THE IMPACT OF A STREAM-DWELLING HARPACTICOID COPEPOD UPON DETRITALLY ASSOCIATED BACTERIA

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Abstract. Natural densities of common stream-dwelling harpacticoid copepods, Attheyella spp., reduced the density and biomass and increased the area-specific and cell-specific production of detritally associated bacteria. Bacterial density was reduced by as much as 58% and rod-shaped bacteria were reduced as much as 27%. Attheyella selectively removed larger rod-shaped bacteria. This resulted in a significant change in the size-frequency distribution of rod-shaped bacteria and a decrease in median cell length by 17-30%. The removal of larger sized cells by Attheyella probably contributed to the observed reduction in bacterial biomass. With copepods present, bacterial biomass was reduced as much as 45%. Estimated rates of ingestion of bacterial carbon by copepods are comparable to values for marine harpacticoids. Bacterial biomass appears to be a more important food source to microdetritivores than to macrodetritivores in streams.

Key words: Attheyella; bacteria; bacterial biomass; bacterial density; bacterial production; bacterial respiration; Copepoda; detritivory; detritus; meiobenthos; stream.

INTRODUCTION
Meiofauna, metazoans ranging in size from 40-500 μm, have been integrated into concepts of detrital dynamics in marine systems, but until recently, they have been largely overlooked in stream environments. The meiobenthos of marine environments has been examined in some detail, and various authors have noted the importance of these organisms in terms of their secondary production and their impact on benthic microflora and detrital processes (Gerlach 1971, 1978, Coull 1973, Tietjen 1980). It has been shown experimentally that selected taxa of the marine meiobenthos can enhance the rate of carbon mineralization, possibly by stimulating microbial activity through predation (Findlay and Tenore 1982). Other research indicates that the meiobenthos as a whole enhances the rate of consumption of detritus by larger deposit-feeding invertebrates (Tenore et al. 1977). Stream meiofauna may perform analogous roles.

Determining the response of the detrital bacterial community to grazing by meiofauna and determining the meiofauna's rate of ingestion of microbial carbon are first steps in investigating the role and significance of the stream meiofauna. Our study describes the impact of a stream-dwelling harpacticoid copepod on the frequency of cell types, density, biomass, and production of detritally associated bacteria and on the respiration of detritally associated microbes. We also estimate the rate of ingestion of bacterial carbon by these copepods. We test the hypotheses that stream meiofauna, through bacterivory, reduce bacterial density and concurrently stimulate bacterial activity.

METHODS
Birch leaves (Betula allegheniensis) were collected at leaf fall in 1982 and 1983 from a forested watershed at the Coweeta Hydrologic Laboratory (CHL), Macon County, North Carolina, USA. Litter traps were placed near a second-order mountain stream, Hugh White Creek (HWC). Leaves from these traps were stored and air-dried for several weeks, then 1.1 cm diameter leaf discs, 4 mg dry mass each, were removed.

Adults of harpacticoid copepods, Attheyella spp., were removed from HWC sediment and used in this experiment. Attheyella illinoisensis and A. obatogamensis are abundant in HWC (O'Doherty 1985, 1988), and A. illinoisensis is considered one of the most common and widely distributed freshwater harpacticoid copepods in the United States (Coker 1934).

Experimental design
We performed a series of three experiments in which we enumerated cell types, estimated biomass, determined productivity, and measured respiration of detritally associated microbes with and without harpacticoid copepods present. These experiments differed principally in the level of copepod density and the rate of water exchange. Scanning electron micrographs allowed visual assessment of the impact of copepod grazing in the first experiment. The impact of copepod presence on bacterial cell size-frequency distribution was examined in the first and third experiments. Bacterial density was measured in all experiments. Bacterial biomass and bacterial production were estimated in the second and third experiments, and microbial respiration was measured in the third experiment.
Experiment 1.—Leaf discs were incubated in 4 L of filtered HWC water (1-μm pore size) at 15°C in the dark for 13 d before use. Filtered stream water (2.5-3 L) was exchanged every 2-4 d during the incubation period. Copepods were distributed to 75 wells in polystyrene tissue culture plates, each well containing 3 mL of filter-sterile stream water and a single preconditioned leaf disc. One-third of the wells received no copepods (treatment NC), 1/3 received 5 copepods (treatment XHC), and 1/3 received 10 copepods (treatment XXHC). Leaf material and copepods were maintained at 15°C and kept in the dark except during sampling periods. Every 2 d throughout the experiment half of the water in each well was exchanged and leaf discs were gently turned over. On days 0, 2.5, 4.5, 8.5, and 14.5, five leaf discs were removed from each treatment and detritally associated bacteria were examined (see Analytical procedures).

Experiment 2.—Leaf discs were incubated in unfiltered HWC water at 15°C in the dark for 9 d before use. Groups of 12 adult copepods were placed in each of 9 flow-through experimental chambers (treatment C). Each chamber contained 33 preconditioned leaf discs. Another 9 chambers contained leaf discs but not copepods (treatment NC). Chambers were immersed in a 15°C water bath (Fig. 1) and received filtered, unrecirculated stream water (0.45-μm pore size) at a rate of 0.88 mL/min, which resulted in a turnover time for the 30-mL chambers of 34 min and a flow rate of 0.002 cm/s. Inlet and outlet ports on each chamber were capped with 48-μm mesh Nitex to prevent loss of copepods. On days 2, 6, and 12, all leaf discs were removed from each of three randomly selected chambers in each treatment and detritally associated bacteria were examined (see Analytical procedures).

Experiment 3.—Leaf discs were incubated for 15 d in the dark at 15°C in 18 flow-through plexiglass chambers (Fig. 1) before use. Each chamber received recirculated, filtered HWC water (11-μm pore size) at a rate of 28 mL/min, resulting in a turnover time for the 57 mL capacity chambers of 2 min and a flow rate of 0.04 cm/s. Chamber ports were capped with PVC fittings covered with 48-μm mesh. Each chamber contained 40 preconditioned leaf discs. Groups of 15 adult copepods were placed in 6 chambers (treatment C), groups of 30 copepods were placed in another 6 chambers (treatment HC) and 6 chambers were left without copepods (treatment NC). On days 3 and 12 after the addition of copepods, all leaf discs were removed from each of three randomly selected chambers in each treatment and detritally associated bacteria were examined (see Analytical procedures).

The density of copepods per amount of leaf material in experiments 2 and 3 (treatment C in each experiment) is representative of high densities of harpacticoid copepods seen on leaf litter in the field (Perlmutter 1988). The densities of copepods in experiment 1 (treatments XHC and XXHC) and in experiment 3 (treatment HC) exceed maximum densities observed in undisturbed streams at CHL. These higher densities (treatments XHC, XXHC, and HC) represent those observed in the field following certain types of perturbation, such as the removal of aquatic insects from a Coweeta stream by a pesticide treatment (Cuffney et al. 1984).

Analytical procedures

Scanning electron micrographs were made of small discs (0.35 cm diameter) removed from each larger leaf disc used in experiment 1. Small discs were prepared for examination with a Philips 505 scanning electron microscope (Parducz 1967).

To count and size bacteria, leaf discs were processed with a Bransonic ultrasonic cleaner, which proved to be essentially 100% effective at removing surface-bound material (D. G. Perlmutter, personal observation). Single discs were placed in scintillation vials containing 10 mL of 5% formalin solution and sonicated for 10 min. Bacteria were counted, their cell length was measured, and they were photographed on Irgalan Black-stained Nuclepore filters using Acridine Orange epifluorescent techniques modified after Hobbie et al. (1977). Filters were examined and photographed on microscope slides with an Olympus microscope (model BHS) equipped for epifluorescence with an EY 455 blue excitation filter.

In experiment 1 bacteria were selected randomly and their lengths measured with an ocular micrometer. One hundred measurements were made on each of five slides from each treatment replicate for every sampling date. In experiments 2 and 3, photomicrographs (1200×) were digitized to determine cell size and volume (Edwards 1987). Photomicrographs taken at 480× magnification were used to provide additional cell size-frequency data for rod-shaped bacteria in experiment 3 (>1000 cells measured per treatment).
Bacteria were counted in either 20 fields (experiment 1) or 10 fields (experiments 2 and 3) on each slide from every treatment. Enumerated bacteria were always categorized as either rods or cocci. Rod-shaped bacteria were divided into two length categories (> or <2 μm in experiment 1 and > or <2.25 μm in experiment 3). Cocci were also divided into two categories (> or <0.5 μm in experiment 1 and > or <0.45 μm in experiment 3).

Bacterial production was estimated using rates of 3H-methyl-thymidine (3H-Tdr) incorporation into DNA following the procedure of Findlay et al. (1984). 3H-Tdr (New England Nuclear, specific activity 740 GBq/mmol) was added to two leaf discs in a 3-mL volume of filter-sterile water. Seven hundred and forty kBq of 3H-Tdr were added per two discs in experiment 2 and 370 kBq were added per two discs in experiment 3. 3H-Tdr was added on days 0, 2, 6, and 12 in experiment 2 and on days 3 and 12 in experiment 3. In both experiments discs were incubated with agitation at 15°C for 1 h (3-h incubation time on day 3 in experiment 3). Isotope dilution series (Moriarity and Pollard 1981) were run in each case to determine naturally occurring endogenous and exogenous pools of thymidine. DNA was extracted from detritally associated bacteria and assayed for radioactivity on a Beckman liquid scintillation counter (model LS 1800) with an external standard to determine counting efficiency.

Bacterial production was calculated as the number of cells produced per hour per leaf disc (2 x 10^9 cells/nmol Tdr incorporated, Bell et al. 1983) and converted to the number of cells produced daily per square centimetre of leaf surface. The number of cells produced was converted to cell biovolume using mean volumes for rod-shaped bacteria and cocci in experiment 2 and mean cell volume for each of four cell categories in experiment 3. In both experiments production was apportioned based on the proportion of total cell number in each cell category. Cell biovolume was converted to biomass carbon using the conversion factor of 2.2 x 10^{-13} g/μm^3 (Bratbak and Dundas 1984).

Microbial respiration for 4-5 leaf discs from selected chambers was measured with a YSI Biological Oxygen Monitor (model 53). Respiration rates were determined over a 2-h period for leaf discs incubated at 12°C.

Statistical analysis

Statistical comparisons of size–frequency distributions of rod-shaped bacteria were made between treatments using a chi-square test. Differences in cell size and/or volume between treatments were tested with a median test at the .05 significance level. This was performed as a chi-square test in a 2 x 2 contingency table (Bhattacharyya and Johnson 1977:542).

Differences in density of bacteria between treatments were analyzed for statistical significance using a treatment x day between-subjects ANOVA which also allowed for an analysis of day effect and day x treatment interaction effect. If treatment effects were found to be significant, a one-factor ANOVA was then performed on treatment differences for each day and statistical significance was assessed with a Fisher’s Protected Least Significant Difference procedure (PLSD, alpha = .05). Bacterial biomass as carbon was estimated as the product of three factors: bacterial density, cell biovolume, and the conversion of cell biovolume to carbon content. Differences in biomass of bacteria between treatments were analyzed with a similar two-factor ANOVA procedure. Rates of bacterial production and the ingestion of bacteria by copepods were not examined statistically because of the assumptions used in the conversion factors involved in their calculation. Treatment differences in microbial respiration were tested with Student’s t tests at the .05 significance level.

The rate at which copepods ingested bacteria was determined from the observed decrease in bacterial density for treatments with copepods as compared to treatments without copepods. The rate of ingestion was estimated after determining bacterial growth in control treatments without copepods using a linear growth equation (Christian et al. 1982). Predicted values for bacterial biomass in treatments with copepods were determined from the linear growth equation and compared to observed values; differences were attributed to copepod feeding.

Results

Fungal growth became visible without the aid of microscopy on the stomatal side of leaf discs shortly after discs were placed in tissue culture plate wells in experiment 1. Scanning electron micrographs illustrate the sequential disappearance of the fungi, bacteria, accumulated debris, and loosened cuticle from leaf surfaces when copepods are present (Fig. 2). The substantial amount of organic material loosely bound to upper and lower portions of leaf discs (Fig. 2a) is noticeably less after 2.5 d in treatments with copepods, and this reduction is greatest at the higher density of copepods (Fig. 2b, c, d). The loss of surface-associated material continues in the presence of copepods (Fig. 2e, f, g) until relatively little debris and few large bacteria remain (Fig. 2h, i, j), with smaller bacteria often seen clustered in microscopic depressions or embedded in the leaf surface (Fig. 2k, l).

Total bacterial density was significantly reduced in the presence of copepods (Table 1, Figs. 3 and 4). Specifically, rod-shaped bacteria were significantly fewer with copepods present (Table 1, Figs. 3–5). Copepods apparently removed larger rod-shaped cells (Table 1, Fig. 3) and bacterial size–frequency distributions of rod-shaped bacteria were significantly shifted toward smaller cell sizes (Figs. 6 and 7). Median length of rod-shaped cells was significantly less with copepods present (Table 2); it was reduced as much as 26% in experiment 1 and 11% and 13% in experiment 3 under
FIG. 2. Scanning electron micrographs of leaf surfaces from experiment 1. Time sequence; day 0 (a), day 2.5 (b, c, d), day 4.5 (e, f, g), day 8.5 (h, i, j). Copepod density: no copepods (a, b, e, and h), 5 copepods per disc (c, f, i), 10 copepods per disc (d, g, j, k, and l). Magnification: 600x (a-j), 525x and 1600x (k, left and right panel, respectively) and 3500x (l). Scale bars: 50 µm (a–k) and 10 µm (l).

lower and higher copepod densities, respectively. The density of smaller cocci was significantly lower with copepods present in experiment 1 on two sampling days, but by the final sampling day these bacteria were significantly more abundant in the presence of the greatest number of copepods.

Changes in bacterial biomass reflected changes in bacterial density, and this was due to the reduction in the number of rod-shaped bacteria coupled with a reduction in their mean biovolume. This resulted in the reduction of bacterial carbon in treatments with copepods (Table 3). Bacterial biomass was significantly less on the final day of experiment 2 with copepods present, and biomass reductions ranged from 37–45%. Bacterial biomass appeared to be reduced in treatments with copepods on the final sampling date in experiment 3, although these differences were not statistically significant due to the high variability in the data. This
Fig. 3. Density of bacteria by cell type and size on leaf discs in experiment 1 for three treatments; □ no copepods, ▲ 5 copepods per leaf disc, and ■ 10 copepods per leaf disc. Density presented as mean ± 1 SE, n = 3.

variability resulted from the propagation of error when density and biovolume measurements were combined in the calculation of biomass.

Bacterial production ranged widely (Table 4). Although production in experiment 2 was similar between treatments, daily turnover rate and production per cell appeared to be greater in the presence of copepods on the last two sampling days. On one day in experiment 3, highest levels of bacterial production, daily turnover rate, and production per cell occurred in treatments with the greatest number of copepods.

Rates of carbon intake by copepods resulting from grazing on bacteria, calculated from changes in bacterial density and biomass, ranged from 0.03-0.47 μg·copepod⁻¹·d⁻¹. Grazing rates in experiment 2 led to an average carbon intake of 0.27 μg·copepod⁻¹·d⁻¹ (range = 0.10-0.47 μg·copepod⁻¹·d⁻¹). Grazing rates in experiment 3 resulted in an average of 0.12 μg·copepod⁻¹·d⁻¹ (range = 0.04-0.23 μg·copepod⁻¹·d⁻¹).

Respiration rates of detritally associated microbes (measured as O₂ consumed per unit leaf surface area per hour) ranged from 0.12 to 0.19 μL·cm⁻²·h⁻¹. Microbial respiration rates did not differ significantly between treatments.

**DISCUSSION**

**Size selection of bacteria by copepods**

The reduction of the median size of rod-shaped bacteria on leaf surfaces in the presence of copepods may reflect the susceptibility of larger microbes to grazing due to their cell size and/or the food-collecting structures of the copepods. Larger microorganisms, projecting higher above the leaf surface, are probably more susceptible to grazing activities on a topographically uneven surface, as indicated by the presence of microcolonies of smaller cells clustered in surface depressions or partially embedded in the leaf matrix. This size-selective impact of grazing has been noted in studies of algae-grazing insect larvae in streams (Sumner and McIntire 1982, Hill and Knight 1988).

*Attheyella*'s feeding structures may be more effective at removing larger and more accessible cells. Unfortunately the feeding mechanisms of harpacticoid copepods have not been investigated as thoroughly as those of calanoid or cyclopoid copepods. Marcotte (1977a) characterized members of the harpacticoid genus *Tisbe* as being raptorial or mixed-feeding omnivores capable of gleaning bacteria or diatoms from...
organic debris or clay minerals. Apparently their food selection is determined by particle size and shape (Marcotte 1977b). Some harpacticoid copepods are described as "plane sweepers" (Hicks 1980 after B. M. Marcotte, personal communication), which preferentially feed upon flat surfaces. Although more information on diet and feeding behavior is needed, there is evidently a degree of specialization among harpacticoids that could result in size-selective grazing.

The removal of larger rod-shaped bacteria results in a pronounced reduction of microbial biomass, which may have an effect on the functioning of the microbial community. In experiment 1 we observed that, along with the reduction in larger rod-shaped bacteria, smaller rod-shaped bacteria were more numerous at the higher density of copepods. Whether this represents compensatory growth remains unknown, as we have no data for microbial activity in this experiment. In experiment 3, at higher grazing pressure, increased bacterial production accompanies reductions of both large and small rod-shaped cells without an increase in the smaller cocci. Determining the mechanisms for bacterial response to bacterivory remains an intriguing question.

**Copepod grazing impact on bacterial density, biomass, production, and respiration**

We found that the extent of reduction of detritally associated bacteria varied in relation to cell size, number of copepods, and possibly the rate of water flow. Under conditions of in situ densities of *Attheyella* but at lower flow rate and lower production (experiment 2 vs. experiment 3), bacterial density and biomass were more reduced. Thus our data suggest that the impact of copepod grazing on bacteria is mitigated by flow rate, and that this may be partially due to the effect of flow rate on bacterial production.

Our work demonstrates that heightened bacterial production often accompanies the removal of rod-shaped bacteria by copepods. This heightened functional response of populations that are grazed has been seen in the compensatory growth of water column and benthic algae (Hargrave 1970, Cooper 1973, McDonald 1985) and in the stimulation of bacterial activity resulting from bacterivory (Johannes 1965, Hargrave 1970, Fenchel 1972, Barsdate et al. 1974, Fenchel and Harrison 1976). Grazing may stimulate bacterial ac-
TABLE 3. Bacterial biomass carbon (μg/cm²) in treatments NC (no copepods), C (nominal copepod density), and HC (twice nominal copepod density). Data are means ± 1 sd (n = 3).

<table>
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<tr>
<th>Experiment 2</th>
<th>Day</th>
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<th>Coci (μg/cm²)</th>
<th>Rods (μg/cm²)</th>
<th>Total (μg/cm²)</th>
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<td></td>
<td>0</td>
<td>NC</td>
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<td>0.853 ± 0.376</td>
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<td>2</td>
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<td></td>
<td>4</td>
<td>C</td>
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<td>0.921 ± 0.076</td>
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<td>8</td>
<td>C</td>
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<th>Coci (&gt;0.45 μm)</th>
<th>Rods (&lt;2.25 μm)</th>
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bacterial carbon incorporated at rates of 5.8, 12, and 24 ng·mg⁻¹·d⁻¹ for Tipula, Peltoperla, and Lirceus, respectively.

These rates are much lower than our estimated assimilation rate of bacterial carbon by *Attheyella illinoisensis*. We determined this rate as follows. Adult female and male *Attheyella illinoisensis* weigh ≈7 and 6 μg, respectively (E. O'Doherty, personal communication); using an adult mass of 6.5 μg results in a calculated mass-specific ingestion rate of bacterial carbon of 5–72 μg·mg⁻¹·d⁻¹. Assuming assimilation efficiencies ranging from 20 to 50% results in estimated carbon assimilation rates ranging from 1 to 56 μg·mg⁻¹·d⁻¹. These rates range up to several orders of magnitude higher than rates observed for leaf-shredding macroinvertebrates. Hence our study indicates that the meio-benthos rather than the macrobenthos more effectively consume what Cummins (1974) has described as the microbial “peanut butter” on the detrital “cracker.” Indeed, this comparison of assimilation of bacterial carbon by *Attheyella* vs. that of larger invertebrates implies important functional distinctions for stream detritivores. Microdetritivores such as *Attheyella*, with assimilation rates on the order of micrograms of bacterial carbon per milligram of animal per day, apparently select detritally-associated microflora, whereas macrodetritivores, with reported carbon assimilation rates on the order of nanograms, assimilate substantial amounts of detrital substrate and much smaller amounts of microbial material.

*Attheyella* is often found among organic debris in shallow, slow-flowing portions of the second-order Appalachian mountain stream High White Creek in the Coweta Hydrologic Laboratory. In this environment copepod populations and other bacterivorous meiofaunal organisms would be expected to reduce significantly the standing stock of detritally associated microbes. Our data indicate that the meiofauna in stream leaf litter could consume up to 22% of daily bacterial carbon production. This is determined by using the estimated meiofaunal density in leaf litter (42 000 individuals/m², Perlmutter 1988) and assuming that 60–80% of these organisms are bacterivorous.
In terms of their own dry mass, animals of the meiofauna may consume from 5 to 72 \( \mu g\cdot mg^{-1}\cdot d^{-1} \) (this study). We assigned stream meiofaunal organisms an average individual dry mass of 2 \( \mu g \). Literature reviews of marine meiofaunal abundance and biomass (Gerlach 1971, Coull 1988) indicate that an average mass for meiofaunal organisms ranges between 1.5 and 2 \( \mu g \) individual. Thus meiofaunal consumption of bacterial carbon is estimated to range from 0.25 to 4.8 mg\( \cdot m^{-2}\cdot d^{-1} \). Bacterial biomass on leaf litter is 82-164 mg/m\(^2\), as determined from bacterial C on leaf surfaces (1-2 \( \mu g/cm^2 \), D. G. Perlmutter, unpublished data) and the dry mass of leaf litter in Hugh White Creek (213 g/m\(^2\), autumn through winter, Perlmutter 1988). Daily turnover of bacterial carbon is estimated as 41% for experiment 2 and 13% for experiment 3 (this study) or an estimated bacterial carbon production rate ranging from 10 to 68 mg\( \cdot m^{-2}\cdot d^{-1} \). When mass-specific rates of consumption of bacterial carbon by the meiofauna are related to rates of bacterial production under our different flow regimes, the meiofauna are estimated to consume between 1 and 22% of daily bacterial production. The importance of the consumption of bacterial production by meiofaunal organisms could be even greater in natural streams where reported rates of bacterial production are lower than in our laboratory study system (Meyer et al. 1988).

We have found that stream-dwelling harpacticoid copepods effectively remove accumulated organic material, fungi, and bacteria from detritus and can enhance production in detritally associated bacteria. We suggest that grazing by copepods, in concert with other meiofaunal organisms, may substantially alter the quality of detritus, influencing the rate of its consumption by larger stream invertebrates. These microdetritivores appear to play a significant role in the detrital dynamics of headwater streams.

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LITERATURE CITED


activity through the release of nutrients (Barsdate et al. 1974, Tietjen 1980) or by increasing the surface area for microbial recolonization (Hargrave 1970, Gerlach 1978).

Respiratory activity of detritally associated bacteria does not appear to be significantly affected by the presence of harpacticoid copepods. Our measurements of respiration of detritally associated microbes are comparable though slightly lower than rates reported by Ward and Cummins (1979). Variability in our measurements of respiration may have masked any effects of copepod grazing. However, a grazing-induced decrease in bacterial biomass without a change in microbial respiration has been reported previously in a study of the effect of soil microarthropods on plant litter decomposition (Paniko and Simonov 1986).

Increases in copepod density resulted in the relatively greater reduction in the density of rod-shaped bacteria except when “overcrowding” apparently interfered with copepod feeding behavior. Although doubling copepod density above “in situ” abundance levels resulted in a 1.5 times greater decrease in rod-shaped bacterial density (experiment 3), doubling copepod density above abundance levels initially higher than “in situ” density did not result in a greater reduction of rod-shaped bacteria (experiment 1). Copepods held at these abnormally high densities were often observed
off of the leaf surface and on the side of their tissue culture plate wells. Under these conditions of "over-crowding" we observed that frequent encounters between copepods on the leaf surface elicited avoidance behavior, which presumably interfered with feeding activities.

**Copepod grazing rates**

Our estimated rates of the ingestion of bacterial carbon by copepods (0.03–0.47 μg·ind·−1·day−1) are comparable to grazing rates reported previously for marine harpacticoid copepods. Vanden Berghe and Bergmans (1981) reported carbon assimilation rates for *Tisbe furcatata* ingesting both bacteria and algae ranging from 0.05 to 0.12 μg·ind·−1·d−1. Assuming assimilation efficiencies ranging from 20 to 50%, these rates would result in carbon ingestion rates ranging from 0.10 to 0.60 μg·ind·−1·d−1. Rieper (1978) estimated carbon ingestion rates for the marine harpacticoid copepods *Tisbe holothuriae* and *Paramphiascella variarenis* as ranging from 1 to 3.5 μg·ind·−1·d−1. Montagna (1984), in his in situ study of marine meiofaunal grazing upon bacteria and diatoms, estimated the ingestion of bacterial carbon by copepods, nematodes, and ostracods to range from 0.042 to 0.53 μg·ind·−1·d−1. The variability in estimated harpacticoid grazing rates stems from differing environmental conditions, experimental procedures, conversion factors and not least, differences among the species of copepods involved.

**Role and significance of the meiobenthos in detrital processing in streams**

In many headwater woodland streams allochthonous organic material, primarily leaf litter, is microbially transformed and subsequently consumed by a variety of macroinvertebrates (Kaushik and Hynes 1971, Petersen and Cummins 1974, Cummins and Klug 1979). In his paradigm of stream structure and function, Cummins (1974) suggests that detrital microbes may serve as the more nutritionally valuable portion of detritus for these invertebrates. Recent evidence contradicts this paradigm. Findlay et al. (1984, 1986a, b) have shown that some stream detritivores, i.e., *Tipula, Peltoperla*, and *Lirceus*, assimilate enough detritus so that the associated bacteria provide only a small fraction of these animals’ nutritional requirements. They report

| Table 1. Summary table for ANOVA for bacterial density. Data are *F* values, with degrees of freedom reported. |
|---|---|---|---|---|---|
| Cell category | Treatment | Day | Treatment x day interaction |
| Total bacteria | Experiment 1 | | |
| Rod-shaped bacteria | 10.61 | 2.46*** | 41.36 | 3.46*** | 5.17 | 6.46*** |
| Large rod-shaped bacteria | 9.11 | 2.46*** | NS | NS | NS | NS |
| Small rod-shaped bacteria | 81.94 | 2.46*** | 6.25 | 3.46** | 3.52 | 6.46** |
| Cocci | NS | NS | NS | NS | NS | NS |
| Large cocci | NS | NS | NS | NS | NS | NS |
| Small cocci | 6.77 | 2.46** | 39.64 | 3.46*** | 5.00 | 6.46*** |
| Total bacteria | Experiment 2 | | |
| Rod-shaped bacteria | 12.29 | 1.12** | 10.10 | 2.12** | 4.58 | 2.12* |
| Cocci | NS | NS | NS | NS | NS | NS |
| Total bacteria | Experiment 3 | | |
| Rod-shaped bacteria | 13.80 | 1.12** | 9.50 | 2.12** | 5.61 | 2.12* |
| Cocci | NS | NS | NS | NS | NS | NS |

* *P < .05, ** *P < .01, *** *P < .001, NS = no significance.*


