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TROPHIC GENERALISTS VS. TROPHIC SPECIALISTS: IMPLICATIONS FOR FOOD WEB DYNAMICS IN POST-FIRE STREAMS[1]

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Abstract. The trophic ecology of 11 benthic macroinvertebrate taxa found in Cache Creek, Yellowstone National Park (YNP) was studied to determine if burned organic matter is an important resource and how resource utilization patterns may be altered in post-fire streams. Laboratory food quality experiments were conducted to determine the growth response of each species when grown on several resource types: burned organic matter, periphyton, unburned coarse particulate material (CPM), and unburned fine particulate material (FPM). The central hypothesis of this research was that benthic macroinvertebrates cannot use burned organic matter as a resource. A secondary hypothesis was that some benthic macroinvertebrates are facultative in trophic function, with the ability to use both allochthonous and autochthonous resources for growth.

Of the 11 taxa studied, only one (*Paraleptophlebia heteronea*) could grow on burned organic matter as a resource, indicating that post-fire food webs probably do not exhibit major shifts in resource utilization to burned material. Two species were generalist detritivores (*P. heteronea, Ameletus cooki*) able to use both natural FPM and CPM resources. Two species were specialist detritivores (*Oligophlebodes sigma, Ephemerella infrequens*) growing only on unburned CPM resources, and two (*Cinygmula mimus, Epeorus albertae*) were specialist herbivores utilizing only periphyton. Five species were generalist herbivore–detritivores (*Baetis bicaudatus, Drunella doddsi, D. coloradensis, D. spinifera, Zapada columbiana*), exhibiting growth on both detritus and periphyton resources.

Based on the experimental results, trophic generalists are common food web components in Yellowstone streams. Two of the most abundant benthic macroinvertebrates during post-fire recovery, *B. bicaudatus* and *Z. columbiana,* were trophic generalists, indicating that some generalists may be disturbance adapted. In this study, published functional feeding group classification did not indicate obligate resource utilization (growth on only one resource type) for most taxa studied. Comparison of a food web for Cache Creek based on functional feeding group classification and one based on the results of this study indicates that the inclusion of generalists in the web results in a more realistic approximation of food web relationships such as the link-species scaling law. Our results suggest that future research should include spatial and temporal aspects of resource switching and generalist resource utilization by individual lotic primary consumers.

Key words: food web; macroinvertebrate; resource utilization; Rocky Mountain stream; trophic generalists vs. trophic specialists; wildfire.

INTRODUCTION

Disturbance of streams by wildfire can affect aquatic macroinvertebrates at spatial scales ranging from microhabitat to entire catchment and temporal scales ranging from days to decades (Minshall 1988, Christensen et al. 1989, Minshall et al. 1989). The 1988 wildfires in Yellowstone National Park (YNP), USA, provided an opportunity to assess the impact of catchment level disturbance on many aspects of stream macroinvertebrate populations and communities in a setting

which has remained relatively unimpacted by humans for >100 yr (Forbes 1893, Mihuc et al., *in press*; G.W. Minshall, *unpublished manuscript*). Previous knowledge of stream responses to fire relates primarily to nutrient dynamics, with few published results available specifically on macroinvertebrates (Minshall et al. 1989, Spencer and Hauer 1991).

The focus of the present research was resource assimilation and food web dynamics among benthic macroinvertebrates in the Cache Creek (YNP) basin, a catchment severely impacted by the 1988 Yellowstone wildfires. Predictions about post-fire responses of benthic macroinvertebrates in streams have included: (1) lower detrital food quality and a temporary reduction of allochthonous resources in post-fire streams, which results in a diminished detritivore component; and (2) an increase in periphyton abundance during early post-

fire years, which should favor the herbivore component (Minshall et al. 1989). Lower detrital food quality is thought to result from a change in organic matter input from unburned detritus to burned material in post-fire streams. Little is known about how primary consumers make use of these altered food resources, or about food web dynamics in post-fire streams.

The central hypothesis of this research was that primary consumers in post-fire streams cannot utilize burned material as a resource. Burned organic matter should be a poor resource for primary consumers because it contains little readily metabolizable organic matter. A secondary hypothesis was that some benthic macroinvertebrate taxa exhibit a generalist functional trophic niche, with the ability to assimilate both allochthonous and autochthonous resources into tissue (Koslucher and Minshall 1973). Among benthic macroinvertebrates, some taxa have mouthparts specialized to ingest food attached to surfaces (scrapers), and some are specialized to ingest "loose" food items of either fine (gatherers) or coarse (shredders) particle size (Cummins 1973). Generalist resource niches, however, may predominate among benthic macroinvertebrates because mouthpart specialization does not necessarily indicate obligate resource utilization (Minshall 1988, Palmer et al. 1993).

Our approach to these hypotheses involved three aspects: (1) the quality of post-fire burned organic matter as a resource for growth of lotic primary consumers, (2) the nature of burned vs. unburned food resources as evidenced by indirect measures of food quality (e.g., microbial density, protein, lipid, ash, and cellulose/lignin content), and (3) the generalist or specialist nature of the trophic niche of primary consumers in post-fire streams (evaluated by growth on potential food resources in post-fire streams). Laboratory growth experiments were conducted to address aspects 1 and 3, assessing food quality among six potential resources, including burned detritus, for 11 species. Resource food quality for each species was defined according to the growth response when grown on a food type.

METHODS

Growth experiments

Taxa studied were chosen for several reasons. They represented either (1) the most abundant species in Yellowstone post-fire streams (*Baetis bicaudatus, Zapada columbiana*), (2) some of the more common species found in Yellowstone streams (*Ephemerella infrequens, Drunella doddsi, Oligophlebodes sigma*), or (3) representatives from the three major functional feeding groups found in Rocky Mountain streams: shredders, scrapers, and gatherers. Taxa studied accounted for one-third of the total community abundance and 57% of the abundance of Ephemeroptera, Plecoptera, and Trichoptera in Yellowstone National Park (YNP) streams and included four of the eight most abundant

species found in Cache Creek, YNP between 1988 and 1992 (*B. bicaudatus, Z. columbiana, E. infrequens, D. doddsi*) (Mihuc et al., *in press*).

The six food treatments used in the growth experiments were (1) periphyton, (2) unburned fine particulate material (FPM), (3) unburned coarse particulate material (CPM), (4) benthic material from a burned stream, Cache Creek, YNP, collected during the first post-fire season, (5) burned fine particulate material (BFPM), and (6) burned coarse particulate material (BCPM). The first three treatments represent the three main resources available to primary consumers in streams located in unburned catchments. The last three treatments represent detrital resources available to primary consumers in post-fire streams. BFPM and BCPM were 100% burned during a controlled burn in the laboratory, while Cache Creek material contained ≈35% burned material (G.W. Minshall, *unpublished data*).

Each food treatment was replicated three times in a completely random design. Growth experiments were conducted in a Controlled Environments (Winnepeg, Manitoba) model 20d0018 environmental chamber at constant temperature (10°C) under a 12:12 light:dark regime. Experimental units (replicates) were 15-L aerated plastic chambers. The chambers had a 25 × 25 cm bottom area (625 cm²) and contained 10–15 L of filtered stream water. Water was filtered through a 53-μm mesh Nitex net. Aeration included a plastic air deflector that served to create a circulating water current in the chambers as in Mackay (1981) to simulate stream flow conditions. The water velocity ranged from 13 to 20 cm/s in each chamber, measured by the rate of dissolution of salt tablets as in Rabeni and Minshall (1977). During each experiment, water was replaced weekly in each chamber with a mixture of 70% filtered stream water and 30% de-ionized water. The dilute water and weekly water change were used to prevent accumulation of nutrients or other water-soluble materials during the experiment. Total dissolved solids and pH were measured weekly in each chamber to insure that levels were maintained at or below natural stream levels. Any FPM accumulations were removed from the CPM and BCPM treatments every 10 d by sieving all food material on a 1-mm mesh screen.

Resources for the unburned FPM and CPM treatments were collected from Amphitheater Creek, YNP, a catchment that was not affected by the 1988 Yellowstone wildfires. CPM was collected from wood/leaf packs using a D-frame dip net and FPM by scooping up the sediment (fine particulate matter) with a bucket and collecting the sample in a 53-μm mesh Nitex net. Material for the FPM treatments (unburned FPM and burned FPM) was sieved through a 1-mm screen to exclude CPM. The BFPM and BCPM treatments used the same material collected from Amphitheater Creek, burned at 400°C for 2 h in a muffle furnace. Burned CPM also included terrestrial leaf litter collected from Amphitheater Creek which was burned at 400°C for 2

TABLE 1. Experimental conditions and stream of origin for each taxon tested in the food quality experiments. Taxa tested in the same experiment are indicated by the same superscript letter.

Taxon	Functional feeding group	Date of experiment	Duration of experiment (days)	N per treatment replicate	Origin of population
Cinygmula mimus	Scraper	July 1992	30	8	Mink Creek, Idaho
Ameletus cooki	Gatherer	September 1992	50[a]	4	Amphitheater Ck, YNP
Zapada columbiana	Shredder	September 1992	50[a]	7	Amphitheater Ck, YNP
Paraleptophlebia heteronea	Gatherer	November 1992	·60[b]	8	Mink Creek, Idaho
Drunella spinifera	Scraper	November 1992	60[b]	5	Mink Creek, Idaho
Ephemerella infrequens	Scraper/shredder	March 1993	45	7	Mink Creek, Idaho
Baetis bicaudatus	Scraper/gatherer	May 1993	22	8	Pebble Creek, YNP
Drunella coloradensis	Scraper	June 1993	40[c]	7	Pebble Creek, YNP
Oligophlebodes sigma	Scraper	June 1993	40[c]	6	Pebble Creek, YNP
Drunella doddsi	Scraper	July 1993	18	6	Gibson Jack Creek, Idaho
Epeorus albertae	Scraper	February 1994	40	8	Mink Creek, Idaho

h in a muffle furnace. The burning simulated crown fire conditions at the soil surface (Wells et al. 1979). The partially burned matter was collected from a third-order site on Cache Creek, YNP using the same technique as unburned FPM. All material for the CPM treatments was washed on a 1-mm mesh screen to exclude fine particulate matter from these treatments. All material was air dried at room temperature prior to use in the experiments. Food was placed in each experimental treatment at least 7 d prior to the beginning of each experiment to allow microbial colonization. Microbial colonization on each food type was monitored using acridine orange staining and direct microscopic epiflourescent enumeration. Colonization generally occurred within 24–48 h, reaching peak densities after 48 h in most treatments (T. B. Mihuc, *personal observation*).

Periphyton was collected by removing rocks from a riffle section of Amphitheater Creek, YNP or Mink Creek (Bannock County, Idaho). In the field, invertebrates were removed from each rock, and the rocks were transported to the laboratory in aerated containers at ambient stream temperature. In the laboratory, 3–4 rocks, and their associated periphyton, were placed in each periphyton replicate at least 7 d prior to an experiment. Rocks were allowed to acclimate to the environmental chamber temperature by placing them in 25 L of unfiltered stream water from the collection site for 24 h. Community composition of field-collected periphyton was compared to laboratory periphyton treatments after 7–14 d of colonization prior to every experiment. Samples were collected by scraping the surface of three rocks randomly drawn from the stream and each rock in the experimental chambers. The number and estimated relative abundance of the diatom and algae taxa in the field and laboratory assemblages were determined for comparison.

Insects for each experiment were collected by overturning substrate in a reach of the study stream and collecting the dislodged invertebrates in a D-frame dip net. The sample was immediately sorted for larvae and nymphs of the taxa desired. To prevent injury to the insects, sorting was done with a plastic 5-mm diameter suction pipette. Insects were transported to the laboratory in aerated containers at ambient stream temperature and were allowed to acclimate in these containers in the environmental chambers for 48 h prior to each experiment. Only early life stages (within 2 mo after egg hatching) or middle life stages (2–6 mo after egg hatching) were used in the experiments. Exact life stages were not determined. Late stages, determined by large size or the presence of well-developed wing pads on nymphs, were not tested to avoid emergence during the experiments.

Experiments were conducted between June 1992 and February 1994 (Table 1). Experiments ranged from 180–600 degree-days in duration. One degree-day is defined as 1°C daily average water temperature. In general, experiments were ≈500 degree-days in duration. Insects were monitored every 5–10 d throughout each experiment, removing dead specimens and recording molting events. Because early life stages were used, experiments were conducted in different seasons depending on the phenology of each taxon. Two taxa were tested together in several experiments (Table 1). Placing species with similar habitat preferences in the same experiment was avoided to minimize competitive interactions. The experimental density (individuals per square centimetre of substrate area) of each species was maintained at or below known field densities for YNP streams (Mihuc et al., *in press*). By using densities well below natural densities and by placing ample food in each treatment replicate, food was not a limiting factor in these experiments. The experiments were designed to test for food quality, not resource quantity. Gut contents of three specimens from each treatment replicate were examined at the end of each experiment to determine if the insects were, in fact, ingesting the food available. Gut contents were prepared as in Mecom and Cummins (1964).

During the experiments, all treatments except the periphyton replicates were covered with black plastic to prevent autotrophic production in these treatments. Therefore only the periphyton replicates were exposed to the 12:12 light : dark lighting regime. While darkness may have affected behavior of the insects, covering the treatments insured that conditions were completely heterotrophic in the detritus treatments. Although diurnal light patterns are known to affect behavior in lotic insects, temperature is probably the most important factor affecting growth in stream insects (Vannote and Sweeney 1980). Darkness did not appear to affect molting behavior since several taxa were observed to molt in the dark treatments during the experiments. Four taxa grew only in the covered treatments, indicating that altered light conditions did not affect feeding patterns or growth.

Dissolved oxygen measurements were taken to determine autotrophic or heterotrophic conditions in each treatment. Dissolved oxygen was measured at 10°C with no insects or aeration present. Measurements were taken in each treatment replicate for a 24-h continuous period during January 1994 using Royce (New Orleans, Louisiana) model 900 dissolved oxygen analyzers and a Campbell Scientific (model ps12) datalogger. Oxygen metabolism was used to determine the extent of photosynthetic (autotrophic) and respiratory (heterotrophic) processes occurring in each treatment. Net daily production of oxygen indicated autotrophic conditions while net oxygen uptake indicated heterotrophic conditions for each of the six resources.

Determination of growth:statistical analyses

For each species, insect mass at the end of the experiment was compared to a pre-treatment sample of 10–15 insects taken at the beginning of the experiment. Individual mass was determined to the nearest 0.001 mg using a Cahn electrobalance after drying for 24 h at 60°C and cooling to ambient room temperature in a desiccator. Dead insect mass was determined if specimens were collected intact with no signs of decay, indicating recent mortality. Decayed insects were not used because mass and time of death were too uncertain. Mortality was assumed to be caused by the failure of the insects to utilize the food presented, not to physical conditions or competition within the treatments. High mortality was observed for most taxa only in the burned treatments. If high mortality had been observed across all food treatments for a taxon, then factors other than resource quality could be implicated. Also, gut content analysis indicated that each taxon, regardless of growth or mortality, was ingesting the material presented in each treatment. In nearly all cases, guts of insects in the burned treatments were at least 50% full, even when no growth occurred.

Significant growth for experimental animals was determined using the nonparametric Mann-Whitney U test ($P < 0.05$) between pre-treatment and post-treatment samples. A nonparametric statistical test was used because the data did not meet the homogeneity of variance assumption for a one-way ANOVA even after log ($x + 1$) transformation. The Mann-Whitney U test was chosen because it is a relatively robust technique for small N ($N < 10$) comparisons. Results are presented as growth rate (milligrams per milligram per degree-day, calculated using a linear growth model as mass change [Δm] divided by pre-treatment mass [m_i] per degree day).

Food quality indices

Food quality indices for each food treatment were determined by measuring percentage protein content using the phenol reagent technique (Lowry et al. 1951), lipid content using chloroform/methanol extraction (Folch et al. 1956), hydrolysis-resistant organic matter (cellulose, lignin) content using ethanol/toluene/ether extraction (Buddington 1980), and ash content. Ash content was determined by ashing a sample of known dry mass at 550°C for 2 h in a muffle furnace and rehydrating the sample at 55°C for 24 h before re-weighing. Samples were taken at the beginning and end of each experiment for all analyses. The unburned CPM treatment was separated into three components for chemical analysis (leaves, twigs, and pine needles). Results are presented as the average percentage mass for each index. Results were similar for samples taken from each experiment and are presented as the average of all samples.

The density of respiring microbes on the surface of each detritus type was determined by CTC (5-cyano-2,3-ditolyl tetrazolium chloride) staining (Rodriguez et al. 1992). Detrital material was stained for 5 min followed by surface counts of fungal and bacterial density (3–5 replicates per detritus type) using direct microscopic epifluorescent enumeration. Fungal and bacterial densities were determined at the beginning, middle, and end of each experiment. Microbe counts are presented as cell density per unit particle surface area. Results were similar between experiments and are presented as the average of all samples. Statistical differences between all food quality indices were determined using a one-way ANOVA (Tukey's honest lsd post-hoc test, $P < 0.01$).

RESULTS

Growth experiments

Experimental results are summarized by the type of trophic niche found (generalist or specialist, herbivore or detritivore). Middle instar *P. heteronea* nymphs were generalist detritivores, growing on several detrital resources (Fig. 1). Of the 11 taxa used in the experiments, only *P. heteronea* exhibited positive growth on the burned FPM and burned CPM treatments. *Paraleptophlebia heteronea* did not use autochthonous periphyton as a resource. *Ameletus cooki* nymphs also
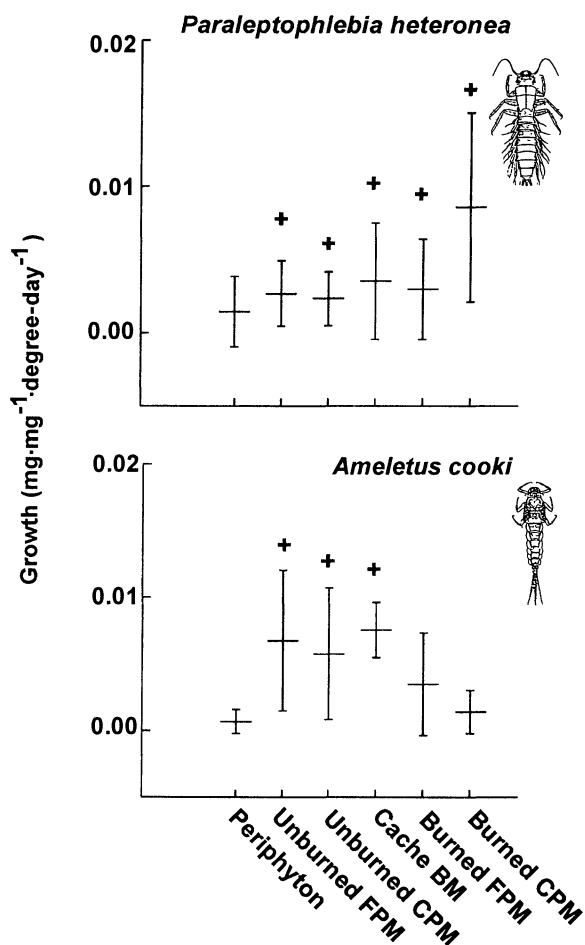
FIG. 1. Growth results for the generalist detritivores *Paraleptophlebia heteronea* and *Ameletus cooki* on each of the experimental treatments. Growth is presented as average mg·mg^{-1}·degree-day^{-1}. Error bars represent ± one standard deviation. + = positive growth (Mann-Whitney U, $P < 0.05$). Drawing of *Paraleptophlebia heteronea* was reprinted from *An Illustrated Guide to the Mountain Stream Insects of Colorado* by J. V. Ward and B. C. Kondratieff (University Press of Colorado, 1992), by permission of the publisher. Drawing of *Ameletus cooki* was reprinted from *The Aquatic Insects of Alberta* by H. F. Clifford (University of Alberta Press, 1991), by permission of the publisher.
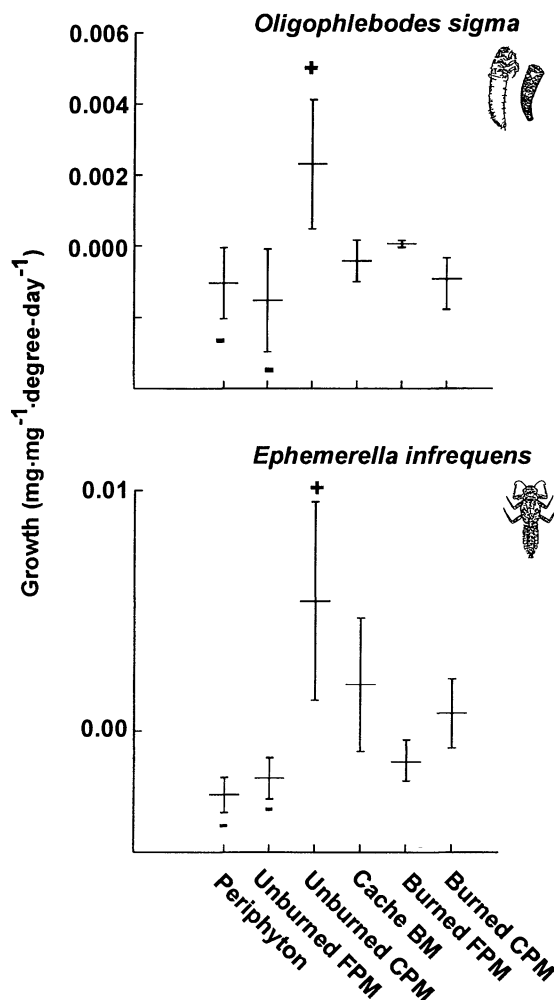

FIG. 2. Growth results for the specialist CPM detritivores *Oligophlebodes sigma* and *Ephemerella infrequens* on each of the experimental treatments. Growth is presented as average mg·mg^{-1}·degree-day^{-1}. Error bars represent ± one standard deviation. + = positive growth (Mann-Whitney U, $P < 0.05$). − = negative growth (loss of mass) (Mann-Whitney U, $P < 0.05$). Drawing of *Oligophlebodes sigma* was reprinted from *Larvae of the North American Caddisfly Genera* by G. B. Wiggins (University of Toronto Press, 1977), by permission of the publisher.

were generalist detritivores, using unburned FPM, unburned CPM, and Cache Creek benthic material as resources for growth (Fig. 1). *Ameletus cooki* did not grow on periphyton or either burned resource (BFPM or BCPM).

The growth results for early instar *Oligophlebodes sigma* larvae and *Ephemerella infrequens* nymphs (Fig. 2) indicate a specialist CPM detritivore niche, growing only on unburned leaf litter (CPM). *Cinygmula mimus* and *Epeorus albertae* middle instar nymphs were periphyton specialists, unable to utilize any of the other five resource treatments for growth (Fig. 3).

Five of the 11 taxa grew on periphyton and at least one detritus resource, exhibiting a generalist herbi-

vore–detritivore niche (Fig. 4). *Baetis bicaudatus* and *Drunella spinifera* nymphs grew only on periphyton and unburned CPM, with no differences in growth between these two resources for either taxon. *Zapada columbiana* showed significant growth on periphyton, unburned CPM, and Cache Creek benthic material with no differences in growth among the three resources. *Drunella doddsi* grew on periphyton and unburned CPM but exhibited higher growth on unburned CPM detritus. *Drunella coloradensis* nymphs grew on both periphyton and unburned CPM, with higher growth on periphyton. *Drunella doddsi* and *D. coloradensis* appear to be adapted for CPM and periphyton utilization,
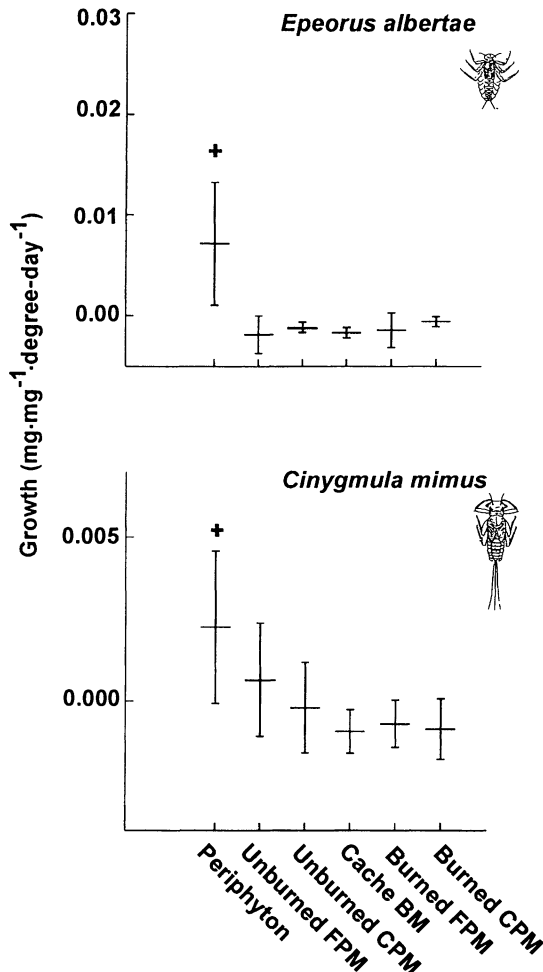
FIG. 3. Growth results for the specialist herbivores *Epeorus albertae* and *Cinygmula mimus* on each of the experimental treatments. Growth is presented as average $mg \cdot mg^{-1} \cdot degree\text{-}day^{-1}$. Error bars represent ± one standard deviation. + = positive growth (Mann-Whitney U, $P < 0.05$). Drawing of *Epeorus albertae* was reprinted from *An Illustrated Guide to the Mountain Stream Insects of Colorado* by J. V. Ward and B. C. Kondratieff (University Press of Colorado, 1992), by permission of the publisher. Drawing of *Cinygmula mimus* was reprinted from *The Aquatic Insects of Alberta* by H. F. Clifford (University of Alberta Press, 1991), by permission of the publisher.

respectively, as indicated by higher growth on these resources.

Only the periphyton food treatment exhibited oxygen production, indicating autotrophic conditions in this food treatment (Table 2). The other five treatments all exhibited net oxygen consumption, indicating heterotrophic conditions (Table 2); this is not surprising given that these treatments were maintained in the dark. Unburned CPM and Cache Creek benthic matter had the highest oxygen consumption rates and were the only treatments other than BCPM that contained any coarse particulate detrital material for microbial colonization. Low oxygen consumption occurred in the unburned

FPM, burned FPM, and burned CPM treatments, probably a result of low microbial densities on these resources. The FPM and BFPM treatments contained large amounts of inorganic sediment, while the BCPM contained large amounts of non-sediment ash. Low microbial densities and, therefore, low respiratory activity would be expected on these food resources, as observed.

The periphyton assemblage in the experimental treatments (21 taxa) was similar to field-collected periphyton in Mink Creek (25 taxa) and Amphitheater Creek, YNP (28 taxa). However, one taxon, *Arthrodesmis* sp., was predominant in the laboratory treatments and not the field samples. The periphyton community in the laboratory assemblage, therefore, was structurally different from field-collected periphyton. The laboratory assemblage, however, remained autotrophic (Table 2), and was functionally similar to periphyton found in natural streams.

Food quality indices

The periphyton and unburned CPM food treatments were higher in protein and lipid content than other resources (Tukey's lsd, $P < 0.01$), suggesting higher food quality (Fig. 5). All three unburned CPM components (leaves, twigs, and needles) had higher cellulose/lignin content (Tukey's lsd, $P < 0.01$), probably making CPM a good resource for detrital microbes that are specialized for the breakdown of these complex polysaccharides (Hofsten and Edberg 1972, Benner and McArthur 1988). Unburned FPM, periphyton, and the three burned treatments were high in ash content (Fig. 5).

Microbial densities were highest on unburned CPM, which was the only food with any fungal colonization, indicating high food quality for detritivores (Fig. 6). Unburned FPM and all three burned treatments had low bacterial densities and no fungal colonization and appeared to be of low food quality (Fig. 6).

DISCUSSION

Based on the growth experiment results, chemical food quality indicators, and microbial densities, unburned CPM appears to be the highest quality allochthonous resource available to lotic primary consumers in post-fire Rocky Mountain streams. Nine of 11 taxa tested were capable of growth on this food resource. None of the other allochthonous food resources appears to be of particularly high quality, with unburned FPM used for growth by two species, Cache Creek benthic material used for growth by three species, and the other two burned food resources used for growth only by one. Periphyton, the only autochthonous resource presented as food in these experiments, also appears to be of high food quality since it was used for growth by 7 of 11 taxa.

Our results suggest that burned material is of little importance as a food resource for primary consumers in post-fire streams. Given the low protein and lipid
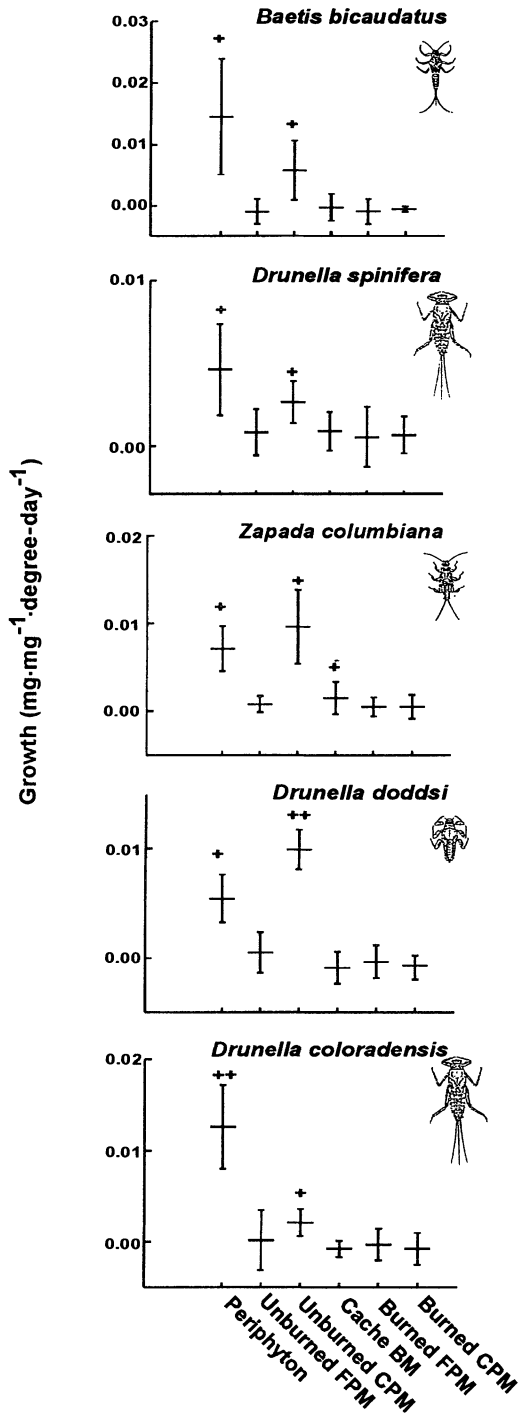
FIG. 4. Growth results for the generalist herbivore–detritivores *Baetis bicaudatus, Drunella doddsi, D. spinifera, D. coloradensis,* and *Zapada columbiana* on each of the experimental treatments. Growth is presented as average mg·mg^{-1}·degree-day^{-1}. Error bars represent ± one standard deviation. + = positive growth (Mann-Whitney U, $P < 0.05$). ++ = higher growth than other positive growth treatments (Mann-Whitney U, $P < 0.05$). Drawings of *Baetis bicaudatus, Drunella doddsi,* and *Zapada columbiana* were reprinted from *An Illustrated Guide to the Mountain Stream Insects of Colorado* by J. V. Ward and B. C. Kondratieff (University Press

TABLE 2. Autotrophy/heterotrophy in each resource treatment. Summary of the oxygen production/consumption measurements. Net oxygen production indicates autotrophic conditions. Net oxygen consumption indicates heterotrophic conditions.

	Net daily oxygen production, consumption (mg·L^{-1}·d^{-1})		Autotrophic or heterotrophic condition
Treatment	Mean	1 SD	
Unburned treatments			
Periphyton	+0.52	0.17	autotrophic
Unburned FPM	−0.15	0.10	heterotrophic
Unburned CPM	−0.58	0.16	heterotrophic
Burned treatments			
Cache Creek BM	−0.59	0.24	heterotrophic
BFPM	−0.17	0.09	heterotrophic
BCPM	−0.18	0.13	heterotrophic

content and high ash content of burned material, it is not surprising that microbial densities were low and that only *P. heteronea* was able to use this resource for growth. *Paraleptophlebia heteronea* prefers gravel/sediment substrate and has a relatively high ingestion rate among aquatic insects (Minckley 1963, Minshall and Minshall 1977, Shepard and Minshall 1984, Smock 1988). This species appears to be adapted to gain nutrition from resources with low organic matter content, such as sediment FPM or, in this case, burned material. Partially burned resources (Cache Creek BM) were used for growth by only three taxa, *A. cooki, P. heteronea,* and *Z. columbiana,* also indicating that most benthic macroinvertebrates are not well suited for utilization of post-fire detrital resources.

The results support the idea that many lotic invertebrates are trophic generalists, capable of using two or more resources for growth. The principal implication of a generalist trophic niche for benthic macroinvertebrates is that food switching may occur when resource availability patterns change, such as may occur in post-fire streams. Food switching has been implicated as important among benthic macroinvertebrates by other investigators (Chapman and Demory 1963, Koslucher and Minshall 1973). Switching can occur within a developmental stage or with ontogenetic shifts between developmental stages. This study provided evidence for switching within a developmental stage, since most experiments covered only one stage of development. Other studies provide possible evidence for ontogenetic shifts (Chapman and Demory 1963, Koslucher and Minshall 1973, Short 1983). The decline in

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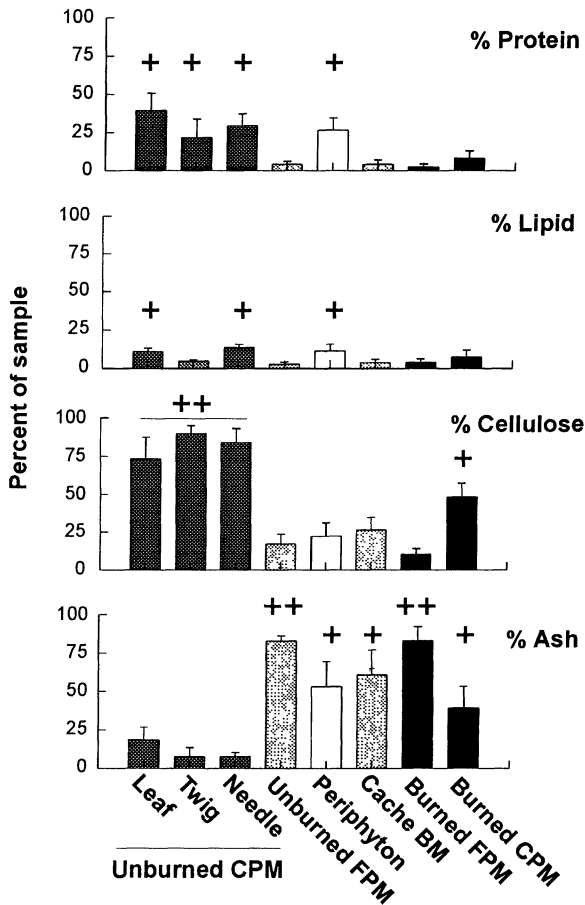
FIG. 5. Chemical food quality indices for each experimental treatment. ++ = higher values than all other treatments (Tukey's lsd, $P < 0.01$). + = higher values than all but ++ treatments (Tukey's lsd, $P < 0.01$).
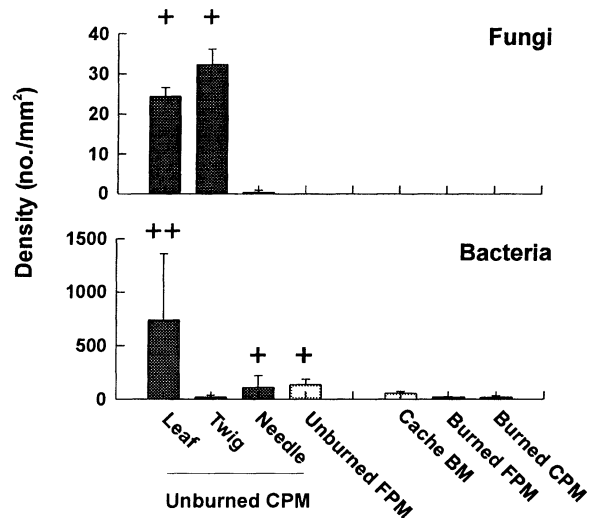

FIG. 6. Densities of fungi and bacteria on the food in each experimental treatment. ++ = higher values than all other treatments (Tukey's lsd, $P < 0.01$). + = higher values than all but ++ treatments (Tukey's lsd, $P < 0.01$).

unburned CPM inputs in a post-fire watershed may result in switching from CPM detritus as a resource to periphyton by some generalist herbivore–detritivores, such as B. bicaudatus, D. doddsi, D. coloradensis, D. spinifera, or Z. columbiana.

Trophic niche and post-fire responses of Cache Creek benthic macroinvertebrates

In terms of trophic ecology, generalist herbivore–detritivores appear best adapted for the changing resource conditions found in post-fire streams, while specialist taxa, particularly CPM detritivores, are not. Two benthic macroinvertebrates, B. bicaudatus and Z. columbiana, were predominant during initial post-fire recovery in Cache Creek. Baetis bicaudatus is the only taxon that increased in abundance and biomass above reference conditions within two seasons of the 1988 Yellowstone fires, while Z. columbiana neither declined nor increased in post-fire streams (Mihuc et al., in press), suggesting that both species are tolerant of the physical conditions and altered resource inputs in post-fire streams. Both species are trophic generalists,

suggesting that generalist resource utilization is favored in post-fire streams.

In terms of habitat preferences, taxa that require stable habitat and/or slow currents declined in abundance and biomass in post-fire streams (Mihuc et al., in press). Therefore, species that require slow flow or stable habitat such as C. mimus, D. coloradensis, D. spinifera, E. infrequens, O. sigma, and P. heteronea would be expected to decline in post-fire streams as a result of habitat instability, regardless of their trophic requirements. Paraleptophlebia heteronea might be expected to thrive in post-fire conditions because of its ability to utilize burned material for growth; however, it has not increased in Yellowstone streams following the 1988 fires. Paraleptophlebia sp. prefer slow currents and stable habitat (Minckley 1963, Minshall and Minshall 1977), and most likely did not increase following the fires because of lack of stable physical habitat or inability to utilize periphyton resources, even though the growth experiment results indicate that it can use burned detrital resources. Decreases in abundance of E. infrequens and O. sigma presumably were related to stable habitat requirements and a CPM specialist trophic niche.

In summary, generalist herbivore–detritivores with a wide range of physical habitat preferences (e.g., B. bicaudatus and Z. columbiana) are well adapted for the conditions found in Yellowstone's post-fire streams. A combination of factors, including trophic relationships and physical habitat preferences, influences the response of each taxon in post-fire streams. Just as each taxon has individual trophic niche requirements, each exhibits individual responses to other aspects of wildfire disturbance.
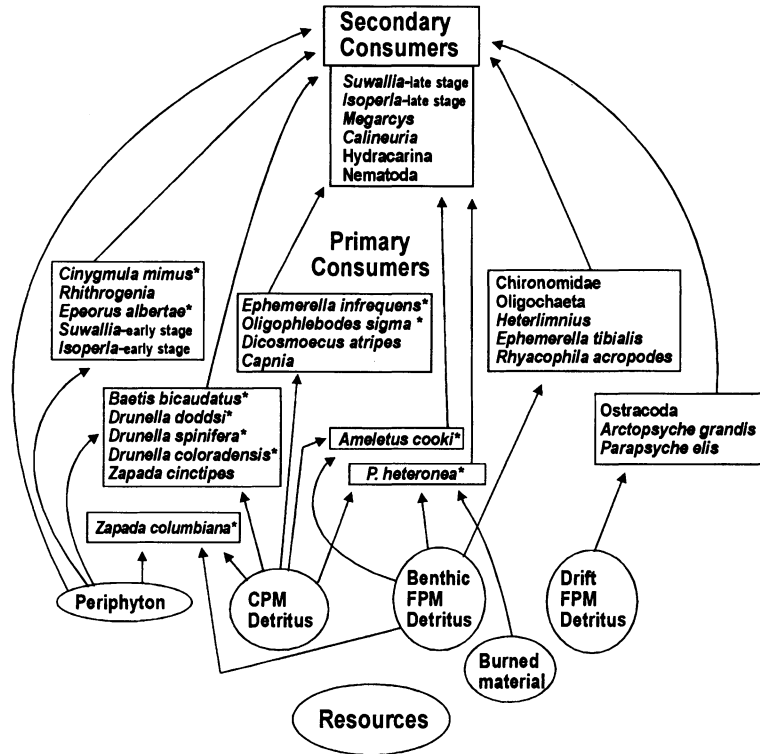
FIG. 7. Food web diagram of Cache Creek, YNP based on the experimental results. * = taxa studied in the growth experiments. *Dicosmoecus atripes* and *Zapada cinctipes* trophic relationships are from Mihuc and Mihuc (*in press*).

Implications for stream food webs

A summary of a generalist food web for Cache Creek based on the results of this study appears in Fig. 7. The food web includes the 29 most abundant taxa found in the Cache Creek basin (Mihuc et al., *in press*). Where specific trophic relationships were not tested, niche relationships were gleaned from the literature (e.g., Mutt-kowski and Smith 1929, Merritt and Cummins 1984). *Dicosmoecus atripes* and *Zapada cinctipes* trophic relationships are from Mihuc and Mihuc (*in press*). Taxa in the generalist food web are grouped into 14 trophic species. A trophic species is an identical set of prey or predators in the food web, including basal, intermediate, and top trophic species (Cohen and Briand 1984). Basal trophic species are the food resources for primary consumers, intermediate species are primary consumers, and top species are secondary consumers in the Cache Creek food web. The use of the term species in this context does not imply a biological species but rather a group of predators or prey with identical link relationships in the web. This study has contributed to the addition of generalist trophic species as intermediates in the food web.

For comparison, a food web for Cache Creek in which functional feeding groups (FFGs) are used as guilds to define trophic species is presented in Fig. 8. In this food web it is assumed that FFGs act as trophic guilds with a primary food resource for each guild so

that shredders utilize CPM detritus, gatherers utilize FPM detritus, scrapers utilize periphyton, and filterers utilize drift FPM (Cummins 1973). The generalist food web has more trophic species, more links, and higher connectance than the food web based on functional feeding groups, mainly because taxa in the generalist web are not restricted to specific trophic relationships by assignment into guilds (Table 3). Connectance is the number of observed links divided by the number of expected links (Paine 1988, Pimm et al. 1991). The generalist food web more closely approximates food web relationships such as the link-species scaling law, which states that the number of links (L) per trophic species (S) is directly proportional, such that there are twice as many links as species: $2(S) = L$, or $S/L = 0.5$ (Briand and Cohen 1984, Pimm et al. 1991). The food web based on functional feeding group structure does not approximate this relationship ($S/L = 1.25$ without fish, 0.85 with fish, Table 3) while the generalist food web does ($S/L = 0.64$ without fish, 0.48 with fish, Table 3).

The increase in the number and types of intermediate trophic species in the generalist web over the FFG web suggests that careful attention should be paid when attempting to lump autecologically similar species into functionally similar groups; in this case placing benthic macroinvertebrates with similar mouthpart morphology (FFG) into trophic guilds. Although some autecologi-
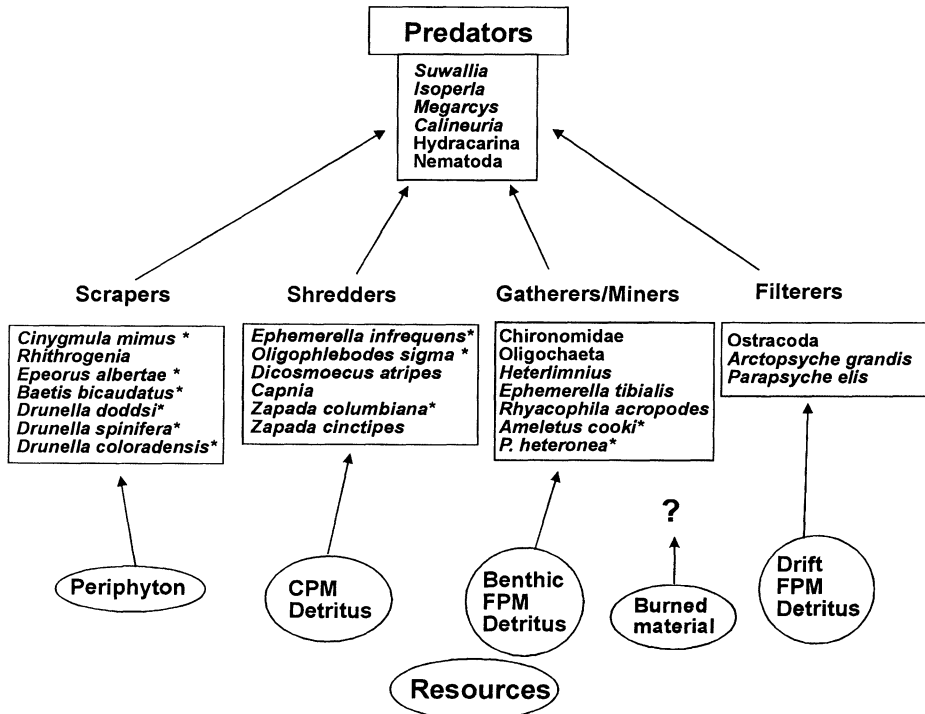
FIG. 8. Food web diagram of Cache Creek, YNP using functional feeding groups as trophic species. * = taxa studied in the growth experiments.

cally similar species probably do exhibit similar functional roles in the community (Harris 1995) the individualistic nature of the species (the fact that each species has a different evolutionary and ecological history) should be considered. Furthermore, similar functional roles for a given parameter may not occur for two autecologically similar species at all points in space and time; for example some generalists may function primarily as detritivores while others function as herbivores at a given point in space or time. Summarizing complex species-associations into oversimplified functional compartments may inhibit progress in our understanding of ecological systems rather than foster it.

An important area of food web research concerns accurate determination of trophic links (Cohen and Briand 1984, Schoener 1989, Warren 1989, Martinez 1993, Closs and Lake 1994). Food web theory is based on published data from many sources, assuming that each investigator has quantified the links in the web accu-

rately and in the same manner. Often trophic relationships are determined based only on what a taxon ingests or by lumping taxa into trophic guilds (Rosenfeld and Mackay 1987, Warren 1989, Martinez 1993). A more accurate approach is to determine resource assimilability for each consumer, with food web links established only for ingested resources that can be assimilated into tissue (sensu Fig. 7). The need for resource food quality data as well as accurate food habits in constructing food webs cannot be overstated, including the need for information about changes in food habits and/or food quality among individual taxa (Pimm and Rice 1987).

Conclusions

The species-specific trophic ecology found for Cache Creek benthic macroinvertebrates supports the view that ecological studies in streams should be based at the species level. The need for complete autecological

TABLE 3. Comparison of the number of trophic "species," links, and connectance between the generalist food web and the food web based on functional feeding groups (FFG web).

Food web	No. trophic species (S)	No. observed links (L)	S/L	No. expected links S(S − 1)/2	Connectance L/[S(S − 1)/2]
Generalist web	14	22	0.64	91	0.242
Generalist web; fish included	15	31	0.48	105	0.295
FFG web	10	8	1.25	45	0.177
FFG web; fish included	11	13	0.85	55	0.236

information is important in heterogeneous systems such as streams where patchiness and patch structure are extremely complex and large-scale generalizations such as ecosystem or landscape patterns are difficult to determine (Townsend 1989, Kotliar and Weins 1990). Much more information about the autecology of species in benthic communities is needed before our understanding of habitat, resource, and time partitioning patterns in streams can become concrete (Ladle 1990), and reliable predictions or interpretations about responses to disturbance such as wildfire will be possible.

Trophic generalists are an important group in postfire streams and are probably important in disturbed streams in general. Because many primary consumers function as generalists, they can exhibit shifts in resource utilization in space and time. Seasonal patterns in food habits have been documented for many benthic consumers, demonstrating seasonal food switching (Chapman and Demory 1963, Koslucher and Minshall 1973, Short 1983). Little information exists about spatial patterns in resource utilization in lotic systems except for patterns based on trophic guilds (Vannote et al. 1980). The prevalence of generalist trophic function among benthic macroinvertebrates suggests that the use of FFGs as trophic guilds may not be appropriate. Functional feeding groups, therefore, should be used with caution to infer systems-level trophic dynamics in streams (e.g., system autotrophy or heterotrophy derived from scraper or shredder abundance or biomass). More information about the role of generalists in stream food webs is needed, including spatial and temporal patterns in resource utilization within and among life stages for lotic consumers, before further generalizations at the systems level can emerge.

LITERATURE CITED

Benner, R., and J. V. McArthur. 1988. Effects of temperature on microbial utilization of lignocellulose detritus in a thermally impacted stream. Microbial Ecology 16:323–330.

Briand, F., and J. E. Cohen. 1984. Community food webs have scale invariant structure. Nature 307:264–267.

Buddington, R. K. 1980. Hydrolysis-resistant organic matter as a reference for measurement of fish digestive efficiency. Transactions of the American Fisheries Society 109:653–655.

Chapman, D. W., and R. L. Demory. 1963. Seasonal changes in the food ingested by aquatic insect larvae and nymphs in two Oregon streams. Ecology 44:140–146.

Christensen, N. L., J. K. Agee, P. F. Brussard, J. Hughes, D. H. Knight, G. W. Minshall, J. M. Peek, S. J. Pyne, F. J. Swanson, J. W. Thomas, S. Wells, S. E. Williams, and H. E. Wright.. 1989. Interpreting the Yellowstone fires of 1988. BioScience 39:678–685.

Clifford, H. F. 1991. The aquatic insects of Alberta. University of Alberta Press, Edmonton, Alberta, Canada.

Closs, G. P., and P. S. Lake. 1994. Spatial and temporal variation in the structure of an intermittent-stream food web. Ecological Monographs 64:1–21.

Cohen, J. E., and F. Briand. 1984. Trophic links of community food webs. Proceedings of the National Academy of Sciences (USA) 81:4105–4109.

Cummins, K. W. 1973. Trophic relations of aquatic insects. Annual Review of Entomology 18:183–206.

Folch, J., M. Lees, and H. Sloane Stanley. 1956. A simple method for the isolation and purification of total lipids from animal tissues. Journal of Biological Chemistry 226:497–509.

Forbes, S. A. 1893. Aquatic invertebrate fauna of the Yellowstone National Park, Wyoming, and of the Flathead region of Montana. Bulletin of the United States Fish Commission for 1891:207–258.

Harris, P. M. 1995. Are autecologically similar species also functionally similar? A test in pond communities. Ecology 76:544–552.

Hofsten, B. V., and N. Edberg. 1972. Estimating the rate of degradation of cellulose fibers in water. Oikos 23:29–34.

Koslucher, D. G., and G. W. Minshall. 1973. Food habits of some benthic invertebrates in a northern cool-desert stream (Deep Creek, Curlew Valley, Idaho-Utah). Transactions of the American Microscopy Society 92:441–452.

Kotliar, N. B., and J. A. Weins. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59:253–260.

Ladle, M. 1990. Long-term investigations of trophic relationships in southern chalk streams. Freshwater Biology 23:113–117.

Lowry, O. H., N. J. Rosebrough, A. L. Farr, and R. J. Randall. 1951. Protein measurement with the folin phenol reagent. Journal of Biological Chemistry 193:265–275.

Mackay, R. J. 1981. A miniature laboratory stream powered by air bubbles. Hydrobiologia 83:383–385.

Martinez, N. D. 1993. Effects of resolution on food web structure. Oikos 66:403–412.

Mecom, J. O., and K. W. Cummins. 1964. A preliminary study of the trophic relationships of the larvae of *Brachycentrus americanus* (Banks) (Trichoptera: Brachycentridae). Transactions of the American Microscopy Society 83:233–243.

Merritt, R. W., and K. W. Cummins. 1984. An introduction to the aquatic insects of North America. Kendall/Hunt, Dubuque, Iowa, USA.

Mihuc, T. B., and J. R. Mihuc. *In press.* Trophic ecology of five shredders in a Rocky Mountain stream. Journal of Freshwater Ecology.

Mihuc, T. B., G. W. Minshall, and C. T. Robinson. *In press.* Responses of benthic macroinvertebrate populations in Cache Creek, Yellowstone National Park to the 1988 wildfires. *In* J.Greenlee, editor. Ecological implications of fire in the Greater Yellowstone. Proceedings of the Second Bi-

ennial Scientific Conference on the Greater Yellowstone Ecosystem, September 20–21, 1993. International Association of Wildland Fire, Fairfield, Washington, USA.

Minckley, W. L. 1963. The ecology of a spring stream, Doe Run, Meade County, Kentucky. Wildlife Monographs 55: 4–123.

Minshall, G. W. 1988. Stream ecosystem theory: a global perspective. Journal of the North American Benthological Society 7:263–288.

Minshall, G. W., J. T. Brock, and J. D. Varley. 1989. Wildfires and Yellowstone's stream ecosystems. BioScience 39:707–715.

Minshall, G. W., and J. N. Minshall. 1977. Microdistribution of benthic invertebrates in a Rocky Mountain (U.S.A.) stream. Hydrobiologia 55:231–249.

Muttkowski, R. A., and G. M. Smith. 1929. The food of trout stream insects in Yellowstone National Park. Roosevelt Wild Life Annals 2:241–263.

Paine, R. T. 1988. Food webs: road maps of interactions or grist for theoretical development. Ecology 69:1648–1654.

Palmer, C., J. O'Keefe, A. Palmer, T. Dunne, and S. Radloff. 1993. Macroinvertebrate functional feeding groups in the middle and lower reaches of the Buffalo River, eastern Cape, South Africa. I. Dietary variability. Freshwater Biology 29:441–453.

Pimm, S. L., J. H. Lawton, and J. E. Cohen. 1991. Food web patterns and their consequences. Nature 350:669–674.

Pimm, S. L., and J. C. Rice. 1987. The dynamics of multispecies, multi-life-stage models of aquatic food webs. Theoretical Population Biology 32:303–325.

Rabeni, C. F., and G. W. Minshall. 1977. Factors affecting microdistribution of stream benthic insects. Oikos 29:33–43.

Rodriguez, G. G., D. Phipps, K. Ishiguro, and H. F. Ridgway. 1992. Use of a fluorescent redox probe for direct visualization of actively respiring bacteria. Applied and Environmental Microbiology 58:1801–1808.

Rosenfeld, J. S., and R. J. Mackay. 1987. Assessing the food base of stream ecosystems: alternatives to the P/R ratio. Oikos 50:141–147.

Schoener, T. W. 1989. Food webs from small to large. Ecology 70:1559–1589.

Shepard, R. B., and G. W. Minshall. 1984. Role of benthic feces in a Rocky Mountain stream: fecal production and support of consumer growth. Holarctic Ecology 7:119–127.

Short, R. A. 1983. Trophic ecology of three winter stoneflies (Plecoptera). American Midland Naturalist 105:341–347.

Smock, L. A. 1988. Life histories, abundance and distribution of some macroinvertebrates from a South Carolina, USA coastal plain stream. Hydrobiologia 157:193–208.

Spencer, C. N., and F. R. Hauer. 1991. Phosphorus and nitrogen dynamics in stream during a wildfire. Journal of the North American Benthological Society 10:24–30.

Townsend, C. R. 1989. The patch dynamics concept of stream community ecology. Journal of the North American Benthological Society 8:36–50.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130–137.

Vannote, R. L., and B. W. Sweeney. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. American Naturalist 115:667–695.

Ward, J. V., and B. C. Kondratieff. 1992. An illustrated guide to the insects of Colorado. University of Colorado Press, Boulder, Colorado, USA.

Warren, P. H. 1989. Spatial and temporal variation in the structure of a freshwater food web. Oikos 55:299–311.

Wells, C. G., R. E. Campbell, L. F. DeBano, C. E. Lewis, R. L. Fredriksen, E. C. Franklin, R. C. Froelich, P. H. Dunn. 1979. Effects of fire on soil. U.S. Forest Service General Technical Report WO-7.

Wiggins, G. B. 1977. Larvae of the North American caddisfly genera. University of Toronto Press, Toronto, Canada.