The influence of environmental predictability/disturbance characteristics on the structure of a guild of mountain stream insects

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Resource overlap in the saprophage/collector-gatherer guild along temporal, trophic and microfacial niche dimensions was determined at two sites in the Upper Colorado River. The amount of resource overlap within the saprophage/collector-gatherer guild in a predictable, benign regulated section of the river was compared with the amount of overlap within the saprophage/collector-gatherer guild of a less predictable, frequently disturbed free-flowing section. Thirty years of daily flow records were used to determine predictability and frequency of disturbance events. Trophic, temporal and microfacial overlap between the two guilds was not significantly different. There was no evidence to support the hypothesis that resource overlap should be reduced or more regularly spaced in guilds inhabiting predictable, benign environments.


Introduction

A guild is a co-occurring group of species, not necessarily related closely taxonomically, that utilize the same resources in the same way (Jakob 1981). The term "guild structure" may refer to several guild characteristics (e.g. Safe 1975, Holmes et al. 1979, Pianka 1960, Hairston 1981); in this study, it refers to the amount of overlap in patterns of resource utilization. Resources are defined as environmental factors directly used by organisms that potentially affect their fitness.

Equilibrium theory (McIntosh 1955) proposes that overlap in resource use among potentially competing species (exploitative competition) should be greater in stochastic, frequently disturbed environments than in more benign, predictable environments (Levins 1968, MacArthur 1972, May and MacArthur 1972, Pianka 1976). Species in more predictable environments may enhance their fitness by minimizing interspecific competition through efficient exploitation of a restricted set of resources, thereby decreasing resource overlap. Species in unpredictable and disturbed conditions, however, may be unable to specialize on specific resource spectra because of the "noisy environment" (MacArthur 1975). In addition, disturbances may maintain populations below their carrying capacities where resources are not limiting (e.g., Harper 1969, Connell 1978, Huston 1979). Therefore, species in unpredictable, disturbed environments may generalize in their use of resources, thus increasing resource overlap (MacArthur and Levins 1967, MacArthur 1975).

This argument is based upon three initial premises: 1) equilibrium communities develop under conditions of low environmental variability, where abiotic factors are not extremely unpredictable or harsh; 2) interspecific competition is an important process under equilibrium conditions, where predation effects are minimized; and 3) resource overlap is inversely related to competition. Although premises 1 and 2 are supported by various ecologists (e.g., Huston 1989, Schoedon and Sans-
ers 1969, Dayton 1971, May and MacArthur 1972, Menge and Slobodkin 1976, Wien 1984; the prevalence of equilibrium conditions and competition in natural communities is a matter of some contention (e.g., Connell 1980; Strong et al., 1984). The proposed relationship between measures of resource overlap and competition (premise 3), however, is somewhat confusing (e.g., Giller 1984), because there need be no relationship between resource overlap and competition if resources are not limiting and if competition does not occur (e.g., Hustich 1978).

Environmental conditions in habitats change on various ecologically-relevant temporal scales (Wien 1984, Chesson 1986). These changing conditions include resource states, abiotic factors, or biotic interaction. Here, we focus on three attributes of temporal environmental variability: 1) the degree of environmental variation in major abiotic factors, 2) the predictability of abiotic factors, and 3) the frequency of disturbance events.

Our objective in this investigation was to relate differences in temperature and discharge variability, predictability and disturbance characteristics between an unregulated stream site and a regulated location to differences in guild structure (resource overlap). We designed the study to investigate the hypothesis that overlap along the temporal, trophic, and microspatial niche dimensions between members of the scraper-collector-gatherer guild would be reduced or more regularly spaced in the less variable, more predictable, disturbance-free site (regulated) than in the more variable, less predictable, frequently disturbed site (unregulated).

Regulated streams provide an excellent testing ground for examining this hypothesis because daily and seasonal temperature and flow fluctuations are reduced and flood events are rare (e.g., Ward and Stanford 1979, 1984). Also, the effects of predation which may reduce competition and allow niche overlap to increase (e.g., Connell 1975, Menge 1976, Peckarsky 1983), were minimal in the regulated site because of the absence of predaceous stoneflies (Rafner and Ward, in press).

Methods
Two sampling sites with similar characteristics, except for the influence of stream regulation, were selected for study. The sites were located in the upper Colorado River basin in the vicinity of Granby Reservoir (Fig. 3), a large deep-release storage reservoir constructed in the 1940s. Both sites were located in rubble riffles of similar gradient, canopy cover, geology, and riparian vegetation at similar elevations (Rader and Ward, in press). An unregulated station (site 1) was located 5 km above Granby Reservoir. Site 3 was located a sufficient distance below Granby Dam (4.0 km) to exhibit at least partial recovery from the altered conditions engendered by the upstream impoundment (Rafner and Ward, in press). These sampling stations will henceforth be referred to as the reference site (site 1), and the recovery site (site 3).

Five mayfly taxa [Baetis spp., Ephemerella infrequens (McDunnough), Drunella grandis (Eaton), Paraleptophlebia heterocea (McDunnough), and Caenis sp. (Dodd)] were examined in the reference site. Six mayfly taxa [Baetis spp., E. infrequens, D. grandis, P. heterocea, Splathronurus occidentalis (Eaton), Epeorus longimanus (Eaton)], and a caddisfly (Gastrocosma ventralis, Banki) were examined in the reference site. Each species has been classified as collector-gatherers and scrapers, except for G. ventralis, which has been classified as a scraper (Merritt and Cummins 1994). Each species utilized the same general food resources (epithoix and benthic detritus) in the same ways (scraping and gathering) and therefore was considered part of the same guild (Rader and Ward 1987). Collectively, the five species in the reference site and the seven species in the recovery site comprised 75% and 87%, respectively, of the total numbers of scrapers and collector-gatherers. For the remainder of this paper the five
taxa in the reference site and the seven taxa in the recovery site will be referred to as the reference guild and the recovery guild.

**Variability-predictability-disturbance characteristics**

Water temperature was measured continuously at both sites for 18 months using Ryan 90-D thermographs. Annual mean daily temperatures, annual coefficients of variation, and annual degree days were determined from daily mean temperatures.

United States Geological Survey (USGS) gaging stations were located a short distance upstream from both the reference and recovery sites. Thirty years (1952 to 1982) of mean daily flow records were used to determine annual mean daily flow, annual coefficient of variation, flow predictability, and key attributes of the flow disturbance regime. Colewell's (1974) index of predictability was used to compare flow predictability above and below Decoy Reservoir. Colewell's index was calculated by grouping the mean daily flow values into eight categories corresponding to the eight rows of a frequency matrix with three hundred sixty-five columns representing the days in a year. Category intervals for both flow and time were chosen to maximize the resolution of the analysis.

Disturbance was defined as the flow necessary to transport the mean substrate particle diameter. Estimations of the geometric mean substrate particle diameter (Lottspeich and Everest 1981) were based on four core samples (25 cm in diameter) taken at each site; two replicates before and two replicates following spring runoff. For further details see Rader and Ward (in press). Before estimating the disturbance flow at each site, it was necessary to estimate the critical tractive force capable of transporting the mean particle diameter. The tractive force is an estimate of the lift and drag exerted on a given particle site at the point of incipient motion (Newbury 1984). On the basis of the tractive force, the flow necessary to transport the mean particle diameter at each site was calculated. For further information see Rader and Ward (in press). Using flow records (thirty years) from above and below the dam a computer program was written to determine the average number of times per year that the flow equaled or exceeded the critical value for incipient motion of the mean particle size (disturbance frequency).

**Trophic overlap**

Gut content analyses were used to determine the diet composition of each taxon within each guild. Gut contents from intermediate to late instars of each species collected during the summer and early autumn (Rader and Ward, in press) were analyzed according to Cummins' (1973) method. Twenty-eight to thirty-five individuals in each taxon at each site were used for the analyses. For further details see Rader and Ward (in press). A proportional similarity index (Whittaker 1975) was used to determine dietary overlap:

\[
\alpha_s = \sum \min (P_s, P_i)
\]

where \(\alpha_s\) is the overlap between the \(s^t\) and \(i^t\) species, and the \(P_s\) is the proportion of the species' diet contributed by the \(k^t\) food category. The value of \(P_s\) ranges from 0 (no food categories in common) to 1 (all food categories used identically).

**Spatial overlap**

Non-glazed, rectangular brick substrates (23 x 19 x 9.5 cm) were used to determine the microspatial distributions of each taxon in both the reference and recovery guilds. Bricks were used because they, unlike natural substrate, have distinct top, sides, front, back and bottom surfaces and because they are readily colored by both periphyton and invertebrates (e.g. Tuchman and Stevenson 1980, Rosenberg and Rosh 1982, Lamberti and Rosh 1985). Sixteen brick substrates were placed lengthwise with the front surface perpendicular to the flow at each site. All brick substrates were placed in the stream one month before sampling. Brick surfaces were sampled in June, July, September and October of 1982 and June of 1983. Sampling of exposed surfaces (top, sides, front and back) consisted of sweeping organisms into a small net (30 x 20 cm opening; 240 μm mesh) that was held immediately downstream from the surface to be sampled. Four replicate samples were taken from each surface, including the bottom surface and interstitials, on each date at each site. The "bottom surface" consisted of: 1) organisms swept from the bottom surface of the brick, and 2) organisms in the top centimeter of gravel, whereas an interstitial sample consisted of substrate organisms from 1-10 cm in depth below the brick. For further details see Rader and Ward (in press).

The same proportional similarity index used to determine dietary overlap was used to determine microspatial overlap. However, \(P_s\) represents the proportion of individuals utilizing the \(k^t\) microspatial category (e.g. top, sides, bottom, etc.).

**Temporal overlap**

The temporal pattern of resource utilization of a population is best expressed as population production (Tolke 1986, Rader and Ward 1987). The temporal pattern of resource utilization by the species in each guild was calculated using the instantaneous growth method (Georganis and Wallace 1985, Benke 1984) or

\[
P = G + B/T
\]

[109]
null model originally developed for flow-averaged phenolog- 
ical data (Poele and Ratkech 1979). This analysis is equiv- 
alent to randomly assigning each of the species within 
a guild a peak production date and then compar- 
ing this random pattern with the observed pattern. 
When a species’ annual production was represented by 
more than one peak, each period of peak production 
was used in the analysis. Siltov (1979) suggested that 
life-history constraints and the seasonal scale may influence 
the outcome of the analysis. For example, if a complete 
year was analyzed and aquatic insects of this study did 
not grow during the winter, then we would expect the 
peak periods of resource utilization of individual species 
2 be aggregated during the winter months of the year. 
However, within the warmer months, the periods of 
peak resource utilization could be regularly spaced. 
Therefore, the null analysis was calculated using 
(ther e four different growth periods: 1) an annual growth period 
(three hundred seventy-five days), 2) an early spring to late 
autumn growth period (two hundred seventy-five days), 
3) a spring growth period (one hundred twenty days), 
and 4) a summer and autumn growth period (one 
hundred fifty-five days). Patterns of peak resource utili- 
ation (aggregated, seasonal, and random) within each of 
these growth periods were analyzed separately for 
each guild

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<th>Results</th>
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**Variability/predictability/disturbance characteristics**

The number of annual degree days (202 vs 1380) and 
the mean annual temperature (5.7 vs 3.6°C) were higher 
in the recovery site than in the reference site. However, 
the coefficient of variation calculated for the annual 
temperature regime (119 vs 64) was greater in the refer- 
ence site. The mean daily flow and variation in mean daily flow 
were greater in the reference site (Tab. 1). Flow at the 
recovery site was much more constant due to the ab- 
sence of annual snowmelt discharge. Cowell’s (1974) 
predictability index was greater below the dam priorit-
Fig. 2. percent volume of each food type consumed by *Barti*s sp. (1), *Paraleptophila heterocera* (2), *Cynips* *ramalei* (3), *Ephemeroptera* *infrequens* (4), *Drosophila* *grandis* (5), *Epeorus* *longimanus* (6), *Siphlonurus* *octoculatus* (7), and *Glossosoma* *ventrale* (8).

ility due to a high constancy component (Tab. 1). Disturbances, defined as flow events necessary to transport the mean substrate particle diameter, occurred far more frequently above the reservoir at the reference site (Tab. 1). Most disturbance flows at the reference site can be attributed to annual snowmelt run-off and spates that occurred in July and sometimes August. There were only three short periods of disturbance flows at the recovery site over the thirty-year period of record. At the reference site, however, there were almost three disturbance events per year (Tab. 1).

Trophic overlap

Both *Barti*s sp. and *C. ramalei* in the reference guild, and *Barti*s sp. and *G. ventrale* in the recovery guild, consumed relatively large proportions of diatoms, whereas the other species were primarily detritivores at both sites (Fig. 2). The dietary composition of *Barti*s sp. and *P. heterocera* was similar at both sites. However, a greater proportion of diatoms was consumed by the primarily detritivorous species, *D. grandis* and *E. infrequens*, at the recovery site. Filamentous algae and animal material represented only a small proportion of the diets of those species that utilized these food categories (Fig. 2). The reference guild had an average overlap of 0.76 (SD = 0.29). The average dietary overlap in the recovery guild was 0.77 (SD = 0.21). A Mann-Whitney-Wilcoxon analysis indicated that trophic overlap within the reference and recovery guilds was not significantly different (P = 0.42).

Microspatial overlap

All species used primarily bottom surfaces except *Barti*s sp. in the reference site and *G. ventrale* and *Barti*s sp. in the recovery site (Fig. 3). However, a greater proportion of individuals in the recovery guild utilized upper surfaces (top, sides, front and back). Microspatial overlap in the reference guild averaged 0.87 (SD = 0.10). The recovery guild had an average overlap of 0.71 (SD = 0.24). Microspatial overlap within the recovery guild at the more variable, unpredictable, frequently disturbed site and the recovery guild at the predictable, undisturbed site was not significantly different (P = 0.14).

Fig. 3. Proportional microspatial distribution of *Barti*s sp. (1), *Paraleptophila* *heterocera* (2), *Cynips* *ramalei* (3), *Ephemeroptera* *infrequens* (4), *Drosophila* *grandis* (5), *Epeorus* *longimanus* (6), *Siphlonurus* *octoculatus* (7), and *Glossosoma* *ventrale* (8).

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Fig. 4. Annual resource utilization curves for *Baetis* spp. and *Paramegahela heteromera* in the reference guild. Production was calculated as mg dry weight m⁻² per time interval.

**Temporal overlap**

Except for one species (*P. heteromera*), the period of maximum production or peak resource utilization in the reference guild occurred between May and July (Figs 4 and 5). Peak resource utilization for *P. heteromera* occurred in the spring (Fig. 4). Most species in the reference guild had a second (smaller) peak in late autumn (Figs 4 and 5). Except for *D. grandis*, the period of peak resource utilization in the recovery guild compared with the reference guild occurred over a similar time interval but was entirely extended from April to August (Figs 6, 7 and 8). The average temporal overlap in resource utilization for the reference guild was 0.42 (SD = 0.16). The recovery guild had an average temporal overlap of 0.39 (SD = 0.20). Temporal overlap in periods of peak resource utilization in the reference guild compared with the recovery guild was not significantly different (P = 0.44). Data on the differences in the magnitude of production among species at the same site and within species at different sites will be presented in a future publication.

The pattern of production and resource utilization of *E. infraquadris* was similar at both sites except that the period of production was extended in the predictable design site (Figs 5 and 7). The pattern of production was also similar at both sites for *P. heteromera* and *D. grandis*. However, production began to peak earlier at the reference site for *F. heteromera*, whereas *D. grandis* began to peak earlier at the recovery site. *Drumella grandis* had a distinct bimodal pattern of production at both sites. *Baetis* spp. demonstrated three production peaks in the recovery site compared with two at the reference site.

Fig. 5. Annual resource utilization curves for *Cinygmula ramayeni*, *Ephemera infraquadris*, and *Drumella grandis* in the reference guild. Production was calculated as mg m⁻² per time interval.
Over the annual growth period, peak resource utilization in both the reference and recovery guilds was not significantly different from random (Tab. 2). Both the recovery and reference guilds were significantly aggregated over the early spring/late autumn, early spring/summer, and summer/late autumn growth periods, except for the recovery guild, which was not significantly different from random over the early spring/late autumn growth period (Tab. 2). Peak periods of resource utilization in the recovery guild at the predictable, infrequently disturbed site was not more widely or more regularly spaced than the reference guild.

Fig. 6. Annual resource utilization curves for Baetis spp., Paraleptophlebia heterocnea, and Epeorus longimanus in the recovery guild. Production was calculated as mg dry weight m⁻² per time interval.

Fig. 7. Annual resource utilization curves for Ephemera infrequens, Drunella grandis, and Siphlonurus occidentalis in the recovery guild. Production was calculated as mg dry weight m⁻² per time interval.
The amount of resource overlap among temporal, trophic and spatial niche dimensions in the scraper/collector-gatherer guilds at the recovery site (predictable, benign) and the reference site (unpredictable, frequently disturbed) was very similar. Although some resources were used somewhat differently (e.g., greater proportions of diatoms were consumed in the recovery site), the amount of resource overlap between sites was not significantly different.

Schroener (1974) suggested that, where competition has been influential, patterns of resource utilization between species should be regularly spaced. Similarly, Van note and Sweeney (1989) suggested that, as a result of interspecific competition, periods of peak resource utilization by species within a given stream functional group (e.g., scrapers, predators, collectors, etc.) will follow a regular temporal sequence. This hypothesis, one of the tenets of the River Continuum Concept (Van note et al. 1980, Matener and Higler 1985), 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 (Van note and Sweeney 1989). Temporal patterns of resource utilization for members of both guilds in this study and

<table>
<thead>
<tr>
<th>Growth period</th>
<th>Annual</th>
<th>Spring/autumn</th>
<th>Spring/summer</th>
<th>Summer/autumn</th>
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<tbody>
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<td>PE(P)</td>
<td>p-value</td>
<td>PE(P)</td>
<td>p-value</td>
<td>PE(P)</td>
</tr>
<tr>
<td>Reference</td>
<td>1.14</td>
<td>0.35</td>
<td>2.33</td>
<td>0.01</td>
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<tr>
<td>Recovery</td>
<td>0.70</td>
<td>0.29</td>
<td>1.96</td>
<td>0.60</td>
</tr>
</tbody>
</table>

a. Random = 1.0; Aggregated > 1.0; Regular < 1.0.

* Statistically significant values.

Tab. 3. A summary of the life history characteristics of each species at the reference (Ref.) and recovery (Rec.) sites. "Uni" and "Bi" represent univoltine and bivoltine life cycles. "Slow" and "Fast" indicate the type of life cycle (Hynes 1970). Values under the "Emergence" category indicate months of emergence.

<table>
<thead>
<tr>
<th>Species</th>
<th>Volinom</th>
<th>Life cycle type</th>
<th>Months of emergence</th>
</tr>
</thead>
<tbody>
<tr>
<td>R. trichogaster</td>
<td>Uni</td>
<td>Bi</td>
<td>Slow</td>
</tr>
<tr>
<td>L. infreques</td>
<td>Uni</td>
<td>Uni</td>
<td>Slow</td>
</tr>
<tr>
<td>D. quadra</td>
<td>Uni</td>
<td>Uni</td>
<td>Slow</td>
</tr>
<tr>
<td>P. nucellaris</td>
<td>Uni</td>
<td>Uni</td>
<td>Slow</td>
</tr>
<tr>
<td>C. ramalxi</td>
<td>Uni</td>
<td>-</td>
<td>Slow</td>
</tr>
<tr>
<td>S. occidentalis</td>
<td>-</td>
<td>-</td>
<td>Slow</td>
</tr>
<tr>
<td>L. longitins</td>
<td>-</td>
<td>-</td>
<td>Slow</td>
</tr>
<tr>
<td>G. ventralis</td>
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