

# 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 scraper/collector-gatherer guild along temporal, trophic and microspatial niche dimensions was determined at two sites in the Upper Colorado River. The amount of resource overlap within the scraper/collector-gatherer guild in a predictable, benign regulated section of the river was compared with the amount of overlap within the scraper/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 microspatial 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.

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## Introduction

A guild is a co-occurring group of species, not necessarily related closely taxonomically, that utilize the same resources in the same way (Jaksić 1981). The term "guild structure" may refer to several guild characteristics (e.g. Sale 1975, Holmes et al. 1979, Pianka 1980, 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.

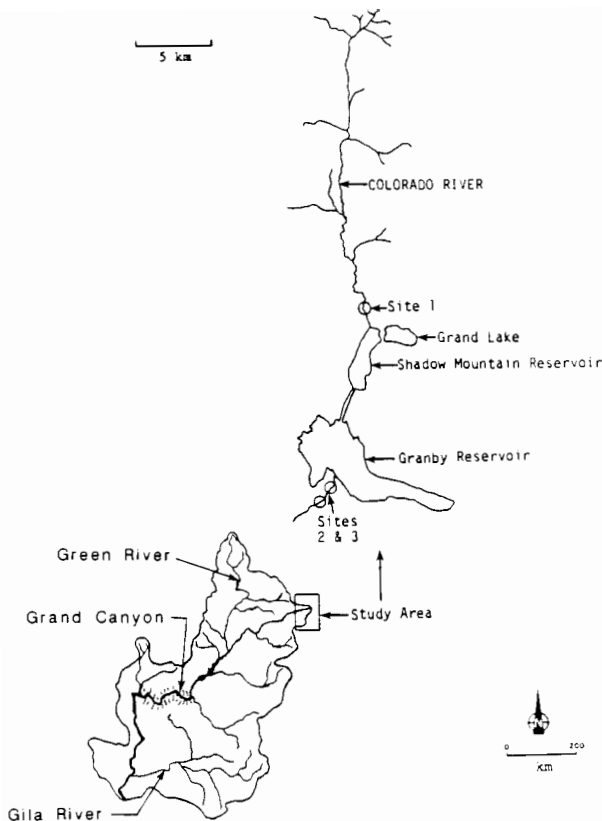
Equilibrium theory (McIntosh 1985) proposes that overlap in resource use among potentially competing species (exploitative competitors) should be greater in stochastic, frequently disturbed environments than in more benign, predictable environments (Levins 1968, MacArthur 1972, May and MacArthur 1972, 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., Hutchinson 1959, Slobodkin and Sand-

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#### COLORADO RIVER BASIN

Fig. 1. The Colorado Basin showing the location of the upper Colorado River, Shadow Mountain Reservoir, Granby Reservoir, Grand Lake and the study sites.

ers 1969, Dayton 1971, May and MacArthur 1972, Menge and Sutherland 1976, Wiens 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., Hurlbert 1978).

Environmental conditions in habitats change on various ecologically-relevant temporal scales (Wiens 1984, Chesson 1986). These changing conditions include resource states, abiotic factors, or biotic interactions. 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, predict-

ability 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 (Rader 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 in the vicinity of Granby Reservoir (Fig. 1), 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 (Rader 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 heteronea* (McDunnough) and *Cinygmula ramaileyi* (Dodds)] were examined in the reference site. Six mayfly taxa [*Baetis* spp., *E. infrequens*, *D. grandis*, *P. heteronea*, *Siphonurus occidentalis* (Eaton), *Epeorus longimanus* (Eaton)], and a caddisfly (*Glossosoma ventrale*, Banks) were examined in the recovery site. Each species has been classified as collector-gatherers and scrapers, except for *G. ventrale*, which has been classified as a scraper (Merritt and Cummins 1984). Each species utilized the same general food resources (periphyton and benthic detritus) in the same ways (scrapping 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) gauging 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. Colwell's (1974) index of predictability was used to compare flow predictability above and below Granby Reservoir. Colwell'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 (Lotspeich and Everest 1981) were based on four core samples (28 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 size at the point of incipient motion (Newbury 1984). Based on 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 dietary 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 analysis. For further details see Rader and Ward (in

press). A proportional similarity index (Whittaker 1975) was used to determine dietary overlap:

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

where  $\alpha_{ij}$  is the overlap between the  $i^{\text{th}}$  and  $j^{\text{th}}$  species, and the  $P \cdot k$  is the proportion of the species' diet contributed by the  $k^{\text{th}}$  food category. The value of  $\alpha_{ij}$  ranges from 0 (no food categories in common) to 1 (all food categories used identically).

#### Spatial overlap

Non-glazed, rectangular brick substrates (23×19×9.5 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 colonized by both periphyton and invertebrates (e.g. Tuchman and Stevenson 1980, Rosenberg and Resh 1982, Lamberti and Resh 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 (30×20 cm opening; 240  $\mu\text{m}$  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 interstices, 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 and 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,  $P \cdot k$  represents the proportion of individuals utilizing the  $k^{\text{th}}$  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 (Tokeshi 1986, Rader and Ward 1987). The temporal pattern of resource utilization by the species in each guild was calculated using the instantaneous growth method (Georgian and Wallace 1983, Benke 1984) or

$$P = G * B/T$$

Tab. 1. Flow characteristics below Granby Dam (regulated) and at the unregulated reference site based on USGS records over a 30 yr period (1952–1982).

	Mean daily flow (m <sup>3</sup> s <sup>-1</sup> )	CV (%)	Colwell's index <sup>a</sup>			Disturbance <sup>b</sup>	
			Predictability	Constancy (%)	Contingency (%)	Mean # yr <sup>-1</sup>	Mean interval (d)
Unregulated regime	1.75	167	0.62	42	58	2.6	93
Regulated regime	1.24	72	0.87	66	34	0.1	3,285

a. Colwell (1974).

b. Flow events which transport the mean substrate particle size.

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 actual annual production curve were inevitably introduced in this procedure; however, the overall pattern of resource utilization is adequately described (Tokeshi 1986). Although calculations were made separately for different generations of bivoltine species, these values were summed to provide a single resource utilization curve.

Population densities were estimated using four to eight sampling units collected for twelve months at each site using a modified Surber sampler (0.09 m<sup>2</sup> opening; 240 μm mesh) and artificial substrates (bricks). Four Surber samples, taken across the width of the stream, were collected monthly at each site. Artificial substrates were sampled during the summer and autumn months. Head-capsule width measurements were used to determine size-frequency plots for life history determinations of each taxon (Rader and Ward, in press). Emergence periods for each species were based on the occurrence of adults and nymphal swollen black wing-pads.

The same proportional similarity index used to determine dietary and spatial overlap was used to determine overlap in temporal patterns of resource utilization. However, P-k represents the proportion of the species' production which occurs over the k<sup>th</sup> sampling interval.

A Mann-Whitney-Wilcoxon non-parametric analysis (Gibbons 1976) was used to determine if the calculated temporal, microspatial and dietary overlap values were significantly greater in the reference guild than in the recovery guild.

#### Resource utilization null analysis

The temporal pattern of resource utilization for the species of both guilds was analyzed separately using a

null model originally developed for flowering phenological data (Poole and Rathcke 1979). This analysis is equivalent to randomly assigning each of the species within a guild a peak production date and then comparing 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. Stiles (1979) suggested that life history constraints and the temporal 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 to be aggregated during the warmer 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 four different growth periods: 1) an annual growth period (three hundred sixty-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 utilization (aggregated, regular and random) within each of these growth periods were analyzed separately for each guild.

## Results

### Variability/predictability/disturbance characteristics

The number of annual degree days (2082 vs 1330) 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 reference 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 absence of annual snowmelt discharge. Colwell's (1974) predictability index was greater below the dam primar-

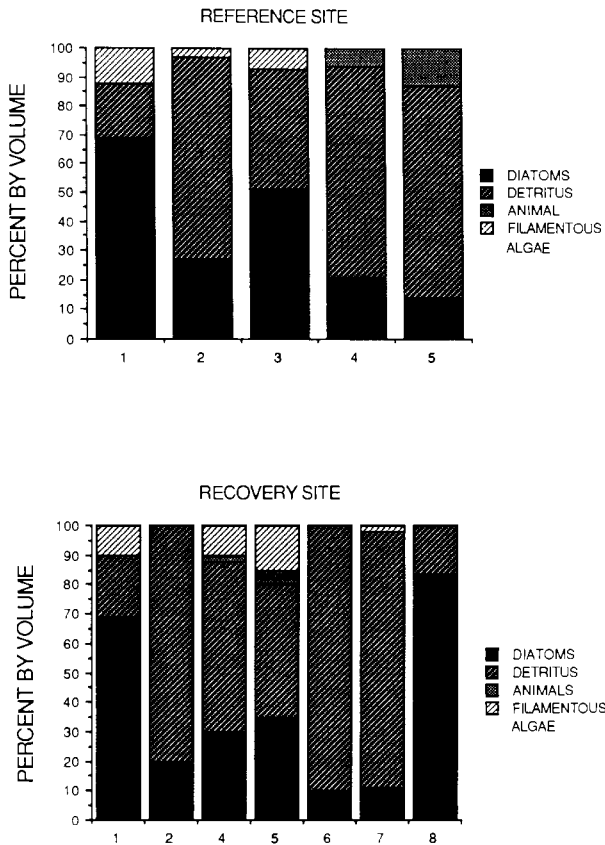


Fig. 2. percent volume of each food type consumed by *Baetis* spp. (1), *Paraleptophlebia heteronea* (2), *Cinygmula ramaleyi* (3), *Ephemerella infrequens* (4), *Drunella grandis* (5), *Epeorus longimanus* (6), *Siphonurus occidentalis* (7), and *Glossosoma ventrale* (8).

ily 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 *Baetis* spp. and *C. ramaleyi* in the reference guild, and *Baetis* spp. 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 *Baetis* spp. and *P. heteronea* was similar at both sites. Howev-

er, 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 *Baetis* spp. in the reference site and *G. ventrale* and *Baetis* spp. 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 reference guild at the more variable, unpredictable, frequently disturbed site and the recovery guild at the predictable, undisturbed site was not significantly different ( $P = 0.14$ ).

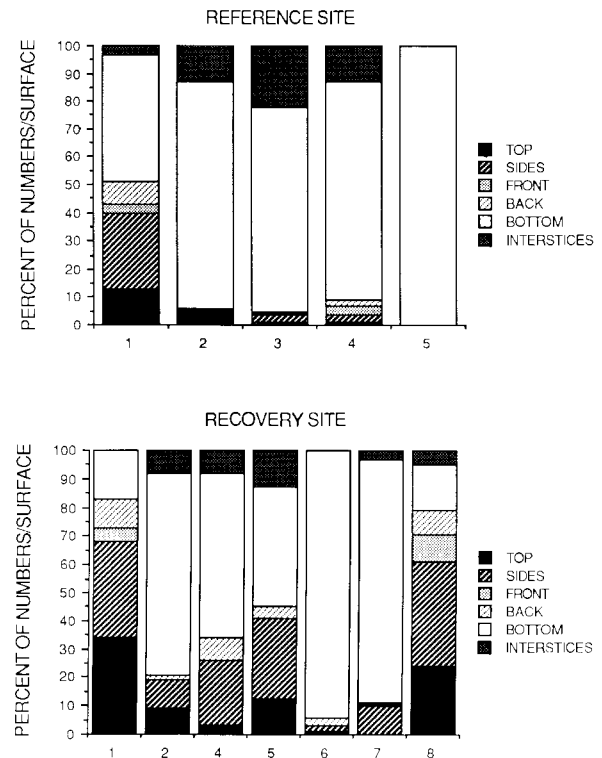


Fig. 3. Proportional microspatial distribution of *Baetis* spp. (1), *Paraleptophlebia heteronea* (2), *Cinygmula ramaleyi* (3), *Ephemerella infrequens* (4), *Drunella grandis* (5), *Epeorus longimanus* (6), *Siphonurus occidentalis* (7), and *Glossosoma ventrale* (8).

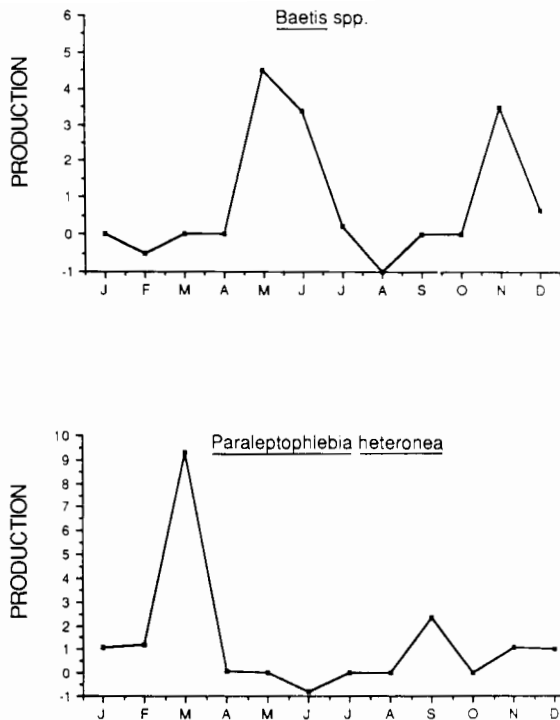


Fig. 4. Annual resource utilization curves for *Baetis* spp. and *Paraleptophlebia heteronea* in the reference guild. Production was calculated as mg dry weight m<sup>-2</sup> per time interval.

#### Temporal overlap

Except for one species (*P. heteronea*), 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. heteronea* 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 usually extended from April to August (Figs 6, 7 and 8). The average temporal overlap in resource utilization for the reference guild was 0.41 (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. infrequens* was similar at both sites except that the period of production was extended in the predictable benign site (Figs 5 and 7). The pattern of production was also similar at both sites for *P. heteronea* and *D.*

*grandis*. However, production began to peak earlier at the reference site for *P. heteronea*, whereas *D. grandis* began to peak earlier at the recovery site. *Drunella 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.

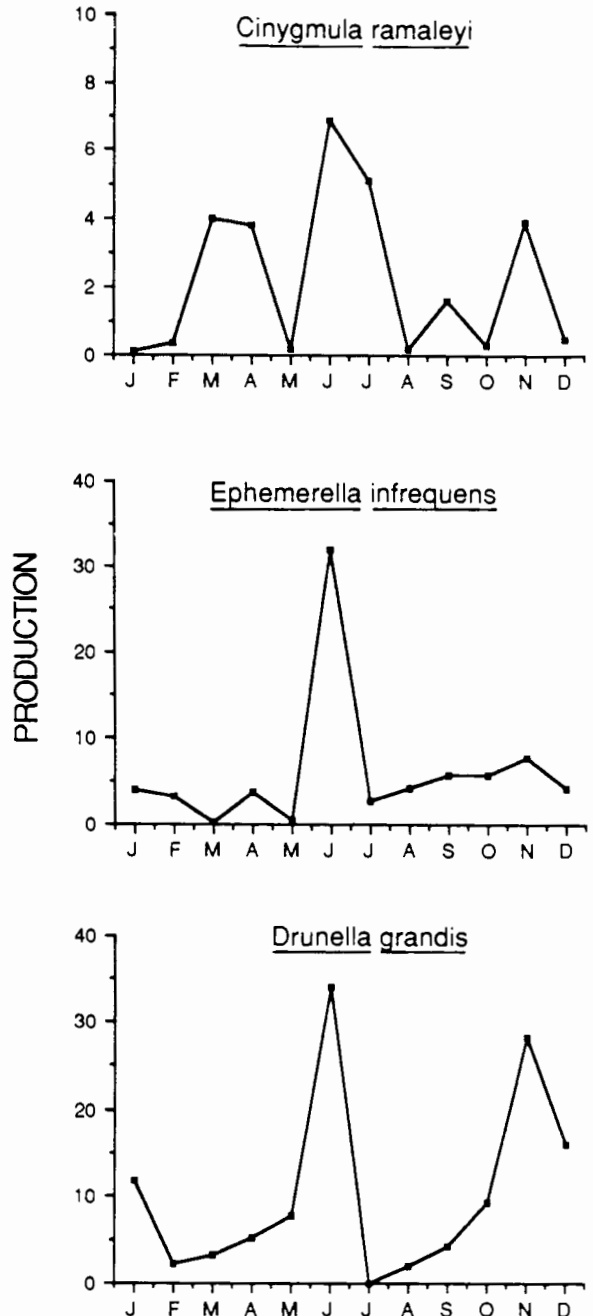


Fig. 5. Annual resource utilization curves for *Cinygmula ramaleyi*, *Ephemerella infrequens*, and *Drunella grandis* in the reference guild. Production was calculated as mg m<sup>-2</sup> per time interval.

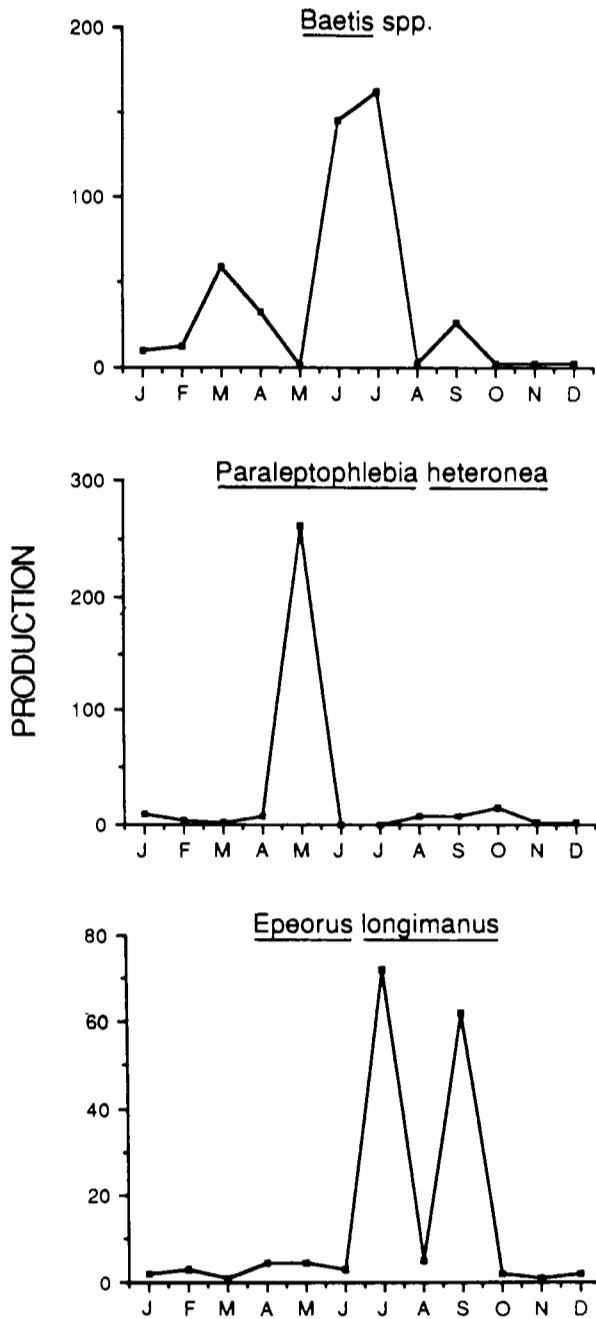


Fig. 6. Annual resource utilization curves for *Baetis* spp., *Paraleptophlebia heteronea*, and *Epeorus longimanus* in the recovery guild. Production was calculated as mg dry weight m<sup>-2</sup> per time interval.

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, ex-

cept 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.

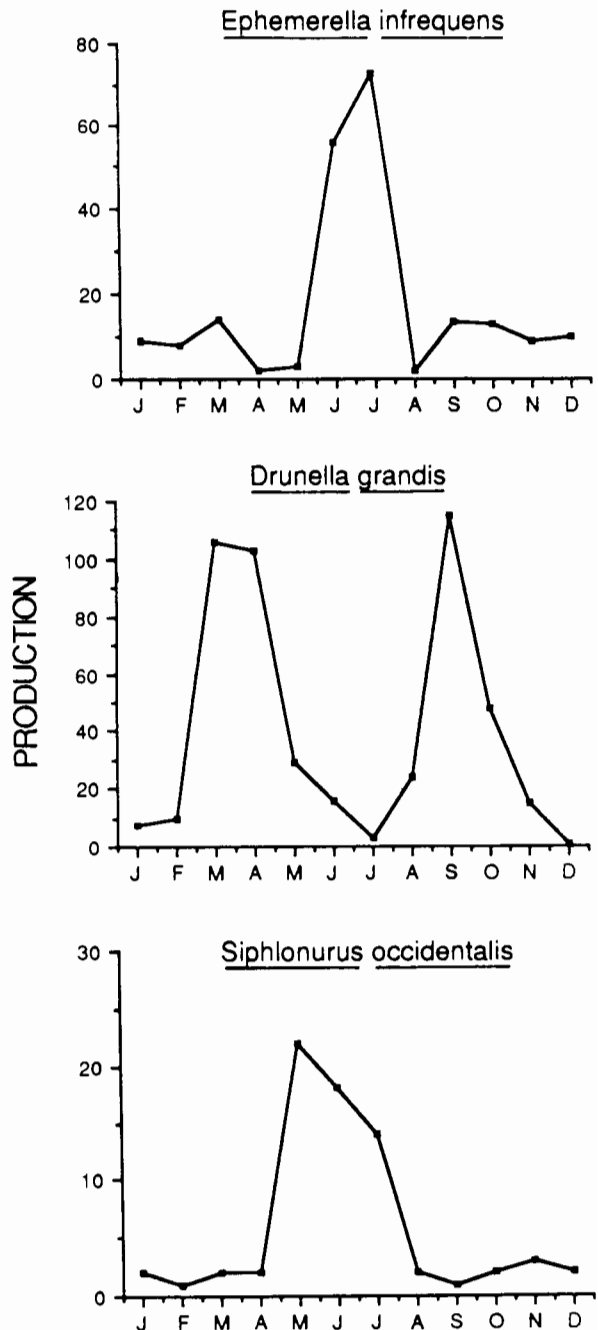


Fig. 7. Annual resource utilization curves for *Ephemerella infrequens*, *Drunella grandis*, and *Siphonurus occidentalis* in the recovery guild. Production was calculated as mg dry weight m<sup>-2</sup> per time interval.

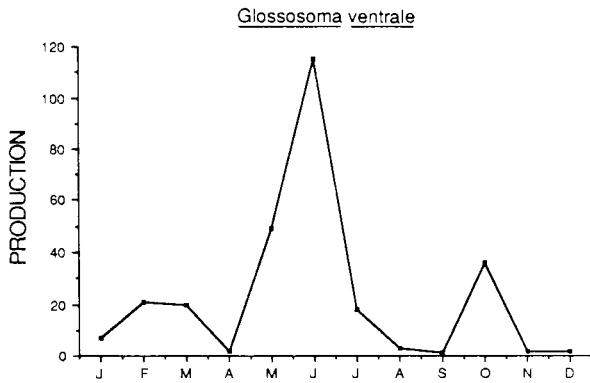


Fig. 8. Annual resource utilization curve for *Glossosoma ventrale* in the recovery guild. Production was calculated as mg dry weight  $m^{-2}$  per time interval.

Tab. 3 summarizes the life cycle events for each species at both sites. Each species in the reference guild had a univoltine slow seasonal life cycle. Of the four species that occurred at both sites, two added at least one new generation per year and three had extended emergence periods at the recovery site compared with the reference site.

## Discussion

The amount of resource overlap along 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.

Schoener (1974) suggested that, where competition has been influential, patterns of resource utilization between species should be regularly spaced. Similarly, Vannote and Sweeney (1980) 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 (Vannote et al. 1980, Statzner 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 (Vannote and Sweeney 1980). Temporal patterns of resource utilization for members of both guilds in this study and

Tab. 2. Null analysis (Poole and Rathcke 1979) for both the reference and recovery guilds for four different growth periods. "P" is the observed variance of the distance between actual peak production periods. "E(P)" is the expected variance of the distance between randomly assigned peak production periods. The ratio "P/E(P)" is a measure of regularity or aggregation. The chi-square statistic  $\chi^2 = kP/E(P)$  with k degrees of freedom, where K = the number of taxa, is a test of the null hypothesis, P = E(P).

	Growth period							
	Annual		Spring/autumn		Spring/summer		Summer/autumn	
	P/E(P) <sup>a</sup>	p-value	P/E(P) <sup>a</sup>	p-value	P/E(P) <sup>a</sup>	p-value	P/E(P) <sup>a</sup>	p-value
Reference	1.14	0.35	2.33*	0.01	2.44*	0.03	5.12*	0.001
Recovery	0.70	0.29	1.06	0.60	2.77*	0.01	4.17*	0.001

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.

Species	Voltinism		Life cycle type		Months of emergence	
	Ref.	Rec.	Ref.	Rec.	Ref.	Rec.
<i>B. tricaudatus</i>	Uni	Bi	Slow	Slow & Fast	5-7	2-9
<i>E. infrequens</i>	Uni	Uni	Slow	Slow	7	6 & 7
<i>D. grandis</i>	Uni	Uni	Slow	Slow	6	6
<i>P. heteronea</i>	Uni	Uni	Slow	Slow	4 & 6	3-6
<i>C. ramaleyi</i>	Uni	-	Slow	-	7	-
<i>S. occidentalis</i>	-	Uni	-	Slow	-	7
<i>E. longimanus</i>	-	Uni	-	Slow	-	7
<i>G. ventrale</i>	-	Uni	-	Slow	-	7



at least one other (Tokeshi 1986) were either aggregated or random depending on the temporal scale or time interval available for growth. Neither the recovery nor the reference guild showed a regular pattern of resource utilization. When compared with appropriate null models, patterns of temporal separation within streams may be more apparent than real.

Based on the results of this study, there was no evidence to support the hypothesis that resource overlap is reduced or more regularly spaced in the scraper/collector-gatherer guild occupying the predictable benign environment in which competition should theoretically be important. Three explanations may account for the rejection of this hypothesis. First, partitioning may have occurred along some unexamined resource dimension. Because niche space is multidimensional (Hutchinson 1958), it is impossible to obtain data on all dimensions (Pianka 1975). Therefore, this explanation is not very satisfying because theoretically it can never be disproven; partitioning could always occur on some unmeasured niche dimension. This study examined resource utilization along three important niche dimensions (Schoener 1974) at ecologically relevant scales and represents one of the first attempts to quantify microspatial utilization on individual substrate surfaces by the mobile mayfly fauna. Therefore, the absence of a reduction in niche overlap in the predictable benign environment was probably not caused by resource partitioning on some cryptic unexamined niche dimension. Second, it is possible that resources at the more predictable benign site were not limiting or limiting for only brief periods of time and, therefore, niche overlap in the recovery guild was not reduced or more regularly spaced than in the reference guild. Finally, it is possible that even though resources were limiting at the more predictable, infrequently disturbed site, resource overlap was not reduced because of the potential influence of intraspecific competition. Whereas interspecific competition tends to reduce resource overlap, intraspecific competition may expand resource utilization, thereby increasing the amount of niche overlap among species of the same guild (e.g., MacArthur 1972, Pianka 1976). Abrams (1980) suggested that patterns of resource overlap within guilds was more closely related to the relative strengths of inter- and intraspecific competition rather than the intensity of interspecific competition alone. Therefore, even if resources were limiting at the more predictable benign site, the influence of intraspecific competition on patterns of resource utilization (increased overlap) may have offset the influence of interspecific competition (reduced overlap).

Life history differences between the two guilds (Tab. 3) were probably caused by the altered thermal regime downstream from the dam (e.g. increased number of degree days). In addition, overall differences in patterns of resource utilization (temporal, trophic and microspatial) between the two guilds were probably caused by

altered abiotic conditions at the recovery site rather than being the result of competition.

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