Food Habits and Dietary Overlap Among Six Stream Collector Species[1]

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Abstract. Food habits were determined monthly over one year for six species of invertebrate collectors in a Colorado trout stream. Detritus formed the bulk of the diet for each species with an algal contribution that was usually $< 10\%$. The vast majority of particles in the foreguts were $< 75\ \mu m$ in size and coincided with the most abundant size class of detritus in the stream. Dietary overlap as measured with Horn's Coefficient of Dietary Overlap was usually > 0.90 for type of food (algae vs. detritus) and particle size. This would indicate that no significant partitioning of food resources occurred among these six species of stream collectors.

Along with space, food is probably the most important resource which influences the distribution and abundance of an animal. Thus, the study of food habits has long comprised an important aspect of stream macroinvertebrate ecology (e.g., Muttkowski & Smith 1929; Hynes 1941; Jones 1950; Chapman & Demory 1963; Richardson & Gaufin 1971; Gray & Ward 1979). These and other studies have provided a great deal of information on stream macroinvertebrate trophic relations and the factors which influence them (see Cummins 1973). However, comparatively little attention has been paid to how food resources are partitioned or shared by stream macroinvertebrates with similar resource requirements. Resource division has been examined in carnivorous stoneflies (Sheldon 1979; Fuller & Stewart 1977) and net-spinning caddisflies (Wallace 1975; Rhame & Stewart 1976). The objectives of the present study are to examine the food habits of the predominant collector-gatherers in a Colorado mountain stream and to determine the degree of dietary overlap among the species.

STUDY AREA

Little Beaver Creek, a tributary of the Cache la Poudre River, is located in north central Colorado in the South Platte River drainage system. It is a third-order stream with a watershed area of 4600 ha. The study site is located in the upper montane zone at an elevation of 2410 m. Here the stream emerges from a narrow valley and is heavily canopied with willows (*Salix* spp.) and alders (*Alnus tenuifolia* Nutt.). Quaking aspen (*Populus tremuloides* Michx.) and ponderosa pine (*Pinus ponderosa* Laws.) are the dominant tree species on the slopes surrounding the stream. Stream width varies from 2 to 10 m and the gradient averages 8%. Substrate consists mainly of rubble in riffles with few pools present. The stream was completely ice-covered (up to 30 cm thick) from mid-November through late March. Maximum water temperatures (12° C) were recorded during July and August while water temperatures of 0° C occured seven months of the year (October - April).

METHODS AND MATERIALS

Food habits of the major collector-gatherers were determined using organisms from benthic samples collected monthly from August through July with a Surber sampler equipped with 243 μm mesh. Several specimens of each species of the same size class (based on head capsule widths) were used in the food habits analysis based on Cummins'

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(1973) method. The entire guts of 3-5 organisms were dissected out and the contents of the foreguts teased onto a depression slide. Material on the slide was dispersed into a beaker containing 25 ml of distilled water and then collected on a 0.45 μm Millipore filter. The filter was then placed onto a microscope slide. One drop of immersion oil was added to the filter which was allowed to clear for 24 h. After clearing, a drop of Permount was added and a cover slip was placed over the filter. The slide was scanned at 400× to identify food items as either detritus or algae. If the food item was somewhat rectangular in shape then the maximum length and minimum width were determined using a Whipple grid. If the item was circular then the diameter was recorded. A total of 200 items or the number present in ten random fields per slide was used in order to insure statistically significant results (Gray & Ward 1979). Dietary overlap was calculated using the method of Horn (1966):

$$C = \frac{2 \sum^{s} X_i Y_i}{\sum^{s} X^2_i + \sum^{s} Y_i^2}$$

Where: C = overlap coefficient; s = food categories; X_i = that proportion of total diet of species X from a given category of food i. Y_i = that proportion of total diet of species Y from a given category of food i. The value of C ranges from 0 (no food categories in common) to 1 (when all food categories are used identically). A value of $C > 0.60$ has been used to indicate biologically significant overlap (Fuller & Stewart 1977; Wallace 1981). The use of the index C as a measure of diet-overlap has been criticized by Hurlbert (1978) because the availability of the food resource is not taken into consideration. This can be of importance when a food category is used by one species but not by other species. Since all food categories were used by all species in the present study, and because of the widespread use of Horn's Index in other studies, it is used in the present analysis of dietary-overlap.

SPECIES STUDIED

Baetis tricaudatus (Dodds) (Ephemeroptera: Baetidae) was among the most abundant macroinvertebrates in Little Beaver Creek. This species is found throughout western North America (Edmunds, Jensen & Berner 1976). Nymphs of *B. tricaudatus were* collected in Little Beaver Creek each month except May. Growth was uneven through the fall and winter but extremely rapid from April to July. The largest standing crop of *B. tricaudatus* was 90 mg/m^2 (dry weight) which occurred in April.

Rhithrogena hageni (Eaton) (Ephemeroptera: Heptageniidae) is a heptageniid mayfly commonly found in Rocky Mountain streams. The nymphs are especially adapted for living in areas of fast current as the gills are modified to form a holdfast structure. Nymphs are therefore found tightly pressed against rocks indicating the nymphs may utilize epilithic organic material as a food source. Adult emergence was observed in July in Little Beaver Creek. Small nymphs were collected in June, however, indicating a long period of emergence. Nymphs grew throughout the winter but the most rapid growth was in the period April through July. Standing crop ranged from zero in May (probably an artifact of the effect of high water on sampling efficiency) to 235 mg/m^2 in October. *R. hageni* was the most abundant macroinvertebrate in the stream in terms of annual mean biomass.

Ephemerella infrequens McDunnough (Ephemeroptera: Ephemerellidae) is a mayfly which occurs throughout western North America (Edmunds et al. 1976). Adults were collected at Little Beaver Creek during June and July; small nymphs appeared in July. Growth occurred through the winter. The highest standing crop was 33 mg/m^2 in January.

Ephemerella grandis Eaton (Ephemeroptera: Ephemerellidae) is another mayfly which is found throughout western North America (Edmunds et al. 1976). Adults were collected near Little Beaver Creek in July and small nymphs appeared in July as well. Nymphs grew throughout the fall and winter. Standing crop reached a maximum of 68 mg/m^2 in October.

Heterlimnius corpulentus LeConte (Coleoptera: Elmidae) is often the only elmid beetle found in high elevation Rocky Mountain streams (Brown & White 1978). Elmid beetles have been reported to feed on algae, fine detritus, leaf litter, and to gouge wood debris (Merritt & Cummins 1978). Larvae of *H. corpulentus* (adults were not used due to very low densities) are considered to be collectors because feeding trials in the laboratory demonstrated that they had little impact on leaf weight loss. The highest standing crop of *H. corpulentus* was 24 mg/m^2 in April.

Zaitzevia parvula Horn (Coleoptera: Elmidae) is another elmid beetle which was very abundant in Little Beaver Creek. *Z. parvula* larvae were most prevalent in January, with a standing crop of 40 mg/m^2.

RESULTS AND DISCUSSION

Collectors in Little Beaver Creek consumed mainly detritus (Fig. 1). Detritus comprised 88-100% of the gut contents of *Baetis tricaudatus*. This detrital contribution is

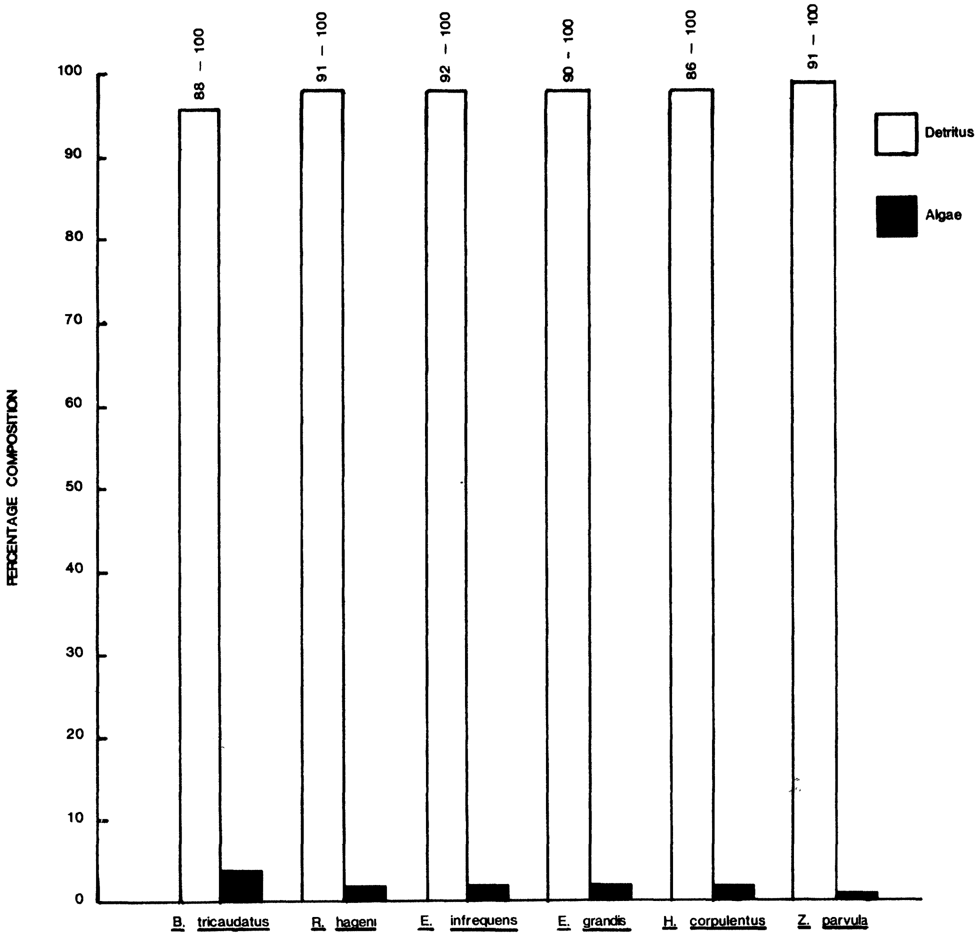

Fig. 1. Food habits of six collector species in Little Beaver Creek, Colorado. Vertical bars represent annual means, the numbers indicate the range of monthly values for detritus. Complement is the percent contributed by algae.

greater than that reported for *B. tricaudatus* in other studies. Gilpin and Brusven (1970) found that nymphs of *B. tricaudatus* fed on 45% algae and 52% detritus in the St. Maries River in Idaho. Gray and Ward (1979) determined overall detritus accounted for 84% of the gut contents of *B. tricaudatus* in Piceance Creek, Colorado, although smaller nymphs were utilizing detritus to a greater degree. Koslucher and Minshall (1973) found a greater contribution by algae in the food of *B. tricaudatus* in a cool-desert in Idaho. Results obatined in the present study are more similar to those for midwestern streams where *Baetis* spp. consumed primarily detritus (Shapas & Hilsenhoff 1976).

Rhithrogena hageni nymphs also were found to feed mainly on detritus (Fig. 1), with gut contents containing from 91-100% detritus. Due to its preference for coarse substrates, especially the sides of boulders (Linduska 1943), it was anticipated that *R. hageni* would ingest larger amounts of diatoms. Gilpin and Brusven (1970) found that the food of *R. hageni* consisted of 55% detritus, indicating a greater use of algae than in the present study. However, Jones (1950) and Shapas and Hilsenhoff (1976) also found that *Rhithrogena* spp. consumed mainly detritus.

Ephemerella infrequens nymphs also apparently subsisted largely on detritus (Fig. 1). Detritus comprised 92-100% of the gut contents. *E. infrequens* and *E. inermis* (a closely related species which could not be distinguished from *E. infrequens*) nymphs in the St. Maries River of Idaho also consumed detritus more than algae (Gilpin & Brusven 1970), but not to the extent as in the present study. Gray and Ward (1979) determined that *E. inermis* gut contents consisted of 98% detritus and 2% algae.

Not surprisingly, *Ephemerella grandis* gut contents (Fig. 1) were composed mostly of detritus (90-100%). The study of Gilpin and Brusven (1970) indicates greater consumption of algae by this species (43%). It has been reported that significant amounts of animal matter may be found in the guts of *Ephemerella* nymphs (Gilpin & Brusven 1970; Shapas & Hilsenhoff 1976). This was not found in the *Ephemerella* examined in the present study nor in *Ephemerella doddsi* nymphs (Short, unpubl. data).

Larvae of the elmid beetles *Heterlimnius corpulentus* and *Zaitzevia parvula* also utilized detritus as a food source to a large extent (Fig. 1) Gut contents of *H. corpulentus* were composed of 86-100% detritus. *Z. parvula* varied from 91-100% detritus. Elmid larvae in two Oregon streams utilized 90-100% algae as food (Chapman & Demory 1963) while elmids in two Virginia streams fed primarily on detritus (Seagle 1982).

A major factor which affects food habits is availability (but see Gray & Ward 1979). Chapman and Demory (1963) related changes in food habits of stream insects to seasonal changes in food availability. Although algal standing crops in Little Beaver Creek were not measured, rock scrapings taken at irregular intervals consisted largely of detritus and yielded few diatoms. Neither filamentous algae nor macrophytes were evident in the stream except for very small growths of the moss *Fontinalis* sp. The analysis of macroinvertebrate food habits shown in Figure 1 may reflect the paucity of algae and overwhelming dominance of detritus.

Another facet of food availability besides food type (i.e., detritus vs. algae) is particle size. Some filter-feeding collectors apparently selectively filter particles from the water column at least partially on the basis of particle size (Wallace 1975). Particle size selection had been demonstrated for deposit-feeding marine macroinvertebrates (Fenchel, Kofoed & Lappalainen 1975) and for oligochaetes in the benthos of lakes (Brinkhurst, Chua & Kaushik 1972), but not for deposit-feeding macroinvertebrates in streams. The mean particle sizes found in the foreguts of the various collector species in the present study are shown in Figure 2. There are no clear seasonal trends for any species and no significant differences between species. All collector species in Little Beaver Creek feed predominately on detrital particles less than 75 μm in size. This is consistent with the

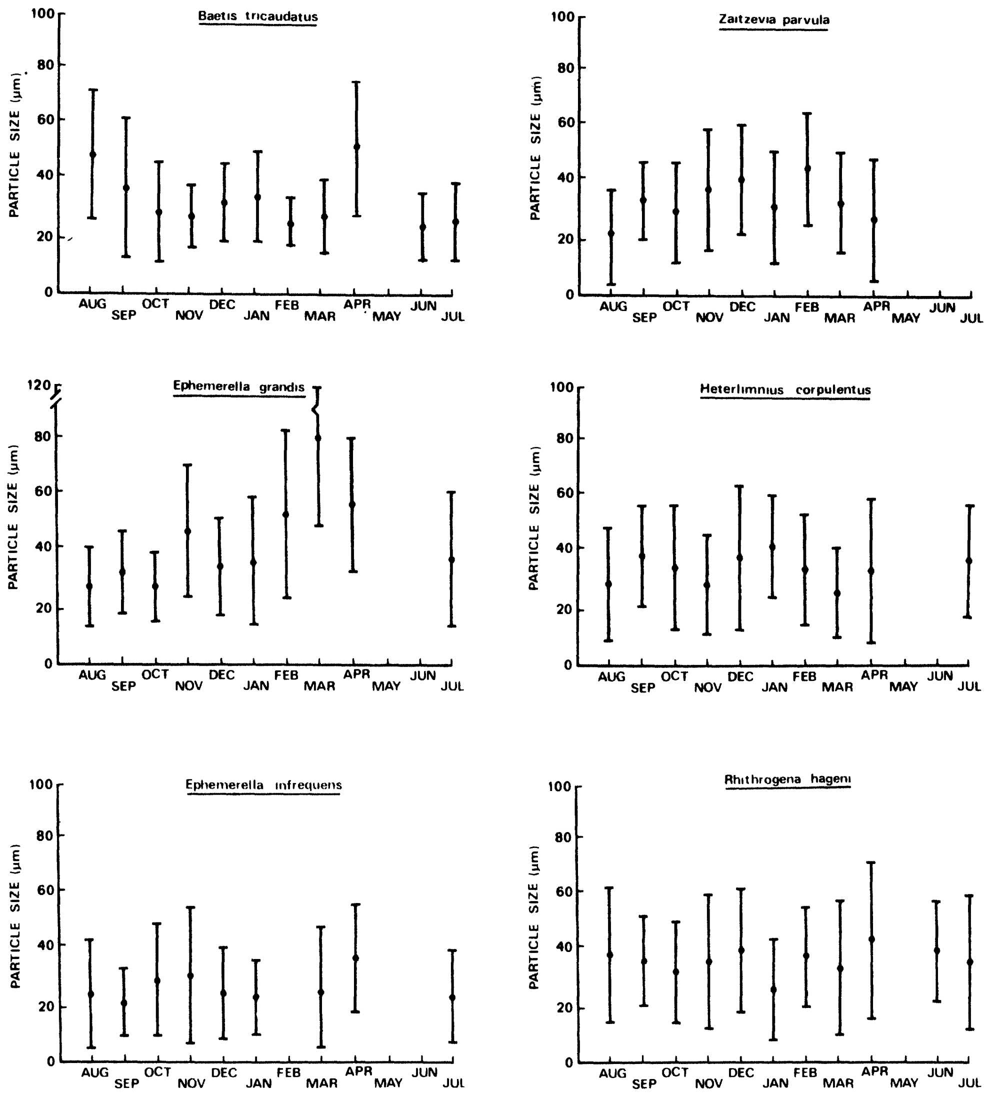

Fig. 2. Particle sizes in the foreguts of six collector species. Values are means ± standard deviations.

particle size distribution of detritus which is also dominated by the fine particulate organic matter (FPOM) fraction (Short & Ward 1981). Thus, deposit-feeding collectors in Little Beaver Creek are feeding on the resource which is most available to them, FPOM. That the collectors were able to ingest such small particles is not surprising. Brown (1961) found that mayfly nymphs fed on Chlorococcales cells less than 20 μm in diameter. Also, it has been reported that some filter-feeding Simuliidae were able to ingest particles less than 1 μm in length (Wotton 1977). Recently, Clifford, Hamilton and Killins (1979) reported that *Leptophlebia cupida* (Ephemeroptera) ingest particles 25-55 μm in size.

To determine the degree of dietary overlap with respect to particle size, ten categories of particle size classes were considered (Table 1). The contribution of each size class to the total number of particles was determined for each species for the entire study period since no significant monthly differences were detected (Fig. 2). All pair-wise Coefficients of Dietary Overlap (C) values were greater than 0.79, indicating biologically significant

TABLE 1

Size class analysis of particles in the foreguts. Values given are the fraction of the total number of particles in each particle size class.

Species	Particle size (μm)									
	0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	90+
Baetis tricaudatus	.16	.19	.30	.10	.10	.12	.01	.01	.01	0
Rhithrogena hageni	.18	.18	.29	.06	.07	.09	.03	.03	.03	.06
Ephemerella grandis	.06	.20	.32	.05	.05	.15	.05	.03	.07	.01
Ephemerella infrequens	.23	.24	.28	.10	.03	.03	.02	.01	.01	.03
Heterlimnius corpulentus	.15	.22	.26	.07	.10	.03	.04	.07	.05	.01
Zaitzevia parvula	.21	.14	.22	.16	.14	.04	.05	.02	.01	.01

overlap among all six species of collectors (Table 2). Values of C for food type (algae and detritus) were greater than 0.95 for all pair-wise combinations. Thus, it appears that no significant partitioning of food resources occurred between the six major collector species in Little Beaver Creek.

How closely related species of stream insects partition resources, or if they even do partition resources, has not been studied thoroughly. Most of the work has been with the net-spinning Trichoptera where partitioning of food resources by different capture net mesh sizes has been demonstrated (Wallace 1975; Malas & Wallace 1977). However, the vast majority of stream insects do not spin nets and in Little Beaver Creek most collectors are deposit-feeders. In one of the few studies on the subject, Grant and MacKay (1969) suggest that temporal separation occurs among many systematically related stream insects so that different stages in the life cycle are present at any one time. They further suggest that this staggering of the life histories might allow ecological segregation through feeding on different sized food particles. Allan (1975) also suggests that differences in body size would allow coexistance to occur, presumably through some means of food resource partitioning. Thus, several questions arise:

1. Do deposit-feeding stream insects select food items on the basis of size? If so, is body size related to food particle size?

2. If food items are selected on the basis of size, does this selection lead to a partitioning of resources amony the deposit-feeding collector guild?

Data collected in the present study indicate that there is no selection for food size. All of the collector species fed mainly on fine detritus less than 75 μm in size. Furthermore, there were no apparent differences in particle sizes ingested throughout the life cycles for any species. There was no significant correlation between particle size ingested and body size (measured as head capsule width) for any of the collector species. This analysis assumes of course that particles are ingested intact and no size reduction occurs as a result of the feeding process (Cummins 1973). The lack of a significant correlation between particle size and body size would tend to support this assumption since if particle size reduction did occur, as the feeding structures grow, larger particles would be expected in the gut. Thus, it appears that the deposit-feeding collectors are sharing a common food resource, the FPOM pool in the stream sediments. No apparent food resource partitioning is occurring, either through food type or particle size. FPOM forms the largest detrital component in the stream so the collectors are utilizing the most available food resource. Therefore, it may be that food quantity is not a limiting factor for stream insects and thus competition for food would not be occurring. Competition between mountain stream insects has not been convincingly documented. This may be due to the harsh physical conditons which are prevalent in mountain stream ecosystems. Such harsh conditions force the biota to adapt to the physical environment and do not allow the development of intense biotic interactions such as competition.

TABLE 11

Coefficients of Dietary Overlap based on particle size for collector species in Little Beaver Creek.

	Baetis tricaudatus	*Rhithrogena hageni*	*Ephemerella grandis*	*Ephemerella infrequens*	*Heterlimnius corpulentus*
Zaitzevia parvula	0.93	0.92	0.79	0.92	0.92
Heterlimnius corpulentus	0.95	0.96	0.85	0.95	
Ephemerella infrequens	0.94	0.96	0.85		
Ephemerella grandis	0.94	0.93			
Rhithrogena hageni	0.98				

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