Microfaunal response to fertilization of an arctic tundra stream

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Summary:

1. As part of a whole-system study, the response of the heterotrophic microfaunal community colonizing artificial substrata (polyfoam units) to fertilization of an arctic tundra stream was followed for 6 weeks during the summer.
2. Dominant heterotrophic microfauna observed included amoebae (approximately 40% of colonizing biomass), rotifers (36% of biomass) and ciliates (25% of biomass).
3. Biomass of heterotrophic microfauna on artificial substrata was not significantly different in a control reach and an experimental reach fertilized with phosphorus (loading rate ten times ambient), but in a reach fertilized with both phosphorus and nitrogen (loading rates ten times ambient) biomass was double that of the control and phosphorus-fertilized reaches. The lack of response in the phosphorus reach was probably due to greater insect grazing as a result of previous phosphorus fertilization of this reach.
4. Abundance of microfauna on epilithic surfaces in the river was higher on rocks from pools than on rocks from riffle areas, but abundance on the artificial substrata was higher than on the natural rocks.
5. The results suggest that microfauna of arctic tundra streams are regulated by grazers and that their importance in transfers among trophic levels is greater in pools than in riffles.

Article:

Introduction

Heterotrophic microfauna (generally defined here as organisms from 20 to 200 Rm) have been studied in lakes and oceans, and numerous reports have noted the importance of these organisms as links between heterotrophic bacteria and zooplankton grazers (e.g. Pomeroy, 1974; Azam et al., 1983). In flowing water systems, the role of bacteria and algae has received attention (cf. Lock, 1993; Kaplan & Newbold, 1993), but far less attention has been paid to dynamics of heterotrophic microfauna (Meyer et al., 1988), especially in low-order streams, where little quantitative data are available (cf. Bott & Kaplan, 1989). Because allochthonous organic matter generally fuels low-order streams (Peterson et al., 1985; Kaplan & Newbold, 1993), heterotrophic microbes and their consumers play important roles in decomposition, nutrient cycling, and production of particulate organic matter from dissolved organics. Thus, the microbial community potentially has a tremendous impact on nutrient spiralling (Newbold et al., 1983) and secondary production in streams.

In contrast to studies of heterotrophic microfauna in streams, studies of abundance and processes of autotrophs, bacteria, larger invertebrates and vertebrates are relatively common. A good example is research on the Kuparuk River in northern Alaska, which has been studied since 1978 and is now part of the Arctic Long Term Ecological Research (LTER) Program at Toolik Lake. Peterson et al. (1993a) have described the biotic components of the Kuparuk River, which include bacteria, algae, macroinvertebrates (insect larvae), and a single fish species, the arctic grayling. Fertilization of the Kuparuk River with phosphorus and nitrogen (in some years) changed the biological processes and populations at all measured trophic levels primarily because of growth stimulation of epilithic diatoms, filamentous algae and bryophytes (Peterson of al., 1993a; Finlay & Bowden, 1994). These changes were documented by assessing the abundance and activity of river flora and

fauna, and they have helped define both food web interactions and processes in the Kuparuk River (e.g. Peterson et al., 1985; Hershey et al., 1988; Gibeau & Miller, 1989; Hullar & Vestal, 1989; Deegan & Peterson, 1992; Miller, DeOliveria & Gibeau, 1992; Peterson et al., 1993a,b; Bowden, Finlay & Maloney, 1994).

The response of organisms in the Kuparuk River to fertilization is also a good example of bottom-up (or resource) regulation of aquatic ecosystems. This concept, along with the idea of top-down control, has been explored extensively in lake systems in recent years (cf. Carpenter, 1988) and also applies in lotic ecosystems as experimental manipulations in the Kuparuk River demonstrate. Peterson et al. (1993a) have constructed a model of interactions in the Kuparuk River that represents the bottom-up effects of nutrient additions on all trophic levels, based on these previous studies. Top-down or grazing interactions are also illustrated in this model. One component whose role is largely unknown, however, is the microfaunal component.

The extensive information available on the Kuparuk River makes it an ideal study site to improve our understanding of the importance of trophic interactions of microbes in the riverine food web. The specific objectives of this study were to characterize benthic microfauna in the 20-200-p.rn size range by examining the organisms that colonized artificial substrata, and to determine the response of these organisms to fertilization of the river with phosphorus alone and with phosphorus plus nitrogen during a summer sampling period (summer of 1989).

Materials and methods

Study site

The Kuparuk River rises in the northern foothills of the Brooks Mountain Range on Alaska's North Slope and flows northward into the Beaufort Sea. At the study site (68°37'N, 149°24'W) it is crossed by the Trans Alaska Oil Pipeline and haul road, and is a meandering fourth-order arctic river which is highly oligotrophic but has a moderately high concentration of dissolved organic carbon (Peterson, Hobbie & Corliss, 1986). Mean channel width at the site is 20 m and the river bottom consists largely of rocky cobbles and boulders (Peterson et al., 1993a). The river is frozen from mid-October to mid-May. Approximately half of the precipitation that falls occurs as snow from September to May and thaw results in high flow over a short interval from mid-May to early June. Summer flows are sustained by springs, lake discharge and local rainfall (Deegan & Peterson, 1992). During this study in the summer of 1989, mean discharge was 2.79 $m^3 s^{-1}$ and ranged from I to 12.6 $m^3 s^{-1}$. Maximum flow occurred during a storm in early August.

Locations on the river are referenced to a common benchmark located about 1 km upstream of the pipeline haul road crossing. Reaches are identified by their position in kilometres below (+) or above (-) this benchmark. Nutrients were added to the stream as aqueous solutions to achieve 10 μg P 1^{-1}, and 100 μg $N1^{-1}$, approximately ten times the normal loading rate. Drippers delivered aqueous solutions of phosphorus (as phosphoric acid) or nitrogen (as ammonium sulphate) plus phosphorus which designated three reaches in the experimental section of the river: control, +P and N + P. The phosphorus (+P) dripper was located at +0.59 km, and the nitrogen plus phosphorus (N + P) dripper at +1.75 km. The control reach was upstream from the phosphorus dripper. A complete description of the experimental site is given in Peterson et al. (1993a).

Field sampling

The sampling method was based on microfaunal colonization of artificial substrates which consisted of polyurethane foam units, or PFUs (Cairns, Kuhn & Plotkin, 1979). Six cylindrical PFUs, 4.4 cm (height) × 3.3 cm (diameter) were secured 10 cm apart on strings. Strings were tied to steel rods pounded vertically into sediments of river riffles so that they remained submerged near the stream bottom at each site. Replicate strings were placed in control and fertilized riffles of river reaches on 1 July, 1989.

Samples were collected weekly. Generally, four to six PFUs were cut from replicate strings at each site, except when high water from a storm in August washed away most strings and only one or two PFUs from each reach were counted on the last sampling dates. Water squeezed from the PFU was collected in a beaker along with two additional rinses of the PFU using river water. The sample was then reduced in volume by reverse-flow

filtration through a 20-µm-mesh net (Dodson & Thomas, 1964). Final volume was adjusted to 60 ml with river water. On each sampling date one or two stream rocks located in riffles adjacent to the artificial substrata were also sampled. Additionally, rocks were occasionally sampled from pools in both the +P and N + P reaches (n = 3 from each) for comparative purposes. Epilithon was dislodged from the exposed upper surface of the rocks (approximately 8 cm in diameter) by rinsing the rock completely using a squirt bottle containing river water. The rinse water was then collected, concentrated by reverse-flow filtration and the volume adjusted to 60 ml as before. All samples were immediately preserved with glutaraldehyde to a 1% final concentration (v/v).

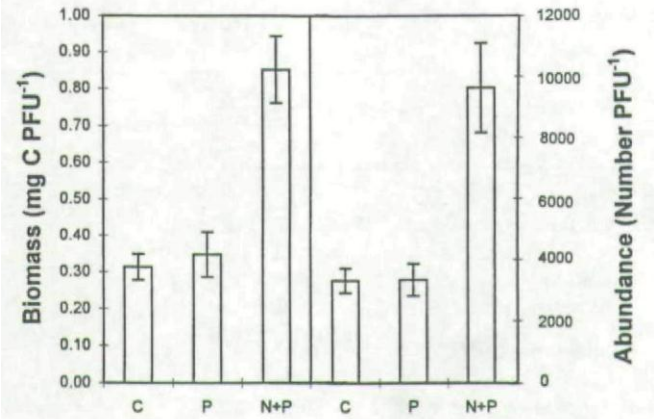

Fig. 1 Mean number and biomass of microfauna on artificial substrata (PFUs) in control and nutrient-amended reaches of the Kuparuk River, 1989. Error bars represent ± 1 SE.

Sample analysis

Organisms were enumerated following the method of Baldock (1986) using Rose Bengal for staining. Rose Bengal stains organic matter, and helps differentiate living organisms from non-living material. This method is especially valuable with one group of organisms, testate amoeba, because without the stain it is impossible to distinguish between a living organism and an empty test (Heal, 1964).

An aliquot of the concentrated sample (0.01-0.5 ml, depending on abundance of organisms) was placed in a test tube. Additional distilled water was added to a volume of 6-8 ml and the sample was stained with one to four drops of a 0.25% Rose Bengal for 1015 min. The sample was then drawn on to an 8.0-µm-pore cellulose acetate filter under gentle vacuum. Filters were then mounted on slides under coverslips in a 43% aqueous sucrose solution. Prepared slides could be stored frozen for several days. Filters were scanned at 200× magnification and organisms were counted, identified and assigned to size classes within broad taxonomic groups for biomass estimations. Organisms were identified using taxonomic guides to protozoa (Jahn & Jahn, 1949; Ogden & Hedley, 1980; Lee, Hunter & Bovee, 1985; Pennak, 1989; Patterson & Hedley, 1992), rotifers (Ruttner-Kolisko, 1974) and meiofauna (Higgins & Thiel, 1988).

Carbon biomass of microbes was estimated based on geometric form, average size of individuals within taxonomic categories, and literature values for specific gravity of wet tissue, fresh weight to dry weight ratio, and carbon content (Heal, 1964; Fenchel, 1975; Ruttner-Kolisko, 1977; Finlay, 1978; Orcutt, 1981; Beaver & Crisman, 1982; Gates, 1984; Carlough & Meyer, 1989; Pace & Pauli, 1989; Putt & Stoecker, 1989; Arndt & Nixdorf, 1991).

Non-parametric statistical analysis (SAS Institute, 1988) was used to assess significance of differences among treatments (control vs. +P vs. N + P).

Results

The benthic microfaunal organisms (20-200 Rm size range) in the Kuparuk River consisted primarily of ciliates, testate amoeboid protozoans (*Difflugia, Arcella, Centropyxis* and some unidentified species) and rotifers (*Trichocerca, Lepdella, Colurella* and other unidentified species). Nematodes were found in low abundance, and gastrotrichs, tardigrades and chironomid insect larvae were seen occasionally but they contributed less than

1% to overall number or biomass in our samples and were not considered further.

Mean density (± SE) of microfauna over the summer was $3.3 \pm 0.4 \times 10^3$ incl.. PFU^{-1} in the control reach, $3.4 \pm 0.5 \times 10^3$ ind. PFU^{-1} in the +P reach, and $9.6 \pm 1.5 \times 10^3$ in PFU^{-1} in the N + P reach (Fig. 1). Coefficient of variation for counts was 60-75% for each taxa, and 92% overall. The pattern of microfauna biomass was similar to that observed for density (Fig. 1). Total microfaunal biomass averaged 0.31 ± 0.04 mg C PFU^{-1} in the control reach, 0.35 ± 0.06 mg C PFU^{-1} in the +P reach, and 0.85 ± 0.09 mg C PFU^{-1} in the N + P reach.

Numerically, ciliates were the most abundant major taxonomic group of microbial fauna, followed by amoebae and then rotifers (Table 1). Ciliate density ranged from 9.2×10^2 ind. PFU^{-1} in the +P reach 1 week after the start of the experiment to 9.5×10^3 ind. PFU^{-1} in the N + P reach after 1 week. Mean ciliate density over the summer was similar in the control and +P reaches, but three times higher in the N + P reach. While ciliates were the most abundant taxa numerically, they comprised only about 25% of the total microfaunal biomass because of their small size (Table 1). Ciliate biomass ranged from 0.03 mg C PFU^{-1} in the +P reach after 1 week to 0.33 mg C PFU^{-1} in the N + P reach after 3 weeks (Fig. 2). Mean ciliate biomass was over twice as high in the N + P reach than in the control or +P reaches.

Table 1 Mean (± 1 SE) abundance and biomass of microfauna on artificial substrata (PFUs) in study reaches of the Kuparuk River, Alaska, 1989

	Reach (*n*)		
	Control (24)	+P (17)	N + P (19)
Density (ind. PFU^{-1})			
Ciliates	$2.07 \pm 0.29 \times 10^3$	$2.27 \pm 0.36 \times 10^3$	$6.55 \pm 1.20 \times 10^3$
Amoebae	$1.04 \pm 0.11 \times 10^3$	$0.93 \pm 0.18 \times 10^3$	$2.69 \pm 0.36 \times 10^3$
Rotifers	$2.16 \pm 0.38 \times 10^2$	$1.43 \pm 0.23 \times 10^2$	$4.05 \pm 0.44 \times 10^2$
All microfauna	$3.33 \pm 0.40 \times 10^3$	$3.35 \pm 0.53 \times 10^3$	$9.64 \pm 1.45 \times 10^3$
Biomass (mg C PFU^{-1})			
Ciliates	0.06 ± 0.01	0.09 ± 0.01	0.21 ± 0.03
Amoebae	0.12 ± 0.02	0.16 ± 0.04	0.33 ± 0.04
Rotifers	0.13 ± 0.02	0.10 ± 0.02	0.31 ± 0.05
All microfauna	0.31 ± 0.04	0.35 ± 0.06	0.85 ± 0.09

Amoebae were the second most abundant organisms and included the testate amoebae Difflugia, Arcella, Centropyxis and at least one unidentified genus. Some naked amoebae were also found but these only comprised 10% of the amoebae. Amoeba density ranged from 2.5×10^2 ind. PFU^{-1} in the +P reach after 1 week of exposure to 4.4×10^3 ind. PFU-1 in the N + P reach after 4 weeks. Mean density of amoebae over the summer was about three times higher in the N + P-fertilized reach than in the control or +P reaches (Table 1). Amoeba biomass constituted about 40% of total microbial biomass, and ranged from 0.04 mg C PFU^{-1} in the +P reach 1 week after the start to 0.57 mg C PFU^{-1} in the +P reach after 5 weeks (Fig. 2). Mean biomass of amoebae in the N + P reach was about twice that found in the control and +P reaches (Table 1).

Rotifers comprised the third most abundant group on a numerical basis and included the genera *Trichocerca*, *Lepedella*, *Colurella*, some Bdelloidea and three additional unidentified genera. Rotifer density ranged from sixty-six ind. PFU^{-1} in the control reach after 1 week to 5.3×10^2 in the N + P reach after 2 weeks. Mean density over the summer was twice as high in the N + P reach as in the control or -1-P reaches (Table 1). Rotifer biomass comprised about 36% of the estimated microfaunal biomass and ranged from 0.04 mg C PFU^{-1} in the +P reach 1 week after artificial substrata were placed in the river to 0.51 mg C PFU^{-1} in the N + P reach after 4 weeks (Fig. 2). Rotifer biomass was nearly three times higher in the N + P reach than in the control or +P reaches (Table 1).

Analysis of variance by ranks (NPAR1WAY, SAS, 1988) revealed highly significant differences in micro-fauna on the PFUs among treatments (control, +P, and N + P reaches). This effect was significant for both numbers and biomass of total microfauna, as well as individual taxa (Table 2). A Duncan's multiple range test performed on the rank transformed data showed that the difference was the result of significantly higher abundance of all

taxa of microfauna in the N + P treatment; there was no significant difference among the control and +P treatments (Fig. 3).

Samples collected from surfaces of rocks in riffles (n = 10, 7 and 8 in control, +P, and N + P reaches, respectively) exhibited high variability in microfaunal populations (CV = 115-138% for counts of individual taxa). Rocks recovered from the +P reach exhibited higher numbers and estimated biomass of microfauna than rocks from the control or N + P reach (Table 3), but neither experimental reach was significantly different from the control (Duncan's multiple range test on rank transformed data). A few rock samples taken from pools in the fertilized reaches (n = 3 from each) exhibited higher numbers (mean = 9.4×10^4 ind. m^{-2}, range = 1.4-19.4) and estimated biomass (mean = 17.7 mg C m^{-2}, range = 4.5-33.5) of microfauna than was found on the rocks from riffles in the fertilized reaches.

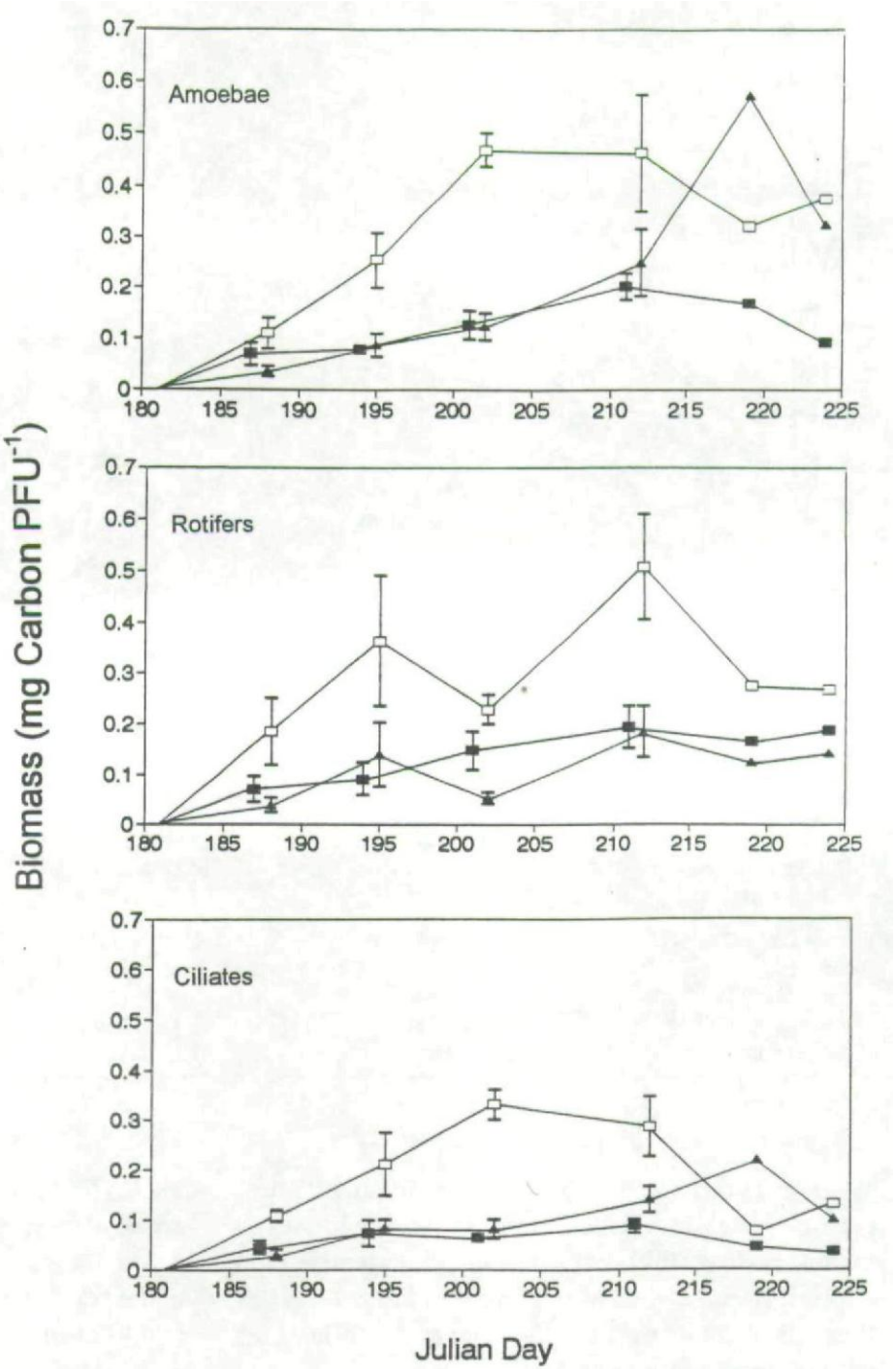

Fig. 2 Biomass of individual microfauna taxa colonizing artificial substrata (PFUs) in control (■), phosphorus (▲), and nitrogen + phosphorus (□) reaches of the Kuparuk River. Error bars represent ± 1 SE when replicate samples were taken.

Table 2 Results of analysis of variance by ranks of microfaunal colonization of artificial substrates in the Kuparuk River. Values are *F*-statistic for sample treatments (control, +P addition, N + P addition) by numbers or biomass of microfauna. All values are highly significant (** = $P < 0.01$)

	Ciliates	Amoeba	Rotifers	Total
Microfaunal number	12.77**	12.59**	18.63**	15.95**
Microfaunal biomass	18.86**	9.54**	12.59**	19.68**

Discussion

Fertilization response

The addition of nitrogen and phosphorus to the Kuparuk River in 1989 resulted in increased microfaunal biomass on artificial substrates, as would be expected from bottom-up stimulation (cf. Carpenter, 1988). Surprisingly, however, the addition of phosphorus alone did not result in significant increases in microfauna over the control despite prior identification of phosphorus as the limiting nutrient in the Kuparuk River (Peterson et al., 1985; Peterson et al., 1993a). This pattern of response to phosphorus was not unique to microfauna on PFUs. Bowden et al. (1992) found that epilithic chlorophyll a, photosynthesis and respiration exhibited a similar pattern of response during the summer of 1989; that is, all of these measures in the N + P reach increased significantly compared to the control reach, but there was no significant difference between the +P and control reaches. Peterson et al. (1985, 1993a) reported similar results for the Kuparuk River in 1985. Both Bowden et al. (1992) and Peterson et al. (1993a) concluded that after several years of phosphorus stimulation of algal productivity, increases in insect biomass and grazing (Miller et al., 1992; M. C. Miller et al., unpubl. data) prevented further accumulation of epilithic algae in the +P reach. The 2 year lag was attributed to long life cycles (1-3 years) of the dominant insects in the Kuparuk River (Peterson et al., 1993a). It is probable that in 1989 insect grazing also masked any effect of algal stimulation in the +P reach, and only with the added stimulation of nitrogen in the N + P reach could the fertilization response outpace macrofaunal regulation. Because microfaunal patterns in 1989 are similar to those of algae, it appears that they are subject to the same predator regulatory constraints as the attached algae.

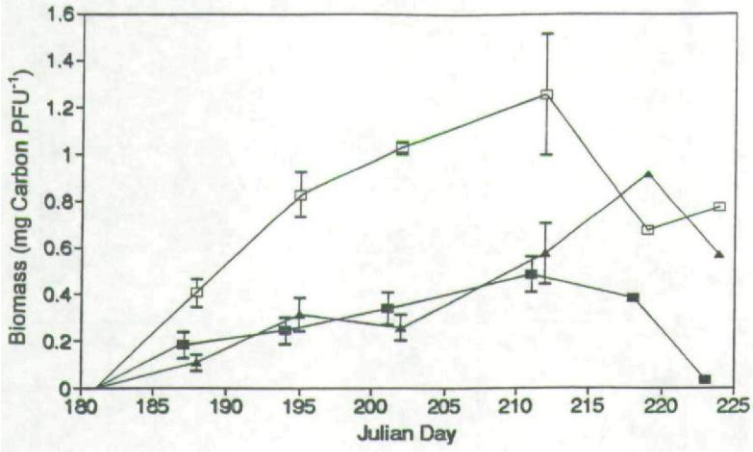

Fig. 3 Total biomass of microflora colonizing artificial substrata (PFUs) in control (■), phosphorus (▲), and nitrogen + phosphorus (□) reaches of the Kuparuk River, 1989.

Table 3 Mean (± 1 SE) abundance and biomass of microfauna on rock surfaces in study reaches of the Kuparuk River, Alaska, 1989

	Reach (*n*)		
	Control (10)	+P (7)	N + P (8)
Density (ind. m^{-2})			
Ciliates	$4.96 \pm 1.13 \times 10^3$	$2.35 \pm 0.56 \times 10^4$	$5.56 \pm 1.62 \times 10^3$
Amoebae	$3.02 \pm 1.12 \times 10^3$	$1.44 \pm 0.41 \times 10^4$	$1.95 \pm 0.66 \times 10^3$
Rotifers	$8.40 \pm 2.04 \times 10^2$	$4.11 \pm 0.85 \times 10^3$	$1.39 \pm 0.80 \times 10^3$
All microfauna	$8.82 \pm 2.31 \times 10^3$	$4.21 \pm 1.11 \times 10^4$	$8.79 \pm 2.73 \times 10^3$
Biomass (mg C m^{-2})			
Ciliates	0.15 ± 0.03	0.92 ± 0.21	0.27 ± 0.07
Amoebae	0.96 ± 0.05	5.36 ± 1.58	0.64 ± 0.30
Rotifers	0.73 ± 0.15	2.82 ± 0.69	1.07 ± 0.54
All microfauna	1.84 ± 0.68	9.11 ± 2.34	1.98 ± 0.85

Artificial substrata

Artificial substrata, such as PFUs, are valuable in assessing responses to perturbation, because they act to reduce variability associated with environmental variables. They are particularly useful in streams where substrata, currents, scouring and predation all contribute to sample variability (Paul et al., 1977). Additionally, studies have noted that organisms colonizing PFUs reflect the species composition of the natural substratum (Cairns et al., 1973; Cairns, Yongue & Boatin, 1979; Henebry & Cairns, 1980). The quantitative comparison of biomass found on artificial vs. natural substrata is more problematic, however, because the surface area available for colonization on PFUs differs from natural substrata in chemical composition and physical structure (B. Niederlehner, Virginia Polytechnic Institute, pers. comm.). We made such comparisons based on an estimate of 134 cm^2 for the surface area of the PFUs we used (H. Vafai, University of North Carolina, Greensboro, pers. comm.). The biomass of microfauna on rock surface samples ranged from 0.005 to 19.89 mg C m2 (mean = 3.92 mg C m^{-2}) compared with biomass estimates in PFU samples from riffles that ranged from 0.007 to 63.6 mg C m^{-2} (mean = 36.93 mg C m^{-2}) on PFUs. The comparison may actually be even closer, however, because the method we used on rock surfaces, rinsing with a squeeze bottle, probably removes only a portion of the microfauna, which are often associated with attached periphyton. This problem appears less important when using PFUs (Cairns et al., 1973). Thus, differences in microfauna abundance between PFUs and rocks are probably less than an order of magnitude.

Comparisons with other studies

Only one other study reports biomass estimates for microfauna on the epilithic surfaces of natural substrata (rocks) in streams (Bott & Kaplan, 1990), although others have reported estimates from stream bed sediments (e.g. Baldock, Baker & Sleigh, 1983). Bott & Kaplan (1990) estimated the average annual biomass of ciliates developing on rocks and porcelain disks in White Clay Creek, Pennsylvania to be 51 mg C m^{-2}, while ciliate standing crops in English chalk streams were about 16 mg C m^{-2} of stream bed (50% of dry weight value reported by Baldock et al., 1983). These values are considerably higher than our estimates of ciliate biomass developing on rocks in the Kuparuk River riffles (0.15-0.92 mg C m^{-2}), but not too different from our total microfauna biomass estimates from rocks in pools in the fertilized reaches (17.7 mg C m^{-2}), or to estimates derived from PFUs (23 mg C m^{-2} in the control reach). Higher values in temperate streams are to be expected as a result of climatic extremes and generally more oligotrophic conditions in arctic streams.

Qualitatively, microfauna community assemblages on rocks and PFUs in the Kuparuk River also differed from those in temperate streams. Testate amoeba and rotifers were major components of arctic stream epilithon but are less common in temperate streams (Baldock et al., 1983; Pennak, 1989). This abundance of amoebae may be attributed to runoff from the surrounding tundra peat or the presence of mosses in the river, as these are characteristic habitats of testate amoebae (Heal, 1964; L. Beyens, University Antwerp, Belgium, pers. comm.).

Microfauna as components of the food web

Microfauna have been identified as important grazers of algae and bacteria in microbial food webs in temperate lake systems (cf. Carpenter, 1988), and they are known to be important agents of nutrient transformation (cf. Fenchel, 1987). In oligotrophic arctic LTER lakes, however, they have been found in low abundance except when the lakes were fertilized (Rublee, 1992). The results of this study seem to suggest a similar limited role for microfauna in low-order arctic rivers. For example, our estimates of microfauna biomass in riffles from the control reach of the Kuparuk (1.8 mg C m^{-2}) are less than 1% of the value of algal biomass estimated from Bowden et al.'s (1992) chlorophyll a data for the same reach, and values estimated from PFUs and rocks in riffles of fertilized reaches are only slightly higher (about 1%). This small proportion of microfauna biomass relative to algal biomass suggests that microfauna are not limited by food resources in riffles. In comparison, Inicrofaunal biomass in pools in fertilized reaches is higher, up to nearly 5% of the value of algal biomass. Thus, microfauna are more likely to be coupled to epilithic algal production in pools than in riffles.

These observations are consistent with Bowden et al.'s (1992) observations of differences between riffle and pool epilithon in the Kuparuk River. They suggested that water flow and insect grazing on riffle rocks limits standing stocks of epilithic chlorophyll *a*. In contrast, epilithic chlorophyll *a* accumulates in the calmer waters

of pools, along with a floc of detrital material, and they noted that nutrient recycling may be important in maintaining production within this biofilm. It is in just such an environment that microfauna may be most important in their roles as both microbial grazers and nutrient recyclers (Fenchel, 1987).

These observations are also consistent with Peterson et al.'s (1993b) model of trophic interactions in the Kuparuk River, based on stable nitrogen isotope signatures which placed little emphasis on microfauna. They reported that of four common insect larvae, two appeared to consume algae directly, while the others had nitrogen isotope signatures which could not link them directly with algal food resources. Peterson et al. (1993b) suggested that reliance on allochthonous detritus or imported organic matter, in addition to algal production, accounted for these signatures. They also noted that actual diets are probably mixtures of various food resources. It is quite possible that, at least in pools, microfauna may comprise a portion of this mixture.

Overall, our results indicate that in low-order arctic rivers heterotrophic microfauna respond to bottom-up stimulation by nutrients, and that their abundance may be limited by predators (top-down control). Their importance in trophic transfers, if any, probably has a strong spatial component (riffles vs. pools). It is evident that additional quantitative information is necessary to improve our understanding of the role of microfaunal communities in food-web dynamics of rivers and streams and resolve these questions. A critical component of such research will be the continued development of methods that allow more direct assessments of microbial communities in streams.

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