td>
<td>This study</td>
</tr>
<tr>
<td><strong>Marine</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0.05-0.06</td>
<td>0.02-0.04</td>
<td>44-56</td>
<td>Dilution, dilution</td>
<td>Landry et al. 1984</td>
</tr>
<tr>
<td>0.10-0.20</td>
<td>0.01-0.31</td>
<td>&lt;1-188</td>
<td>Size fract., size fract.</td>
<td>Wright and Coffin 1984</td>
</tr>
<tr>
<td>0.03-0.21†</td>
<td>0.02-0.04</td>
<td>17-133</td>
<td>Dilution, dilution</td>
<td>Ducklow and Hill 1985</td>
</tr>
<tr>
<td>0.005-0.02†</td>
<td>0.01-0.03‡</td>
<td>71-300</td>
<td>[3H]tdr, decrease in [3H]DNA</td>
<td>Servais et al. 1985</td>
</tr>
<tr>
<td>0.01-0.08</td>
<td>0.02-0.18</td>
<td>40-45</td>
<td>Inhibitors, inhibitors</td>
<td>B. Sherr et al. 1986</td>
</tr>
<tr>
<td>0.10-1.03‡</td>
<td>0.18-0.78</td>
<td>19-183</td>
<td>Inhibitors, inhibitors</td>
<td>Taylor and Pace 1987</td>
</tr>
<tr>
<td>0.05-0.52‡</td>
<td>0.01-0.19</td>
<td>5-223</td>
<td>[3H]tdr, fluor. tracers</td>
<td>McManus and Fuhrman 1988</td>
</tr>
</tbody>
</table>

* Incorporation of [3H]thymidine.
† Instantaneous rates (h^-1).
‡ Assuming all loss due to grazing.
§ Grazing and production estimates made at different times.
∥ Instantaneous rates (d^-1).

protists with short generation times to keep pace with a rapidly increasing bacterial food supply and dampen the oscillations of their abundance. Populations rise and fall in relation to the balance struck between growth rates and loss rates, and availability of nutrients, including that released by grazing, is likely to factor in the growth of bacteria (Güde 1988; Wright et al. 1987). Although there is no assurance that grazing is the dominant control of bacterial population.
dynamics, the empirical relationship (Fig. 2) does support the thesis (Azam et al. 1983) that grazing and bacterial production are closely coupled much of the time. It does not preclude the possibility that bacterial production and grazing can become uncoupled.

The grazing community—Ours is the first field study to determine seasonal patterns of bacterivory by all members of a freshwater planktonic community. Phagotrophic flagellates dominated bacterivory at all times and were responsible for 55–99% of the total bacterivory on an areal basis. Of them, the heterotrophic (unpigmented) flagellates dominated grazing throughout the year. In September, they cropped 20% of the bacterial standing stock per day and 77% of daily bacterial production at 2 m (but see cautions above). Total abundances of heterotrophic flagellates ranged from $2 \times 10^3$ to $4 \times 10^3$ ml$^{-1}$, which is in the range common for heterotrophic flagellates in freshwaters (Güde 1986; U.-G. Berninger pers. comm.). Our data support the interpretation of results from studies with inhibitors (Scavia and Laird 1987), size fractionation (Güde 1986), and abundance correlations (Riemann 1985) that, at most times, heterotrophic flagellates are the major bacterivores in lakes.

Phagotrophic phytoflagellates (mixotrophs) were the second most important group of bacterivores, accounting for 2–45% of bacterivory on an areal basis. Mixotrophs showed a strong seasonal pattern of impact. In winter and early spring they contributed up to 79% of the grazing at a given depth. They consisted primarily of the colonial chrysophytes Dinobryon and Chrysostephanosphaera and the unicell Ochromonas and showed a depth-related pattern of impact that changed as the large colonies settled to deeper water at the end of the bloom. Community composition, abundances, and individual grazing rates were similar to those found in another study of freshwater mixotrophs (Bird and Kalff 1986). Bird and Kalff (1986) found that Dinobryon had a greater grazing impact than crustaceans, rotifers, and ciliates combined. Their method did not measure grazing by heterotrophic flagellates, however, and, until our study, the importance of mixotrophs as seasonal dominants of total community bacterivory was unknown. Our findings emphasize the importance of including chloroplast-containing phagotrophs in estimates of community bacterivory.

Ciliated protists were the third most important group of bacterivores. Bacterivorous ciliates composed 14–90% of the ciliate community. They were seasonally important throughout spring and summer when they contributed up to 18% of total bacterivory on an areal basis. Halteria, Strombidium, Uronema, Cyclidium, Vorticella, Epistyliis, and Stokesia were all common bacterivores. They ranged in size from 10 to 60 µm for solitary forms and up to 250 µm for colonies. Ciliates are also common grazers of bacteria in marine systems where they are generally believed to play a secondary role to the flagellates (Fenchel 1980; Azam et al. 1983). In some marine environments, however, ciliates may be the major consumers of bacterioplankton (Sherr et al. 1987). They may also be more important bacterivores in other freshwater systems.

The rotifers Gastropus, Hexarthra, Filiinia, Anuraeopsis, Keratella, and Kellicottia were bacterivorous and accounted for 13% of the community grazing in June and 2% in September (Fig. 1). Abundances of bacterivorous rotifers were maximal in June (70–400 liter$^{-1}$), agreeing with summer maxima from a previous study in Lake Oglethorpe (Orcutt and Pace 1984). Their brief seasonal occurrence and low relative impact make them minor bacterivores in this community. Our detection of bacterivory in rotifers agrees in general with the findings of other researchers (Bogdan et al. 1980; Starkweather 1980; Bogdan and Gilbert 1987). Keratella cochlearis and K. bostoniensis have been previously identified as relatively efficient grazers of bacteria (Bogdan et al. 1980; Bogdan and Gilbert 1987). Keratella cochlearis and K. bostoniensis have been previously identified as relatively efficient grazers of bacteria (Bogdan et al. 1980; Bogdan and Gilbert 1987). Keratella cochlearis and K. bostoniensis have been previously identified as relatively efficient grazers of bacteria (Bogdan et al. 1980; Bogdan and Gilbert 1987).
In the case of Kellicottia, the difference could be due to the size of the bacterium (1.8–3.1 μm) used by Bogdan et al. (1980) compared to the smaller 0.57-μm microspheres that we used. Both K. cochlearsis and K. bostoniensis are more efficient at grazing larger particles (Bogdan et al. 1980; Bogdan and Gilbert 1987).

Crustaceans were unimportant as bacterivores in Lake Oglethorpe. Copepods and nauplii were not observed to ingest bacteria-sized particles, in agreement with other recent studies in marine and freshwater (Paffenhofer 1984; Bogdan and Gilbert 1987). The minor role for crustaceans as direct consumers of bacterial production (Table 4) has been seen in other field studies (Riemann 1985; Güde 1986). Cladocerans, however, may make a larger contribution to grazing mortality of bacteria on some occasions. In a humic lake where phytoplankton production was low, Kankaala (1988) estimated that daily consumption by Daphnia longispina was 3–48% of the bacterial biomass in the epilimnion. Riemann (1985) found that zooplankton >50 μm (dominantly Daphnia spp.) ingested 48–50% of bacterial net production in an enclosure without fish. Güde (1988) suggested that cladocerans ingest bacteria less efficiently than algae, but may influence bacterial community composition. During periods of “clear water” in Lake Constance there was a regularly observed shift from a mixed composition of small, filamentous and aggregated forms of bacteria to a homogeneous population of small cells (Güde 1988). The microsphere method used in the present study estimates grazing only on unattached bacteria and would underestimate bacterivory of cladocerans if they ingest bacterial aggregates. In Lake Oglethorpe, however, only 3–10% of the bacterioplankton are attached, suggesting that this pathway of direct bacterivory is minor.

The impact of cladoceran grazing on bacterioplankton is likely to change with the species composition of both the cladocerans and the available food spectrum. Cladocerans differ in their ability to collect bacteria (Pace et al. 1983; Porter et al. 1983), and many ingest smaller particles less efficiently than larger ones (DeMott 1985). We found that Daphnia and Ceriodaphnia from Lake Oglethorpe ingested 0.57-μm microspheres at twice the rate in 1.0-μm-filtered lake water (bacteria only) compared to whole-lake water with a natural community of flagellates and other particles. This finding suggests that bacterioplankton may be grazed more heavily by crustaceans if larger prey are reduced, as during clear-water periods. It contrasts with the results of Porter et al. (1983), who found enhanced bacterivory in the presence of larger particles. Although Porter et al. (1983) found the mean clearance rate of bacteria by D. parvula adults was 43% higher in whole-lake water than on bacteria alone, variability was also much greater. Nagata and Okamoto (1988) also found differences in daphnid grazing in various mixtures of radioactively labeled size fractions. They found no significant difference in grazing rates on <1-μm particles, however, in the presence or absence of non-labeled <25-μm particles. Dual label experiments with several other cladocerans did not indicate increased clearance in the presence of larger particles (DeMott 1985). Obviously our understanding of cladoceran bacterivory in the presence of other particles is incomplete.

The degree to which bacterial production is available to higher trophic levels in freshwater systems is dependent on the extent and efficiency with which secondary consumers crop the primary bacterivores, i.e. the heterotrophic and mixotrophic flagellates and, to a lesser extent, the ciliates. Cladocerans are the major grazers of particles in the size range of the 2-8-μm flagellates and can feed on 10-200-μm ciliates, although with reduced efficiency (Porter et al. 1979). Cladocerans consume heterotrophic flagellates and large, pliable colonies, including those of the mixotroph Dinobryon (Tappa 1965; Sanders and Porter 1987). Although copepods may have a significant impact on ciliates (Porter et al. 1979), they are less efficient at cropping particles in the size range of flagellates (E. Sherr et al. 1986; Bogdan and Gilbert 1987). In many lakes, cladocerans are an important food source for predatory fishes and invertebrates. Consumption of bacterivorous flagellates and ciliates by crustaceans is therefore the likely,
albeit indirect, link between bacterial production and the classic planktonic food web.

References


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