Resource utilization, overlap and temporal dynamics in a guild of mountain stream insects

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SUMMARY. 1. Resource utilization was quantified for six mayfly (Ephemeroptera) and one caddis (Trichoptera) species comprising a lotic scraper/collector-gatherer guild across three niche dimensions (temporal, trophic and spatial). Based on trophic differences and inferred microspatial utilization, the members of this guild separated into two groups: (1) cryptic detritivores and (2) exposed algivores.

2. Each species demonstrated a slow seasonal univoltine life cycle except for *Epeorus longimanus* (Eaton) and *Baetis tricaudatus* (Dodds) which were fast seasonal univoltine and multivoltine, respectively.

3. Temporal sequencing of periods of peak resource utilization were not demonstrated by the members of this guild. A null analysis indicated that periods of peak resource utilization were aggregated.

Introduction

Comparatively few studies of lotic macro-invertebrates provide data on patterns of resource utilization along more than one resource dimension (Cummins, 1964; Grant & Mackay, 1969; Hildrew & Edington, 1979; Sheldon, 1972). Most investigations have examined interactions between pairs of potentially competing, often congeneric, species (Hart, 1983). However, there is no compelling reason to limit the possibility of resource partitioning to just two or three species utilizing a single resource along one niche dimension. Spatial and temporal patterns of species coexistence may depend upon a tendency for each species to specialize in resource use, thereby reducing or eliminating the negative affects of interspecific competition (MacArthur & Levins, 1967; May & MacArthur, 1972). It is now accepted that observed ecological patterns

should be evaluated against appropriate null models before deriving any inference from them (e.g. Grant & Schluter, 1984). Vannote & Sweeney (1980) hypothesized that as a result of interspecific competition, periods of peak resource utilization by species within a given stream functional group will follow a seasonal sequence. This hypothesis is one of the tenets of the River Continuum Concept (Vannote *et al.*, 1980) and is consistent with the view that community development is a process of assembling numerous species into discrete functional groups, thus leading to efficient annual use of stream resources through temporal specialization (Vannote & Sweeney, 1980). This temporal pattern has been observed within guilds of filter-feeding, shredding and grazing caddisflies and shredding stoneflies (Cather & Gaufin, 1976; Oswood, 1976; Vannote & Sweeney, 1980). Only two studies, however, have compared this pattern against appropriate null models. Georgian & Wallace (1983) found that within a scraper guild, the peak periods of resource utilization

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were more regularly spaced than would be expected by chance alone. In contrast, Tokeshi (1986) found that the mean overlap in temporal resource utilization for nine species of epiphytic chironomid larvae was significantly larger than expected from a null model analysis.

The purpose of this study was to quantify resource utilization along three niche dimensions (temporal, trophic and spatial) among the members of a scraper/collector-gatherer guild (*sensu* Jaksic, 1981) in a Rocky Mountain stream. The temporal pattern of resource utilization was determined using a null model analysis.

Methods and Site Description

Two study sites (above and below a proposed reservoir) were located in the upper montane zone at altitudes of 2556 and 2281 m a.s.l. on a fourth order reach of the Cache la Poudre River in northern Colorado. The canopy was open and the riparian vegetation consisted primarily of willows (*Salix* spp.) and some alders (*Alnus tenuifolia* Nutt.). Ponderosa pine (*Pinus ponderosa* Laws) and some quaking aspen (*Populus tremuloides* Michx.) were the dominant tree species on the slopes surrounding the stream. The stream at both sites was ice covered for about 4 months, remained near 0°C for 6 months, and attained an annual

maximum of 20°C. Other physico-chemical conditions were similar at the two sites (soft water, circumneutral pH, high gradient, well-oxygenated).

Sampling was confined to rubble riffles, the predominant substrata. Three (November–January) or four (March–October) sample units were taken with a Surber sampler (0.09 m² area; 240 μ m mesh) at each site each month (except February) for 1 year. Sample units from both sites (six to eight replicates) were used to determine species population densities. Using samples from both sites to determine population densities was justified given the physico-chemical similarities between sites. Also, a community similarity index (Whittaker, 1975), an expression of the degree to which two sites are alike based on the relative abundances of species, indicated a 76% similarity between sites for the total macroinvertebrate fauna and a 93% similarity for members of the guild. In addition, nymphal growth rates and adult emergence patterns were similar at both sites. Immatures were sorted and preserved in 5% formalin.

Four mayfly species (*Rithrogena hageni* Eaton; *Epeorus longimanus* Eaton; *Baetis tricaudatus* Dodds; and *Drunella grandis* Eaton) have been classified as scrapers/collector-gatherers (Merritt & Cummins, 1984), whereas *Drunella doddsi* (Needham) and the caddisfly *Glossosoma* sp. have been designated scrapers. A sixth mayfly, *Ephemerella infrequens*

TABLE 1. The size range (head width in mm), date collected and numbers of individuals used to determine gut contents for each category

Species	Size	Head width (range)	No.	Date collected
<i>Rithrogena hageni</i>	Small	0.80–1.20	10	19 Aug.
	Large	2.20–2.50	10	21 Sept.
<i>Epeorus longimanus</i>	Small	0.45–0.60	12	29 March
	Large	2.00–2.40	10	29 May
<i>Ephemerella infrequens</i>	Small	0.50–0.80	10	21 Sept.
	Large	1.20–1.35	10	19 June
<i>Drunella grandis</i>	Small	0.70–0.95	10	19 Aug.
	Large	1.80–1.90	10	21 Oct.
<i>Drunella doddsi</i>	Small	0.75–0.95	10	21 Sept.
	Large	1.25–1.65	10	21 Oct.
<i>Baetis tricaudatus</i>	Small	0.20–0.40	16	21 Sept.
	Large	0.85–1.20	10	19 Aug.
<i>Glossosoma</i> sp.	Small	0.25–0.35	16	21 Oct.
	Large	0.80–0.95	10	19 June

(McDunnough) was classified by Merritt & Cummins (1984) as a shredder, but this and previous studies of Rocky Mountain streams (e.g. Short & Ward, 1980) indicate that it is a collector-gatherer. Each species utilized the same general food resources (algae and detritus) in the same ways (scraping, and collecting and gathering) and therefore was considered part of a single guild (scraper/collector-gatherer). Collectively, the seven species comprised 79% of the total numbers of scrapers and collector-gatherers. Other representatives of this feeding guild were not sufficiently abundant to include in the analysis.

Trophic niche analysis

Gut contents were analysed from both small (early instars) and large (late instars) individuals of each species (Table 1) according to Cummins' (1973) method. The entire gut was dissected and the contents were teased onto a depression slide. Material on the slide was dispersed into a beaker containing 25 ml of distilled water and then drawn onto a 0.45 µm Millipore filter. A drop of clearing solution was added to the filter which was allowed to clear for 24 h before it was mounted permanently on a slide. The slide was scanned at 200× to identify food items as either detritus, diatoms, filamentous algae or animal material. The numbers of items present in ten random fields per slide were used to characterize the gut contents. After following the same procedure, Gray & Ward (1979) found that ten fields adequately represented the slide contents. Horn's (1966) index was used to calculate dietary overlap:

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

where C = overlap coefficient; s = number of food categories; X_i = the proportion of total diet of species X from food category i ; Y_i = the proportion of total diet of species Y from food category i . The value of C ranges from 0 (no food categories in common) to 1 (all food categories used identically).

Temporal niche analysis

Following identification, all specimens not used for examination of gut contents were

divided into 0.1 mm head capsule width size classes and dried at 60°C for 48 h. Box plots (Velleman & Houghlin, 1981) were used to summarize the growth of each species (Fig. 1). Growth analyses and collections of adults obtained by sweeping riparian vegetation each

FIG. 1. Box plots for each species on each sampling date. Plus signs indicate median population sizes and the vertical length of boxes represents the size range over which 75% of the individuals are found. The vertical lines, extending from one or both ends of the box, indicate the size range over which 90% of the individuals in each population are found. Separate points represent clusters of individuals (outliers) that are exceptionally larger than or smaller than the median population size. The total number of individuals used are indicated above or below each plot.

month were used to determine life cycle characteristics for each species.

The pattern of resource utilization of a population is best expressed as population production because it includes both the population density and body size composition (Tokesi, 1986). Species production for each sampling interval was calculated using the instantaneous growth method (Benke, 1984) or

$$P = G \cdot B/T,$$

where B is the arithmetic mean population biomass (dry weight) on the two adjacent sampling occasions, T is the time interval in days, and G is the instantaneous growth rate. G is calculated as

$$G = \ln W_{t+1} - \ln W_t$$

where W_{t+1} and W_t denote geometric mean individual dry weights at times $t+1$ and t . Deviations from the true production curve were inevitably introduced in this procedure; however, the overall pattern of resource utilization is adequately described (Tokesi, 1986). Calculations were made separately for different generations of the bivoltine species *Baetis tricaudatus*. Separate calculations were also made for different cohorts of poorly synchronized, univoltine species. In both cases the production over a given time interval for different cohorts or generations representing a single species was summed to provide a single resource utilization curve. The temporal pattern of peak production for the species of this guild was analysed using a null model developed for flowering phenological data (Poole & Rathke, 1979). This analysis is equivalent to randomly assigning each of the species a peak production date and then comparing this random pattern to the observed pattern. Because production was essentially zero for 4 months of the year (November–February), none of the randomly assigned peak production values were allowed to fall within this time period. Therefore, this model incorporated the effects of winter and ensured that all peak production estimates occurred randomly but outside the four winter months. The resource utilization curves for *B. tricaudatus*, *D. grandis* and *D. doddsi* were bimodal; peak production occurred in the spring and in autumn. Both peaks were used for these three species.

Temporal overlap among species was calcu-

lated using proportional similarity as an index of overlap (Whittaker, 1975):

$$\alpha_{ij} = \sum_k \min(P_{ik}, P_{jk})$$

where α_{ij} is the overlap between the i th and j th species, and P_{ik} and P_{jk} are the proportions of the species' production which occur over the k th sampling interval. Simulation studies have demonstrated that proportional similarity estimates overlap over a wide range with lower bias and better precision than other commonly used indices (Ricklefs & Lau, 1980; Linton, Davies & Wrona, 1981). This same procedure was used by Georgian & Wallace (1983) to determine the pattern of peak production for another guild of scrapers.

Spatial niche analysis

A 'missing value' correlation analysis (Sokal & Rohlf, 1981) was used to detect negative spatial associations. The numbers of each species in seventy-seven sample units (0.09 m^2) collected over the year were used in this analysis. Missing values, indicated by a -9 , corrected for the absence of immatures due to life cycle events (e.g. emergence or egg development). When encountered, the computer would ignore missing values, but distinguish them from 0 which indicates immatures were present but not in that particular sample. Negative associations between species pairs may indicate spatial segregation at the 0.09 m^2 scale. Normal probability plots and scatter diagrams verified parametric assumptions.

Results

Food overlap

Species pair-wise comparisons based on Horn's (1966) dietary overlap index for large individuals (late instars) separated the species into two groups: (1) algivores and (2) detritivores. Group 1 species (*Glossosoma* sp., *Drunella doddsi* and *Baetis tricaudatus*) consumed primarily diatoms with small proportions of detritus and filamentous algae (Fig. 2a). Group 2 species (*Rhithrogena hageni*, *Epeorus longimanus*, *ephemerella infrequens* and *Drunella grandis*) consumed primarily detritus along with some diatoms, animal mate-

FIG. 2. The per cent volume consumed of each food type (detritus, diatoms, filamentous algae and animal material) by (a) large individuals of each species and (b) small individuals.

rial and filamentous algae (Fig. 2a). Both groups demonstrated high ($C > 0.95$) within-group overlap but low ($C < 0.58$) between-group overlap (Table 2). *Baetis tricaudatus* ($C = 0.58$ and 0.50) overlapped moderately with *R. hageni* and *D. grandis* because it consumed relatively larger amounts of detritus (Fig. 2a).

Small individuals (early instars) also separated into two distinct dietary groups. Group 1 species (*Glossosoma* sp. and *B. tricaudatus*)

consumed primarily diatoms (Fig. 2b) and demonstrated very little ($C < 0.21$) overlap with Group 2 (Table 2). Group 2 species (*D. doddsi*, *D. grandis*, *R. hageni*, *E. longimanus* and *E. infrequens*) consumed primarily detritus (Fig. 2b). *Drunella doddsi* switched groups as growth and development proceeded (Table 2). Early instars were detritivorous, whereas later instars were primarily algivorous.

Spatial overlap

If competition has influenced the spatial utilization of the members of this guild and if the appropriate scale has been examined, then competition theory predicts that spatial separation represented by negative correlations among guild members should be found (e.g. Schoener, 1974; Hart, 1983). No significant pair-wise correlations were found at the 0.09 m^2 scale when the densities of each species within Surber samples were compared (Table 3). Spatial utilization on a smaller scale (e.g. preferences for specific rock surfaces, top, side or bottom) was not quantified in this study.

Temporal overlap

Life cycle descriptions and events are summarized in Table 4. All species except *B. tricaudatus* were univoltine. All species except *E. longimanus* were slow seasonal (eggs begin to hatch soon after oviposition and growth occurs over a long period to maturity; Hynes, 1970). *Epeorus longimanus* over-wintered in the egg stage (fast seasonal) and completed its entire growth in the spring (Fig. 1). *Drunella grandis* and *D. doddsi* were well synchronized species where a single generation was represented by a single cohort. The other species were less synchronized and one generation was represented by more than one cohort. Cohorts were recognized by pulses of early instar larvae. Emergence (late summer and/or autumn) and growth (spring and autumn) occurred during approximately the same time periods for each species (Fig. 1).

The seven species of this guild were represented by ten production peaks. When all seven species of the guild were included, the temporal pattern was significantly more aggregated than would be expected by chance

TABLE 2. Pair-wise comparisons of Horn's dietary overlap index for small (above and to the right of the diagonal) and large (below and to the left) individuals of each species. Values range from 0 (no categories in common) to 1 (all categories used identically). Values delineated by rectangular boxes are comparisons between species in different groups (algivores versus detritivores). Values outside rectangular boxes are within-group comparisons.

	<i>R. hageni</i>	<i>E. longimanus</i>	<i>E. infrequens</i>	<i>D. grandis</i>	<i>D. doddsi</i>	<i>B. tricaudatus</i>	<i>Glossosoma</i> sp.
<i>R. hageni</i>		0.98	0.99	0.99	0.99	0.12	0.20
<i>E. longimanus</i>	0.91		1.00	0.99	0.99	0.10	0.18
<i>E. infrequens</i>	0.92	0.94		0.98	0.99	0.10	0.18
<i>D. grandis</i>	0.96	0.89	0.96		0.99	0.12	0.20
<i>D. doddsi</i>	0.44	0.13	0.17	0.37		0.11	0.20
<i>B. tricaudatus</i>	0.58	0.33	0.31	0.50	0.96		0.99
<i>Glossosoma</i> sp.	0.41	0.20	0.18	0.38	0.97	0.99	

TABLE 3. Correlations based on the number of individuals collected in a 0.09 m² area, from June 1981 to May 1982. The *r* values range from -1 (perfect inverse association) to 0 (random association) to +1 (perfect direct relationship). There were no significant ($P=0.05$) negative or positive correlations.

	<i>R. hageni</i>	<i>E. longimanus</i>	<i>E. infrequens</i>	<i>D. grandis</i>	<i>D. doddsi</i>	<i>B. tricaudatus</i>	<i>Glossosoma</i> sp.
<i>R. hageni</i>	—						
<i>E. longimanus</i>	0.28	—					
<i>E. infrequens</i>	-0.09	-0.13	—				
<i>D. grandis</i>	0.01	-0.01	0.10	—			
<i>D. doddsi</i>	0.38	0.05	0.10	0.55	—		
<i>B. tricaudatus</i>	0.07	0.04	0.45	-0.10	-0.11	—	
<i>Glossosoma</i> sp.	-0.03	0.16	0.20	-0.15	-0.01	-0.22	—

TABLE 4. A summary of the general life cycle characteristics of each species

	Voltinism	Type	Cohorts per generation	Emergence
<i>R. hageni</i>	Univoltine	Slow seasonal	2 or 3	July and August
<i>E. longimanus</i>	Univoltine	Fast seasonal	1 or 2	July and August
<i>E. infrequens</i>	Univoltine	Slow seasonal	2 or 3	July and August
<i>D. grandis</i>	Univoltine	Slow seasonal	1	July
<i>D. doddsi</i>	Univoltine	Slow seasonal	1	June
<i>B. tricaudatus</i>	Multi-voltine	Slow and fast seasonal	?	May–October
<i>Glossosoma</i> sp.	Univoltine	Slow seasonal	1 or 2	July and August

($P=0.11$). However, the pattern for three Group 1 species, represented by five production peaks, was not significantly different from random. Also, the pattern for the four Group 2 species, represented by five production peaks, was not significantly different from random.

Temporal overlap in production for all members of this guild was high and ranged from 0.37 to 0.81 (Table 5). If past competition and

coevolution has influenced the temporal overlap in production within this guild then species using similar food types (species within groups) should have a smaller overlap than species using different food types. A Mann-Whitney-Wilcoxon non-parametric analysis (Gibbons, 1976) indicated that the pair-wise temporal overlap values within Groups 1 and 2 were not significantly smaller than the overlap values between species in Groups 1 and 2 ($P=0.433$).

TABLE 5. Temporal overlap values between species calculated as proportional similarity. A Mann-Whitney-Wilcoxon non-parametric test indicated that values outside the rectangular box were not significantly different from values delineated by the box. Values delineated by the rectangular box are comparisons between species in different groups (algivores versus detritivores). Values outside the rectangular box are within-group comparisons.

	<i>R. hageni</i>	<i>E. longimanus</i>	<i>E. infrequens</i>	<i>D. grandis</i>	<i>D. doddsi</i>	<i>B. tricaudatus</i>	<i>Glossosoma sp.</i>
<i>R. hageni</i>	—						
<i>E. longimanus</i>	0.64	—					
<i>E. infrequens</i>	0.43	0.56	—				
<i>D. grandis</i>	0.67	0.44	0.46	—			
<i>D. doddsi</i>	0.62	0.39	0.58	0.61	—		
<i>B. tricaudatus</i>	0.76	0.51	0.70	0.66	0.62	—	
<i>Glossosoma</i> sp.	0.81	0.37	0.57	0.60	0.63	0.73	—

Discussion

Dietary differences separated these scraper/collector-gatherers into two groups (cryptic detritivores and exposed algivores). Data from a concurrent study (Rader & Ward, unpublished) on species preferences for specific rock surfaces indicates that *Drunella grandis*, *Ephemerella infrequens*, *Epeorus longimanus* and *Rithrogena hageni* (Group 2) prefer crevices and substrate undersides (cryptic habitat), while *Baetis tricaudatus*, *Drunella doddsi* and *Glossosoma* sp. (Group 1) prefer exposed rock surfaces. Hamilton & Clifford (1983) while examining the feeding habits of mayflies in three Alberta streams also classified Group 1 species as surface feeders and group 2 species as interstitial feeders. Therefore, dietary differences between groups 1 and 2 of this study probably reflected differences in microhabitat utilization rather than food specialization by species with special micro-spatial distributions.

The temporal pattern of resource utilization demonstrated by this guild did not support Vannote's (1978) hypothesis that species within the same guild or functional group should be sequentially organized so as to minimize periods in which similar resources are being used. If we had found a regular pattern among the species resource utilization curves then competition would be one of the likely mechanisms, among a few alternatives, capable of producing this pattern. As it is, com-

petition is probably unimportant in structuring the temporal organization of this guild. However, population densities and production may still be influenced by competition that occurs too infrequently to produce life-cycle adjustments and temporal separation.

It is also possible that competition has influenced the amount of temporal resource overlap among a few species of this guild without producing a regular pattern of peak resource utilization. If this were the case, then we would expect some of the pair-wise species production overlap values to be small. For example, Georgian & Wallace (1983) found that a scraper guild demonstrated a regular pattern of temporal peak production with remarkably small values of temporal overlap (ranging from 0.00 to 0.29) among species annual production curves. The amount of temporal overlap of species annual production curves for the members of this guild was high and ranged from 0.39 to 0.81. In addition, the pattern of peak resource utilization was aggregated for the guild as a whole and no different from random within Groups 1 and 2. For these reasons, we found no evidence supporting the hypothesis that interspecific competition has influenced the temporal patterns of resource utilization within this guild. Evidence suggests that in this stream, and other similar Rocky Mountain streams (Ward, Zimmermann & Cline, 1986), physical components may be more important than competitive interactions in structuring zoobenthic assemblages.

Acknowledgments

This study was supported by a research grant to J. V. Ward from the Colorado Experiment Station. The authors wish to thank Neal Voelz, LeRoy Poff and Henry Zimmermann for their review of this manuscript.

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(Manuscript accepted 13 May 1987)

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