Habitat partitioning among the mayfly species (Ephemeroptera) of Yuccabine Creek, a tropical Australian stream

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Summary. This study examines the distributions among microhabitats of 12 detritivorous species of mayfly in Yuccabine Creek, an upland tropical rainforest stream. Analysis of data from regular benthic sampling and from in situ experiments using implanted substrata showed that although all species occurred in all the microhabitats examined, different species had significantly different peaks of abundance in different microhabitats, leading to distinct partitioning of the available habitat. The observed patterns of distribution were closely associated with the distribution of fine detritus deposits (FPOM). In the absence of FPOM in fast-flowing regions of the stream, leaf litter was the prime determinant of species distribution. Current velocity and substratum particle size influenced the distribution of the detritus and leaf litter. Abundance of mayflies was greatest in the pool habitat for all except two of the species.

Key words: Resource partitioning – Seasonal habitats – Mayfly – Rainforest stream – Experimental ecology

Since the pioneering research of Percival and Whitehead (1929), considerable effort has been directed toward study of the distributional patterns of stream invertebrates. Much of the early research was aimed at the description of habitat requirements of individual species, without particular reference to community structure (Gee 1982). Most studies of resource utilisation in streams have been of temperate (e.g. Rabeni and Minshall 1977) or subarctic systems (e.g. Ulfstrand 1967, 1975), and comparable studies of tropical aquatic invertebrates are scarce.

Only three long-term studies of tropical upland streams exist (Bishop 1973; Dudgeon 1984 *et seq*; Pearson et al. 1986 *et seq*) and detailed studies of resource utilisation among tropical stream insects are absent. It is of considerable interest to determine the ways in which available resources are utilised within tropical stream communities because of the high species diversity in tropical systems (Bishop 1973; Pearson et al. 1986).

It has been suggested that the small-scale distribution of stream macroinvertebrates is the result of speciesspecific responses to biotic factors such as competition (Magdych 1979; Hart 1983, 1985), environmental variables such as current velocity, substratum particle size, and food sources (Cummins and Lauff 1969; Rabeni and Minshall 1977) or both. Additional abiotic factors such as temperature and chemical composition of the water usually may be disregarded when micro-distributions are studied, as they tend to be of greatest influence on largescale distributions, but remain constant on the local scale (Ulfstrand 1967).

This study examines habitat partitioning by the mayfly species of Yuccabine Creek, a small upland rainforest stream. Yuccabine Creek is a tropical stream and has a high diversity of invertebrate species (Pearson et al. 1986); however, the number of mayfly species for a single site (13+) is not high when compared with temperate streams (e.g. in Victoria - Chessman 1986) or other tropical streams (in Malaysia – Bishop 1973). Nevertheless, mayflies form a large component of the detritivoredominated insect community within Yuccabine Creek (33% by numbers of the whole fauna; other major groups include Trichoptera, 25%; Elminthidae, 12%; and Chironomidae, 18%; - Pearson et al. 1986). We have shown that the nymphs of all species but one (*Mirawara*) sp., a predator) are detrivorous with almost completely overlapping diets (Hearnden and Pearson in press). Although we have no evidence of competitive interactions between the mayfly species, it is possible that they occur, especially towards the end of the dry season as stream width diminishes and faunal densities rise (unpublished data). It is therefore of extreme interest to ask whether these species show any partitioning of their habitat use or preference.

This study uses two approaches to examine habitat use by the mayfly species. The first analyses descriptive data which associate counts of mayflies from benthic samples with habitat attributes (cf., for example, Bovbjerg 1970; Neill 1975; Malas 1976; Gee 1982). The

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second examines mayfly colonisation of various substrata implanted in the stream. By using trays of implanted substratum in a three-way factorial design, the more obvious habitat features – substratum particle size, leaflitter availability and current velocity – were tested for their influence on the distributions of mayfly species. Although it may be preferable to examine all species of the community at once, the mayflies were selected for practical reasons: (a) the diets of the Yuccabine Creek mayflies were established (Hearnden and Pearson in press); (b) they form a coherent taxonomic group with overlapping diets; and (c) it is assumed that if partitioning of resources does occur among species of the Yuccabine Creek community, it will be most obvious within such a group.

Methods

Study site

The study site was located at Yuccabine Creek, a rainforest stream situated at 600 m elevation in the Cardwell Range (18° 12' S, 145° 45' E), in tropical north Queensland. The site and its fauna have been described by Pearson et al. (1986). The vegetation of the surrounding catchment is mainly mesophyll vine forest (Webb 1959). The stream consists of alternating pools and riffles with the bed composed of rocks, predominantly 0.01 m² to 0.06 m² (cross-sectional area), with interspersed boulders up to 1 m². Patches of up to 1 m² of gravel, sand and leaf litter exist in isolated regions of the stream bed and all are present in smaller quantities below rocks. Yuccabine Creek is strongly seasonal with maximum discharge and temperature in the summer months (December to April).

Field distributions

Monthly field sampling of a 50-m section of riffle was performed as described by Pearson et al. (1986). On each occasion up to 20 random benthic kick-samples were taken with a net of 400 µm maximum mesh size, the area of each sample being $1/16 \text{ m}^2$. For each replicate, all leaf litter was retained for dry-weight measurements, and the dominant substratum size was recorded. Current velocities were measured within the area of each sample unit using a Marsh-McBirney current meter. The mayflies from each sample were identified and counted. Counts were transformed to log₁₀ (x+1) to normalise the frequency distribution of the counts (Zar 1984). A multiple regression and analysis of variance of regression were performed for each species against the three independent variables - leaf litter dry weight, rock size and current velocity (expressed as a percentage of the maximum current velocity recorded for each month). For each species, a model was derived that related species' distribution to these three variables.

Habitat selection experiment

A habitat selection experiment was performed from mid-June to mid-July 1986 in adjacent sections of pool and riffle. Both sites were even in depth (0.25-0.30 m), of similar stream-bed width (5-6 m) and had similar canopy cover (70-80%). The period chosen for the study was one in which stream discharges are usually stable and there is little chance of spate or rapid contraction of the stream. Trays of substratum were positioned in the stream bed and were left for 30 days to allow colonisation by invertebrates (see Benson and Pearson 1987a). The trays consisted of moulded 0.3-mm aluminium, 314 mm long, 254 mm wide and 48 mm deep. Substrata used

in the trays were taken from the stream bed close to the site. Four sizes were used: size 0, sand of 1.5 mm mean diameter; size 1, pebbles of 39.6 mm mean diameter; size 2, cobbles of 67.5 mm mean diameter; and size 3, small rocks of 162.4 mm mean diameter. These categories encompassed most of the size range that occurred at the site, but excluded the larger rocks. Duplicates of each rock size were combined with 30-mm mesh packs containing whole, decaying leaves of approximately 20 g dry weight, taken from the stream. The leaf litter pack was placed on the bottom of the tray underneath the rocks without restricting access for benthic insects to the leaf litter.

This procedure resulted in eight different combinations of substratum. Each combination was replicated four times to produce 32 trays each for pool and riffle, within which the trays were randomly assigned to their position on the stream bed. Each tray position in the stream was excavated so that when the tray was placed on the bottom, the lip was level with the surrounding substratum. This allowed colonisation to occur from the benthos as well as the drift. Current velocity was recorded at each tray prior to retrieval. Five benthic samples were taken downstream of both pool and riffle to allow comparison of the naturally occurring mayfly fauna with that colonising the trays.

Travs were retrieved from downstream to upstream. On retrieval, a net with mesh aperture of 90 µm was placed directly behind the tray to catch any detritus or fauna that drifted or swam off the tray as it was lifted. The contents of each tray were washed and brushed over a 90-µm mesh sieve to remove all fauna. If a leaf-pack was present, leaves were emptied into a plastic bag with the washed sample and the wire-bag scrubbed. Trays containing sand substratum were emptied straight into a plastic bag with any organisms or detritus that was collected in the net. The resultant sample was then preserved in 70% alcohol. In the laboratory, each sample was washed through a series of sieves (2.8 mm/250 μ m/180 μ m/90 μ m). Large particles such as leaves and wood fragments were washed and discarded. The 2.8 mm and 2.8 mm-250 µm fractions were then sorted using a magnifying lens. Initial inspection of the first ten 180-90 µm fractions showed that the 250 µm mesh size collected all the mayflies in the sample. For sand samples, 1.4-mm and 500-µm sieves were added to the above series and each fraction was sorted separately. For all samples, the >90 μ m organic fraction was separated from sand, etc., by elutriation, vacuum-filtered, air dried and weighed.

The mayflies were identified and counted, and the counts were transformed to $\log_{10}(x+1)$. A three-factor analysis of variance was performed to examine the simultaneous and interactive effects of the three treatments, namely current, rock-size and leaf litter, on the distribution of mayfly species in the trays.

Inter-ocular distance of the primary eyes of each nymph was measured as an index of age (Tsui and Hubbard 1979). When more than 50 nymphs of a particular species were present, only the first 50 nymphs encountered were measured. These data were used to analyse size-frequency distributions of each species within the eight substratum types for each site.

An index of the breadth of resource utilisation (Levins 1968) was calculated for each species using the Simpson–Yule index applied to the distribution of the individuals between the resource states (in this case, the different substratum combinations from the pool and the riffle) (see Southwood 1978):

$$\beta_i = \left(\sum_{i=1}^n \frac{N_i^2}{N_t^2}\right)^{-1}$$

where N_i is the number of individuals of the species in the *i*th resource state, and N_i is the total number of individuals in all (=n) the resource states.

The proportional overlap in resource utilisation between two species (i and j) was estimated by:

$$\theta_{ij} = 1 - 0.5 \left(\sum_{k=1}^{n} p_{ik} p_{jk} \right)$$

Species	Variable	В	r^2	F	Р
Atalophlebioides sp. 1	SUBSTRATE	-0.047	0.042	7.94	0.005
Atalonella sp. 1	LEAF LITTER	0.017	0.118	24.09	< 0.001
Atalonella sp. 2	CURRENT LEAF LITTER Equation	$-0.003 \\ 0.027$	0.251 0.222 0.473	29.97 51.34	<0.001 <0.001
Atalonella sp. 3	LEAF LITTER	0.005	0.036	6.74	< 0.010
Atalonella sp. 4	CURRENT	0.006	0.178	39.04	< 0.001
Atalonella sp. 5	CURRENT LEAF LITTER Equation	-0.004 0.013	0.128 0.171 0.299	26.38 18.55	<0.001 <0.001
Atalophlebia sp.	CURRENT LEAF LITTER Equation	-0.003 0.017	0.319 0.247 0.566	41.97 58.98	<0.001 <0.001
Atalomicria sp.	SUBSTRATE CURRENT LEAF LITTER Equation	0.048 - 0.006 - 0.013	0.152 0.197 0.222 0.571	32.27 22.03 16.95	< 0.001 < 0.001 0.001
Baetis sp. Tasmanocoenis sp.	Not significant Not significant				
Mirawara sp.	CURRENT LEAF LITTER Equation	$-0.002 \\ 0.005$	0.092 0.119 0.211	18.92 12.06	< 0.001 < 0.001
Jappa sp. 1	CURRENT	-0.001	0.036	6.66	0.012
<i>Ulmerophlebia</i> sp.	CURRENT LEAF LITTER Equation	-0.002 0.016	0.254 0.219 0.473	30.50 50.43	<0.001 <0.001

Table 1. Regression analyses for all species in relation to microdistribution preference for the three variables, current, leaf litter, and substratum. Parameters are: *B*, the standardised regression coefficient, r^2 , the proportion of the variance accounted for by the variable or the equation, *F*, the variance ratio for a variable or equation, and *P*, the associated probability. n = 182samples

where p_i is the proportion of species *i* in a particular resource state (k), p_j is the proportion of species *j* in a particular resource state, and *n* is the total number of resource states (Schoener 1974a). Values can range from 0 (no overlap) to 1.0 (complete overlap).

Results

Field distributions

The results of the multiple regression analyses for each species are presented in Table 1. For each significant variable, values for the partial regression coefficient, variance attributable to that variable, variance ratio and associated probability are indicated.

For two species, Tasmanocoenis sp. and Baetis sp., none of the three variables explained any variance in the distributions. On the other hand, all three variables were significant in the model for Atalomicria sp. In all other models, either one or two variables were significant for the regression. The two habitat variables that had the greatest influence on micro-distribution were the amount of leaf litter present and the current velocity. Both were significant for the models of Atalonella sp. 2, Atalonella sp. 5, Atalophlebia sp., Mirawara sp., and Ulmerophlebia sp. The distributions of Atalonella sp. 1 and Atalonella sp. 3 were influenced by leaf litter alone. For Jappa sp. 1 and Atalonella sp. 4, the single important variable was current velocity. The influence of substratum by itself was significant only for the distribution of Atalophlebioides sp. 1. It should be noted that in some cases



Fig. 1. Mean dry weights (\pm 1 SE) for fine particulate organic matter (FPOM) collected from each treatment combination in pool and riffle trays. *Rock Size* 0, sand; 1, pebble; 2, cobble; 3, small rock; *closed circles*, leaf litter present; *open circles*, leaf litter absent

Table 2. Responses of fine particulate organic matter (FPOM) (dry weight) in the habitat-tray experiment tested using a 3-way ANOVA. Responses to each main treatment, second- and third-order interaction are shown with associated probability value (P)

FР Source of Sum of df Mean Variation Squares Square CURRENT 86.065 86.065 296.072 < 0.0011 ROCK 15.479 3 5.160 17.750 < 0.001 LEAF 14.101 1 14.101 48.510 < 0.001 < 0.001 $\mathbf{C} \times \mathbf{R}$ 15.288 3 5.096 17.530 < 0.001 $C \times L$ 8.612 8.612 29.627 1 2.915 3 0.972 3.342 0.027 $R \times L$ $C \times R \times L$ 2.473 3 0.824 2.836 0.048 47 Residual 13.662 0.291 Total 159.867 62

Table 3. Mean densities $(\pm 1 \text{ SE})$ of each species collected in Surber samples from pool and riffle sites. A indicates absence from samples

Species	Pool	Riffle
Atalophlebioides sp. 1	68.4 ± 13.4	28.0 ± 1.1
Atalophlebioides sp. 2	$2.0\pm~0.8$	А
Atalonella sp. 1	А	А
Atalonella sp. 2	4.8 ± 1.5	5.0 ± 1.2
Atalonella sp. 3	$0.4\pm~0.2$	0.1 ± 0.3
Atalonella sp. 4	$0.2\pm~0.2$	3.8 ± 1.5
Atalonella sp. 5	3.2 ± 1.4	11.8 ± 2.1
Atalophlebia sp.	9.4 ± 2.8	0.8 ± 0.5
Atalomicria sp.	5.6 ± 2.4	8.0 ± 2.7
Baetis sp.	36.2 ± 8.1	42.5 ± 2.4
Tasmanocoenis sp.	$0.8\pm~0.6$	0.8 ± 0.3
Mirawara sp.	$0.4\pm~0.4$	А
Jappa sp. 1	$5.8\pm~0.7$	1.8 ± 0.6
Ulmerophlebia sp.	$20.0\pm~2.2$	2.0 ± 0.7



Fig. 2A-H. Significant first-order interactions for each species to experimental treatments. Data shown are the transformed cell means (+1 SE). A Atalophlebioides sp. 1, B Atalonella sp. 2, C Atalonella sp. 4, D Atalonella sp. 5, E Atalophlebia sp., F Baetis sp., G Tasmanocoenis sp., H Ulmerophlebia sp. Treatments where P > 0.05 are shown as NS. Significance values for each species are shown in Table 4. Rock Size 0, sand; 1, pebble; 2, cobble; 3, small rock; Current R, riffle; P, pool; LL+, leaf litter present: LL-, leaf litter absent

Table 4. Responses of all commonly occurring species in the habitat-tray experiment tested using a 3-way ANOVA. Responses to each main treatment, second- and third-order interaction are shown with associated probability value (P)

Table 4. Continued

with associated probat	mity valu	.c (1)			
Source of	Sum of	df	Mean	F	Р
Variation	Squares	5	Square		
Atalophlebioides sp. 1	n=1370)			
CURRENT	4.416	1	4.416	33.449	< 0.001
ROCK	2.104	3	0.701	5.312	< 0.001
LEAF	0.025	1	0.025	0.191	0.664
C×R	0.728	3	0.243	1.837	0.153
C×L	0.005	1	0.005	0.040	0.843
R×L	0.394	3	0.131	0.995	0.403
$C \times R \times L$	1.259	3	0.420	3.178	0.032
Residual	6.205	47	0.132		
Total	15.283	62			
Atalonella sp. 2	n=959				
CURRENT	2.255	1	2 2 5 5	26.085	< 0.001
ROCK	0 507	3	0 169	1 956	0 134
LEAF	11 447	1	11 447	132 394	< 0.001
$C \times R$	0 249	ŝ	0.083	0.960	0.420
CxL	0.506	1	0.506	5 8 5 1	0.120
R×I	0.500	3	0.282	3 265	0.012
$C \times R \times L$	0.123	3	0.041	0.473	0.702
Residual	4.064	47	0.086		
Total	0.264	62			
Atalonella sp. 4	n=25				
CURRENT	0.174	1	0.174	8.105	0.007
ROCK	0.331	3	0.110	5,133	0.004
LEAF	0.156	1	0.156	7.270	0.010
C×R	0.098	3	0.033	1.515	0.223
C×L	0.334	1	0.334	15.567	< 0.001
R×I.	0.057	â	0.019	0.891	0.453
$C \times R \times L$	0.161	3	0.054	2.503	0.071
Residual	1.009	47	0.021	-	
Γotal	2.332	62			
Atalonella sp. 5	n=89				
CURRENT	1.379	1	1,379	19.814	< 0.001
ROCK	0.142	3	0.047	0.672	0.573
LEAF	0.884	1	0.884	12 537	0.001
C×R	0.126	3	0.042	0 596	0.621
C×L	0.040	1	0.040	0.570	0.021
R×I.	0.040	à	0.040	0.575	0 623
K ^ L)	0.140	2	0.042	0.593	0.022

$ \begin{array}{l} \mathbf{R} \times \mathbf{L} \\ \mathbf{C} \times \mathbf{R} \times \mathbf{L} \end{array} $	0.126 0.350	3 3	$0.042 \\ 0.117$
Residual	3.314	47	0.071
Total	6.356	62	

Source of	Sum of	df	Mean	F	Р
Variation	Squares		Square		
Atalophlebia sp.	n = 284				
CURRENT	7.764	1	7.764	133.716	< 0.001
ROCK	0.464	3	0.155	2.665	0.059
LEAF	1.387	1	1.387	23.882	< 0.001
$C \times R$	0.572	3	0.191	3.286	0.029
$C \times L$	0.340	1	0.340	5.849	0.020
$R \times L$	0.915	3	0.305	5.254	0.003
$C \times R \times L$	1.012	3	0.340	5.861	0.002
Residual	2.729	47	0.021	_	
Total	15.191	62			
Baetis sp.	n=3612	2			
CURRENT	1.575	1	0.575	29.256	< 0.001
ROCK	1.927	3	0.642	11.933	< 0.001
LEAF	0.048	1	0.048	0.894	0.349
$C \times R$	0.627	3	0.209	3.886	0.015
Č×L	0.159	1	0.159	2.949	0.093
R×L	0.202	3	0.067	1.252	0.302
$\mathbf{C} \times \mathbf{R} \times \mathbf{L}$	0.086	3	0.029	0.531	0.663
Residual	2.530	47	0.054	-	
Total	7.212	62			
Tasmanocoenis sp.	n = 54				
CURRENT	0.589	1	0.579	25.026	< 0.001
ROCK	1.951	3	0.650	28.079	< 0.001
LEAF	0.008	1	0.008	0.359	0.552
$C \times R$	0.535	3	0.178	7.710	< 0.001
C×L	0.024	1	0.024	1.050	0.311
R×L	0.026	3	0.009	0.371	0.774
$C \times R \times L$	0.053	3	0.018	0.762	0.521
Residual	1.088	47	0.023	_	
Total	4.285	62			
<i>Ulmerophlebia</i> sp.	n=134				
CURRENT	1.965	1	1.965	33.912	< 0.001
ROCK	0.782	3	0.261	4.499	0.007
LEAF	0.122	1	0.122	2.114	0.153
$C \times R$	0.708	3	0.236	4.074	0.012
C×L	0.101	1	0.101	1.737	0.194
$R \times L$	0.430	3	0.143	2.472	0.073
$C \times R \times L$	0.639	3	0.213	3.675	0.019
Residual	2.723	47	0.058		
Total	7.541	62			

positive, indicating selection, or at least non-avoidance, of litter accumulations.

significant relationships explained relatively small proportions of the variance (indicated by r^2).

1.655

0.189

It is interesting to note the nature of the partial regression coefficients for each variable. All but one of the significant relationships with current were negative, suggesting avoidance by most species of the regions of faster flow. Conversely, Atalonella sp. 4 had a positive relationship with current and was found predominantly in samples where current velocity was 80-100% of the maximum. All significant relationships with leaf litter were

Habitat selection experiment

During the course of the experiment, the recorded temperature range for Yuccabine Creek was 14-19° C which falls within the normal range for the time of year (Benson and Pearson 1987b). Current velocities (\pm SE) measured at each tray were 8.87 ± 0.22 cm \cdot s⁻¹ for the pool and 45.8 ± 2.44 cm \cdot s⁻¹ for the riffle.



Fig. 3A-F. Significant secondorder interactions for each species to experimental treatments. Data shown are transformed cell means $(\pm 1 \text{ SE})$ for each significant pair of treatments. A Atalonella sp. 2, B Atalonella sp. 4, C Atalophebia sp., D Baetis sp., E Tasmanocoenis sp., F Ulmerophlebia sp. Probability values are shown for each significant treatment pair. LL+. leaf litter-present; LL-, leaf litter absent; 0, sand (open circle); 1, pebble (closed circle); 2, cobble (open triangle); 3, small rock (closed triangle)

The mean weights of fine particulate detritus (FPOM) collected from the different tray combinations at each site are shown in Fig. 1. A three-way analysis of variance (Table 2) performed on the data demonstrated that the distribution of this FPOM was dependent on all three treatments. The amount of detritus retained in the riffle trays was reduced by the faster current flow. Within each site, the larger detritus weights were found in the smallest substratum sizes and generally decreased with increasing particle size. This was particularly evident in the pool trays. Within each substratum size, trays containing leaf litter packs retained up to, and sometimes double, the weight of detritus found in the trays without a leaf litter pack. These general trends result from increased trapping of detritus within the interstitial spaces of the smaller particle sizes. Leaf litter packs trap extra detritus as well as adding to deposits via *in situ* production of detritus resulting from invertebrate shredder activity.

Mean numbers of mayflies in the bottom samples are presented in Table 3. *Atalonella* sp. 1 did not occur in any sample. Abundance of most species was similar in pool and riffle, or lower in the riffle samples, and overall abundance was much higher in the pool. Two species, Atalophlebioides sp. 2 and Mirawara sp., were present in pool samples, but absent from the riffle samples.

Five of the 13 species that colonised the experimental trays were not included in the analysis as they occurred infrequently. These species were Atalophlebioides sp. 2 (n=6), Atalonella sp. 3 (n=6), Atalomicria sp. (n=14), Mirawara sp. (n=4), and Jappa sp. 1 (n=9). For the remaining eight species, probability values for the main effects and interaction effects are presented in Table 4. The responses of each species to the treatments are shown in Figs. 2-4. Though significant preferences existed for all species, there were no cases of a species being absent from habitat combinations other than its own preferred set of choices. Figure 5 summarises these responses and suggests major groupings (A-C) based on significant relationships. This classification is not intended to be a set of definitive criteria to classify the individual species into rigid groups; rather it is presented to highlight the different habitat preferences shown by the mayflies on the basis of the biotic and abiotic influences that have been examined.

On the largest scale, preference for pool or riffle was clear for all species; thus, the species can be divided into



Fig. 4A–C. Significant third-order interactions for each species to experimental treatments. Data shown are transformed cell means (± 1 SE). The responses are shown for each rock size, with and without leaf litter, in pool and riffle. A *Atalophlebioides* sp. 1, **B** *Atalophlebia* sp., **C** *Ulmerophlebia* sp. Probability values are displayed for each species *Closed circles/dashed line*, leaf litter present; *open circle/solid line*, leaf litter absent; 0, sand; 1, pebble; 2, cobble; 3, small rock

two major groups on the basis of current preference (see below). Six of the eight species predominated in the pool trays (Fig. 2A, D–H). *Atalonella* sp. 2 (Fig. 2B) and *Atalonella* sp. 4 (Fig. 2C) were more abundant in the riffle.

1. Riffle preferring species (Group A). Characteristic features of this group (*Atalonella* sp. 2 and *Atalonella* sp. 4), were preferences for trays with leaf litter (Fig. 2B, 2C) and selection for leaf litter trays within the riffle (Fig. 3A, 3B). Availability of leaf litter also influenced the choice of substratum for *Atalonella* sp. 2. It was non-selective in the presence of leaf litter, but preferred pebble and cobble substrata when leaf litter was absent (Fig. 3A). *Atalonella* sp. 4 selected for the rock substratum (size 3, Fig. 2C) and was not influenced by leaf litter availability.

2. Pool preferring species. This group can be subdivided on the basis of selection for a particular main effect:

(a) selection on the basis of leaf litter availability (Group B): this group, consisting of *Atalophlebia* sp. and *Atalonella* sp. 5, demonstrated a preference for leaf litter

(Table 4, Fig. 5). Atalonella sp. 5 showed a straightforward relationship with this variable (Fig. 2D). The preferences of Atalophlebia sp., however, were more dependent on current and rock size. Its selection for leaf litter trays (Fig. 2E) was considerably higher in the pool than in the riffle (Fig. 3C). Substratum choice was also influenced by leaf litter. Sand and pebble substrata became the more preferred rock size when leaf litter was available (Fig. 3C). For Atalophlebia sp., a significant third order interaction indicated that cobble/leaf litter trays were preferred in the riffle and sand/leaf litter trays were preferred in the pool (Fig. 4B).

(b) selection on the basis of substratum size (Group C): this group included *Tasmanocoenis* sp., *Ulmerophlebia* sp., *Baetis* sp., and *Atalophlebioides* sp. 1 (Table 4). Selection for sandy substratum was demonstrated by *Tasmanocoenis* sp. (Fig. 2G) and *Ulmerophlebia* sp. (Fig. 2H), but with a much greater significance in the pool trays (Fig. 3E, 3F). The preference of *Atalophlebioides* sp. 1 for pebble substratum was less pronounced, though significant (Fig. 2A). The preference shown by *Baetis* sp. for pebbles and cobbles became less



pronounced when the interaction with current was considered (Fig. 3D). This interaction decreased the importance of these rock sizes in the pool trays. More complicated interactions existed for Atalophlebioides sp. 1 and Ulmerophlebia sp. in the presence of leaf litter. No particular preference for leaf litter was evident at the main effect level or at any second-order interaction level involving leaf litter (Table 4). However, significant thirdorder interactions were apparent. For both species, mean numbers were consistent across the substratum types without leaf litter, generally decreasing with respect to increasing particle size. In the presence of leaf litter, this pattern was modified for the riffle trays, with the tendency toward greater abundance in leaf litter trays. It is interesting that this tendency for increased numbers in riffle/leaf litter trays relative to pool/leaf litter trays was common to all species except Baetis sp., though the relative importance of the trend was only significant for Atalophlebioides sp. 1 (Fig. 4A) and Ulmerophlebia sp. (Fig. 4C).

There was no significant separation by different size classes of any one species among the different types of substratum in the trays, and no size frequency analyses are presented.

The calculated indices for individual niche breadth (β) and proportional niche overlap (θ) for all species pairs are shown in Tables 5 and 6. Niche breadth varied considerably among the species. *Atalonella* sp. 4 and *Tasmanocoenis* sp. occupied rather small spatial niches compared with the other species (Table 5).

Within the riffle-preferring species, niche overlap was small ($\theta = 0.45$). For pool preferring species, θ -values were higher ($\theta = 0.56$ -0.79). The degree of overlap of pool species with the two riffle-preferring species,

Fig. 5. Summary of the major preferences exhibited by all species in the experiment to current, leaf litter, and rock size treatments. Major groupings are indicated by the letters A, B and C. RO-R3 indicate rock sizes. All links shown indicate significant preferences (Table 4, 3-way ANOVA, P < 0.05)

Table 5. Niche breadth indices for each species calculated using the Simpson-Yule Index, for all species where n > 20. The values for β indicate the extent to which species utilise the spectrum of available resources ($\beta_{max} = 16$)

Species	β
Atalophlebioides sp. 1	9.1760
Atalonella sp. 2	7.4414
Atalonella sp. 4	3.1726
Atalonella sp. 5	9.0733
Atalophlebia sp.	7.2053
Baetis sp.	12.5319
Tasmanocoenis sp.	3.8268
Ulmerophlebia sp.	7.7263

Atalonella sp. 2 and Atalonella sp. 4 is consistently low, as expected (Table 6). Tasmanocoenis sp. also showed low overlap with other species except Ulmerophlebia sp. These species had similar habitat preferences but Tasmanocoenis sp. had a clearer association with sandy substratum (82.6% by numbers) than did Ulmerophlebia sp. (36.5% by numbers); hence for Ulmerophlebia sp., there was higher proportional overlap with other pool-preferring species.

Discussion

In his review of resource partitioning in ecological communities, Schoener (1974b) nominated habitat segregation as the most commonly observed ecological strategy for the division of resources available to individual populations within a community. For Yuccabine Creek, the

1 Atalophlebioides sp.1							
2 Atalonella sp. 2	0.4732						
3 Atalonella sp. 4	0.2499	0.4500					
4 Atalonella sp. 5	0.7311	0.4525	0.2733				
5 Atalophlebia sp.	0.6827	0.3545	0.2186	0.7950			
6 Baetis sp.	0.6820	0.4445	0.3213	0.6702	0.5795		
7 Tasmanocoenis sp.	0.3850	0.3093	0.1695	0.3650	0.4317	0.3417	
8 Ulmerophlebia sp.	0.7075	0.4142	0.1946	0.6693	0.6652	0.5663	0.5918
	1	2	3	4	5	6	7

Table 6. Proportional niche-overlap for all species pairs (where n > 20) for the spatial resource dimension. Values of θ indicate how much of the available resource is used in common by each pair. (0.00 = no overlap; 1.00 = total overlap)

field data and the tray experiment showed that there can be distinct partitioning of the available habitat within the stream bed. Although there was no single controlling factor, all species showed significant bias towards either pool or riffle, and there were significant interactions with one or both of the other treatments (Table 4). These results concur with studies of temperate streams where combinations of factors have been shown to be of more importance than any single habitat feature (Ulfstrand 1967; Rabeni and Minshall 1977; Teague et al. 1985; Williams and Moore 1985).

The multiple regression analysis of the field data gave the best statistical fit to the data, but, because of the correlation between independent variables, it cannot necessarily provide the most appropriate causal explanation for distributions. For example, current and leaf litter commonly feature together in the models (Table 1); however, the distribution of leaf litter is strongly influenced by current velocity (Rabeni and Minshall 1977). Factorial experiments are more useful in separating the effects and interactions of the significant variables controlling micro-distribution.

As the analysis of the field data was based on samples from throughout a year, it was not expected that strong relationships with environmental variables would be found as both the variables and possibly the animals' requirements change throughout the year. The strength of some relationships, therefore, is interesting, and suggests consistency in responses through the year. We have yet to perform the necessary experiments to test whether habitat preferences change with season and with developmental stage for each species.

The tray experiment showed that for all but two species a preference for the pool habitat was predominant. The negative relationships revealed in the regression models also demonstrated the preference for the lower current velocities, or the avoidance of faster currents. Rock size was also of significance in habitat preference and often involved interactions with leaf litter and current. Thus, as suggested by Minshall and Minshall (1977), the substratum acts as a multi-factor variable. Variables not examined in this study, such as texture of the substratum, or micro-spatial complexity (Hart 1978), and degree of compaction (extent of interstitial spaces),

as well as particle size, may affect species composition and abundance. High current velocity and rock size are more likely to be primary factors for collector-filterers such as caddisflies (Edington 1968), simuliid larvae (Culp et al. 1983) and the shrimps Australatya striolata of Yuccabine Creek (Smith 1987) that rely on optimum flow characteristics for their filtering mechanisms and need specific attachment sites on rock surfaces. The importance of low current for the collectors may be in its role as a provider of detrital food, which clearly accumulates in patches of low current velocity. For the mayflies, which are predominantly collector-gatherers of fine detritus, the distinct partitioning of the habitat is perhaps surprising. Notwithstanding this partitioning, most species did occur throughout the habitats presented, indicating the ability of most species to inhabit a range of habitats, or possibly selection of the optimal microhabitat within the habitat offered. Close study of microdistribution with respect to individual rock surfaces and so on would help elucidate this problem.

It is interesting to note the response of each species to the availability of leaf litter and organic detritus. In the riffle, where detritus deposits are relatively small, densities of all species were greater in the leaf litter trays as compared with non-leaf litter trays. In contrast, in the pool, where detrital deposits are extensive, the densities of each species in leaf litter trays and non-leaf litter trays did not show such a marked difference. Detrital deposits were substantially higher in the pool than in the riffle. As food, in the form of organic detritus deposits, was less available in the riffle trays, leaf litter may have assumed a greater importance as a food resource, or detrital trap, for detritivores. Furthermore, the leaf-packs offer an organised, stable substratum, in addition to their ability to accumulate potential food items. In the pool, with low currents and large detrital deposits, leaf litter would be less important as a food source or a substratum. Thus, it appears that the detritus and leaf litter were of primary importance in mayfly micro-distribution; but it is the current velocity and substratum particle size that determine the distribution of these detrital and litter deposits (Orth and Maughan 1983).

In the riffle areas of Yuccabine Creek, litter and fine detritus accumulate under and between rocks and other obstructions, resulting in a patchy distribution (Pearson et al. 1986). It is possible, therefore, that the patchiness and extent of detrital and litter deposits strongly influence population densities of mayflies (and other species) in the riffle. In the pools, natural accumulations of litter are considerably larger and decline only during the wet season spates, concomitant with a decline in invertebrate densities (unpublished data).

It is thus probable that the significantly greater detrital deposits in the pool trays account for species' preferences and the higher total number of individuals found in the pool (Reice 1980; Fahey 1985; McCulloch 1986). However, other factors may produce or contribute to this effect. For example, Benson and Pearson (1987b) have shown that pools are depositional sites for drifting insects in Yuccabine Creek. In the present study there were long sections of riffle (200-400 m long) and shorter pool sections (5-10 m long) upstream of the pool and riffle sites. Hence in this region of riffle-dominated stream, pools would be expected to contain higher densities of organisms as the result of such deposition, although in this region, by their sheer extent, riffles contribute much greater proportions of the total populations of the stream.

Comparison of the apparent habitat preferences shown in the field and experimental data show some agreement and some discrepancies. For example, while current was shown to be significant in both situations for Atalonella sp. 2 and Atalonella sp. 4, for other species it was significant in the field but not the experiment. Similarly, leaf litter was variously significant for different species. The best explanation for the discrepancies is in the lower degree of resolution of microhabitat differences in the field samples. Each sample could quite easily contain a mixture of the microhabitat features, with only the predominant ones being employed in the analysis. This highlights a problem of habitat description in streams which, in their riffle sections at least, are remarkably heterogeneous. The tray experiment was done for this very reason – to separate out more explicitly each of the designated habitat variables.

With respect to interspecific competition for resources such as space, there is need for considerable caution when interpreting measures of resource overlap (Hart 1983; McAuliffe 1983). Demonstration of resource overlap can be evidence neither for nor against the existence of competition (Colwell and Futuyama 1971; Sale 1974). Overlap may simply reflect similarities and differences in the species' independently evolved foraging strategies and tolerances to local conditions (Ebeling and Laur 1986), and thus the species may be distributed about the stream bed to their own best advantage, independently. However, this may result in competition if densities are high enough.

With the drying of the stream in the dry season, the amount of usable habitat in the riffles diminishes gradually (Pearson et al. 1986), leading to a concentration of animal populations. During this period resources may become limiting, and it is the period, if any, during which competition between species may occur. The seasonal nature of the stream may thus be a factor that influences competitive interactions between species. In the summer wet season populations may be reduced below the levels at which competition might occur by spates and increasing stream size which disperse and dilute the fauna (Benson and Pearson 1987a), and by insect emergence (Benson and Pearson 1988). We plan to examine the effects of increasing densities of mayflies on habitat preferences and perhaps refuges in further studies.

It is unlikely that the results from Yuccabine Creek are typical for tropical streams generally as the character of other streams, especially in the wet equatorial tropics, can be very different. For example, the Gombak in Malaysia is unlike Yuccabine Creek in that it maintains high base flows throughout the year, and it has a much more diverse mayfly fauna, probably including mostly obligate lotic species (29 species at a site comparable with Yuccabine Creek: Bishop 1973). In such a stream there is no seasonal concentration of populations caused by reducing flows, and so there is no potential for the possible seasonally-enhanced competitive interactions discussed above. However, this does not deny the possibility of other types of interactions. Study of a rich fauna in a virtually aseasonal stream would clearly be most informative.

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