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Diel Migration and Microhabitat Distribution of a Benthic Stream Assemblage

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Macroinvertebrate microspatial distributions were determined on nonglazed brick substrates at three sites on the upper Colorado River. Site 1 was located above a reservoir, whereas Sites 2 and 3 were located 0.4 and 4.0 km, respectively, downstream from a deep-release dam. Replicate samples from each substrate surface (top, sides, front, back, and bottom) and from the interstices below brick substrates were collected during the day (ca 14:00–16:00) and at night (ca 21:00–23.00) in the summer and autumn of 1982. Although most macroinvertebrates occurred on "bottom" surfaces, "top," and "side" surfaces and the interstices were often utilized. Macroinvertebrates were least abundant on "back" and especially "front" surfaces. Total macroinvertebrate density on upper substrate surfaces was not significantly different at night compared with the day. However, there was a 47% increase in the density of *Baetis* spp. on upper surfaces during the night at Site 1, a diel shift in benthic substrate utilization that corresponded to drift periodicity. The density of *Baetis* spp. on upper surfaces during the night compared with the day was not significantly different at Sites 2 and 3. Large-sized *Baetis* spp. at Site 1, but not at Sites 2 and 3, used a greater proportion of upper substrate surfaces at night compared with the day.

Nous avons mesuré la microrépartition spatiale des macroinvertébrés sur des substrats de brique non vernie à trois sites du cours supérieur du Colorado. Le site 1 se trouve au-dessus d'un réservoir, tandis que les sites 2 et 3 sont situés respectivement à 0,4 et 4,0 km en aval d'un barrage à déversoir bas. Nous avons recueilli de façon répétée des échantillons sur chaque surface du substrat (dessus, côtés, devant, derrière et dessous) et dans les interstices au-dessous des substrats de brique pendant la journée (14h00 à 16h00 env.) et pendant la nuit (21h00 à 23h00 env.) au cours de l'été et de l'automne 1982. Si la plupart des macroinvertébrés se retrouvaient sur les surfaces du dessous, ils occupaient aussi souvent celles du dessus et des côtés, ainsi que les interstices. Les animaux étaient moins abondants sur les surfaces de derrière, et encore moins sur les surfaces de devant. La densité totale des macroinvertébrés sur les surfaces supérieures des substrats ne marquait pas de différence significative entre le jour et la nuit. On notait toutefois une augmentation de 47 % de la densité de *Baetis* spp. sur les surfaces du dessus pendant la nuit au site 1, modification nycthémérale de l'utilisation du substrat benthique qui correspondait à la périodicité de la dérive. La densité de *Baetis* spp. sur les surfaces du dessus la nuit par rapport au jour ne présentait pas de différence significative aux sites 2 et 3. Les *Baetis* spp. de grande taille, au site 1 mais non aux sites 2 et 3, utilisaient une plus grande proportion de la surface supérieure des substrats la nuit par rapport au jour.

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Several studies, both correlative and experimental, provide information concerning the factors which influence the microhabitat distribution of benthic macroinvertebrates in streams (e.g. Linduska 1942; Cummins 1964; Egglishaw 1969; Kohler 1983; Kovalak 1976; Rabeni and Minshall 1977; Hart 1978; Wise and Molles 1979; Reice 1980; Culp et al. 1983; Flecker and Allan 1984). These studies have examined patterns of macroinvertebrate distribution at a variety of spatial scales ranging from small plots to single stones. Very few studies, however, have used individual rock surfaces. Macroinvertebrates respond to environmental variables (e.g. current velocity and food patchiness) which vary over individual rock surfaces. The first objective of this study was to determine the microspatial distribution (substrate surface selection) of the macroinvertebrate assemblage at an unregulated, and a regulated and at a recovery site on the Upper Colorado River. We chose these sites in order to investigate the influence of stream regulation (flow constancy and high periphyton density) on the use of substrate surfaces by macroinvertebrates.

Diel changes in macroinvertebrate micro-habitat distributions can be related to explanations of diel drift periodicity (e.g. Allan et al. 1986). If periods of peak densities on upper substrate surfaces correspond to periods of peak drift then both active and passive mechanisms may explain the diel pattern of drift. However, if density on upper substrate surfaces and in the drift do not correspond, then active mechanisms must be operating. The second objective of this study was to determine the pattern of diel movements in the substrate and discuss its significance with respect to potential drift mechanisms.

Allan (1978 and 1984) found that a greater proportion of insects in larger size classes demonstrated a pattern of nocturnal drift. He suggested that large nymphs would tend to drift at night because of a greater mortality risk during the day due to

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size-selective predation by drift-feeding fish. In a nearly fishless stream, Casey (1987) found that small, not large, mayflies showed a diel shift in benthic substrate utilization by moving onto exposed surfaces at night. The third objective of this research was to determine if a greater proportion of large *Baetis* spp. nymphs utilized upper substrate surfaces during the night compared with daylight hours at three sites with abundant trout populations.

Methods

Site Descriptions

Three sampling stations (rubble riffle sites) were located in the upper Colorado River in the vicinity of Granby Reservoir in the state of Colorado, USA. Except for the influence of stream regulation, sites were similar with regard to elevation (2426–2593 m a.s.l.), gradient (0.006–0.009), canopy cover, geology, abundant trout populations, and riparian vegetation. The first site, an unregulated free-flowing riffle, was selected as a reference site. Site 2, 0.4 km downstream from Granby Dam, was located in an intensely regulated stream section. Site 3, located 4.0 km downstream from Granby Dam, exhibited at least partial recovery from the effects caused by the upstream impoundment. Complete site descriptions can be found in Rader and Ward (1988 and 1989).

Macroinvertebrate Micro-Habitat Distributions (Objective 1)

Microspatial distributions of the macroinvertebrate fauna were determined on dark brown, nonglazed, rectangular brick substrates (23 × 19 × 9.5 cm). Bricks with similar texture across all surfaces were chosen. Clay substrates are commonly used in benthic studies because they provide a uniform size and shape and because they are readily colonized by both periphyton and invertebrates (e.g. Kovalak 1979; Rosenberg and Resh 1982; Lamberti and Resh 1985; Tuchman and Stevenson 1980). Sixteen brick substrates were placed at 1-m intervals in four rows on the stream bed at each site with the long axis parallel to the flow. All brick substrates were placed in the stream 4 wk prior to sampling. Periphyton succession and accumulation on bare substrate requires approximately 3 wk (e.g. Korte and Blinn 1983; Reisen and Spencer 1970; Tuchman and Stevenson 1980). Brick surfaces were sampled for animals in June, July, September, and October of 1982 and June of 1983. Sampling of upper surfaces (top, sides, front, and back) consisted of sweeping (by hand) organisms into a net (30 × 20 cm rectangular opening; 240-μm mesh) positioned immediately downstream from the surface to be sampled. Eight different bricks were randomly chosen and used to sample four "top" surfaces and four "side" surfaces (one surface/brick). Four bricks were used to sample four "front" and four "back" surfaces. The "bottom" surface and "interstices" were sampled on four previously unsampled bricks. The "bottom" surface sample consisted of: (1) organisms swept from the bottom surface, and (2) organisms in the top centimetre of gravel, whereas the "interstices" sample consisted of organisms inhabiting the substrate from 1–10 cm below the brick. Before sampling the "bottom" and the "interstices," all organisms clinging to exposed surfaces were gently swept downstream. Then the brick was lifted and organisms on the "bottom" surface and for approximately 1 cm into the underlying gravel were swept into a Surber sampler (240-μm mesh). The substrate beneath the brick was agitated to approximately 10 cm and the dislodged organisms were swept into a second Surber sampler. All macroinvertebrates were preserved in 5% Formalin before sorting, identification, and enumeration. Microdistributional results based upon brushing macroinvertebrates from substrate surfaces could be biased for those species responsive to human movements. By quickly placing the net in position without disrupting the flow over the substrate, most macroinvertebrates on upper surfaces could be accurately sampled. For example, *Baetis* spp. nymphs were surprisingly docile in responding to human movements. However, data on *Cinygmula* spp., an extremely agile mayfly nymph (Allan et al. 1986), were excluded from this study because of its quick running response to human movements.

An analysis of variance was used to determine significant relationships between the dependent variable (macroinvertebrate density) and three main effects ("Position," "Site" and "Diel"). "Position" had six levels (top, sides, front, back, bottom, and interstices), whereas "Site" had three levels (Sites 1–3). "Diel" had two levels (day versus night samples). Macroinvertebrate density was calculated by dividing the area (cm^2) of each surface into the number of individuals collected per sample. Interstitial surface area was assumed to be 2× the bottom surface area. This assumption probably underestimated the amount of interstitial space and therefore, exaggerated the density estimates of the shallow interstitial habitat (<10 cm). Periphyton and detritus dry weight were included in the analysis as a covariate. The dry weights of periphyton (primarily filamentous green algae) and detritus (>240 μm) were determined from the same samples used to estimate macroinvertebrate densities on individual surfaces. Diagnostic procedures indicated that macroinvertebrate density and periphyton dry weight required a log transformation to stabilize the variance.

Diel Epibenthic Movements (Objective 2)

The prevalence of immigration and emigration in most stream communities (e.g. Townsend and Hildrew 1976) made it necessary to determine macroinvertebrate density on both the top and bottom of substrates during the day and at night. Four "top," "sides", and "bottom" surfaces and "interstices" were sampled at night between 21:00 and 23:00 at each site in July, September, and October (1982) on the same days that mid-afternoon (ca 14:00–16:00) samples were collected. Bricks used to sample "side" surfaces during the day were used at night to sample "top" surfaces, whereas bricks used to sample "top" surfaces during the day were used for "sides," and "bottom" surfaces and "interstices" at night. Sampling the same brick but different surfaces during the day and again at night did not appear to affect the night samples because mobile organisms (e.g. *Baetis* spp.) had adequate time to recover and slow-moving and sessile organisms were unaffected. A battery-operated head lamp covered with red cellophane was used to locate brick substrates at night. Macroinvertebrates were collected in nets, as opposed to direct observations, because visual surveillance (especially at night) was difficult on the "top" and "side" surfaces. However, drift from upstream sources could have biased our results if drifting nymphs represented a substantial portion of the total number of nymphs collected. Since sampling events were of short duration (<30 s), this concern seemed unwarranted.

An analysis of variance was used to determine if there were significant relationships between the dependent variable and three main effects ("Surface," "Site," and "Diel"). Total macroinvertebrate density and *Baetis* spp. density were used as

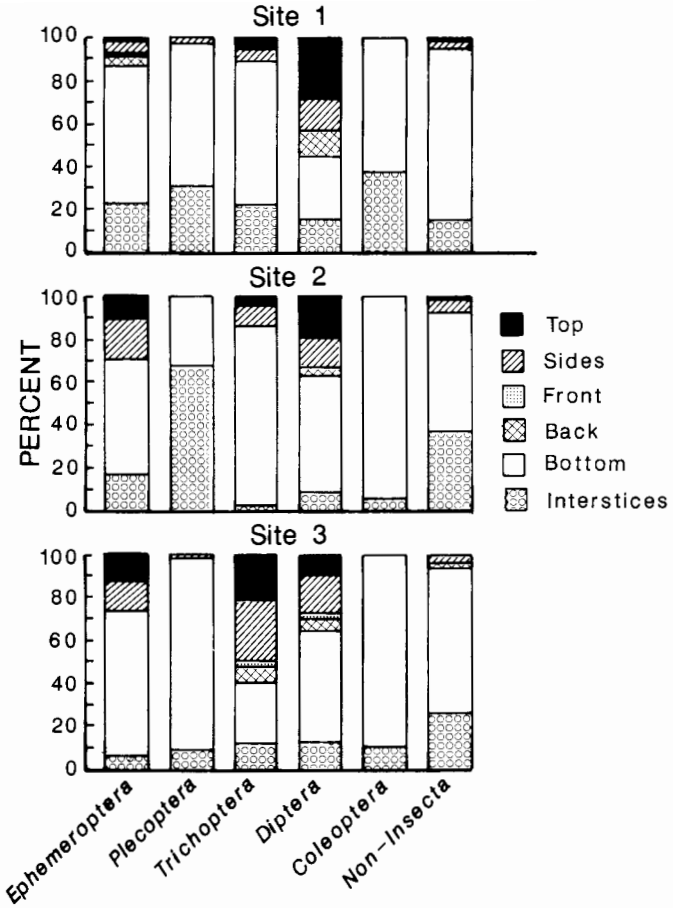

FIG. 1. Percent of macroinvertebrate density by taxonomic orders utilizing brick substrate surfaces and the interstices at each site. "Non-Insecta" included Turbellaria, Nematoda, Oligochaeta, *Hydra* spp. and Hydracarina.

response variables in separate analyses. "Surface," "Site," and "Diel" were the same as above.

Baetis Body Size/Diel Relationship (Objective 3)

Baetis spp. nymphs were collected from each surface during the day and night as described above. All nymphs were dried at 60°C for 48 h and placed in one of four size classes (0.01–0.25, 0.251–0.5, 0.51–0.75, and >0.751 mg). An analysis of variance was used to determine if there were significant relationships between the response variable (*Baetis* spp. density) and three main effects ("Position," "Size," and "Diel"). "Position" had two levels, "exposed" (combined samples from top and side surfaces) and "concealed" (combined samples from bottom and interstices), whereas "size" had four levels corresponding to the four size classes. "Diel" was the same as described above.

Results and Discussion

Macroinvertebrate Micro-Habitat Distributions (Objective 1)

As expected, macroinvertebrates did not utilize all surfaces equally; "Position" of invertebrates on substrate surfaces was a significant ($P<0.001$) main affect. Table 1 summarizes the density data for selected taxa at each site. Although most macroinvertebrates occurred on the "bottom" surface, both "top" and "side" surfaces and the interstices were often utilized (Fig. 1). Only an occasional chironomid or the tricopteran *Glossosoma* spp. occurred on "front" surfaces which were oriented perpendicular to the force of the flow (Table 1). Nor were macroinvertebrates abundant on the "back" surfaces where flow tends to spiral in turbulent vortices (Osborne et al. 1985). The Diptera, Trichoptera, and Ephemeroptera (minus *Baetis* spp. and *Cinygmula* spp.) utilized a greater proportion of exposed surfaces ("top," "sides," and "front") compared with the Plecoptera, Coleoptera, and non-Insecta, which utilized primarily "bottom" surfaces and interstices (Fig. 1).

Macroinvertebrate micro-habitat distribution differed significantly ($P<0.001$) between sites and the abundance of macroinvertebrates on substrate surfaces was significantly ($P<0.001$) correlated ($r^2 = 0.96$) with the dry weight biomass of periphyton and detritus. Species eliminations and reductions and habitat modifications (dense growths of filamentous algae) resulting from stream regulation (see Rader and Ward 1988) account for the site differences. Periphyton density on upper substrate surfaces and detritus accumulations were strongly correlated with macroinvertebrate density because both are important determinants of macroinvertebrate microdistributions (e.g. Minshall 1984). None of the interactions between the main effects from the analysis was significant.

Except for *Baetis* spp. which will be considered separately, *Pseudocloeon* spp. and *Siphlonurus occidentalis* (Eaton) were the primary Ephemeroptera utilizing exposed surfaces at Site 1 (Table 1). However, thick mats of filamentous green algae at Sites 2 and 3 allowed a greater percentage of typically cryptic mayflies (*Ephemerella infrequens*, McDunnough; *Drunella grandis*, Eaton; *Paraleptophlebia heteronea*, McDunnough) to occupy exposed surfaces. Dorso-ventrally flattened heptageniid mayflies (*Epeorus longimanus*, Eaton; *Epeorus albertae*, McDunnough and *Rhithrogena hageni*, Eaton) primarily utilized "bottom" surfaces at each site. Although the Plecoptera at Site 2 preferred the interstitial habitat (Fig. 1), only two taxa (*Amphinemura banksi*, Baumann and Gaufin; *Isoperla* spp.) were collected. The much more diverse plecopteran fauna at Sites 1 and 3 (Rader and Ward 1988) preferred "bottom" surfaces (Table 1). *Glossosoma* spp. were rare at Site 2 but accounted for most of the Trichoptera occupying exposed surfaces at Sites 1 and 3. At Site 2, *Rhyacophila* spp. found in the filamentous algae were the only Trichoptera using exposed surfaces. The most abundant Trichoptera (*Arctopsyche grandis*, McLachlan and *Rhyacophila* spp. at Site 1, *Hesperophylax designatus*, Banks and *Oligophlebodes minutus*, Ulmer, at Site 2 and *Lepidostoma ormeum*, Rambur and *Glossosoma* spp. at Site 3) primarily inhabited "bottom" surfaces and/or the interstices (Table 1). Chironomids and simuliids were the dominant dipterans on exposed surfaces at each site, whereas a variety of taxa utilized "bottom" surfaces and the interstices (e.g. *Hexatoma* spp., *Wiedemania* spp., *Bezzia* spp., *Atherix* spp. and numerous chironomid species). The Coleoptera exclusively used concealed surfaces (Fig. 1). A greater standing crop of sedimentary detritus at Site 1 compared with both sites downstream from the dam (Rader and Ward 1988) may account for the larger percentage of Coleoptera using the interstitial habitat at Site 1. At all three sites, *Hydra* spp. were the major non-Insecta inhabiting "top" and "side" surfaces, whereas the turbellarian *Polycelis coronata* (Girard), Hydracarina, and

TABLE 1. The mean densities (numbers/cm^2) of selected taxa are shown for each substrate surface during the day and night at each site. Values in parentheses represent the standard deviation for each mean. Surfaces 1, 2, 3, 4, 5, and 6 represent top, sides, front, back, bottom, and interstices, respectively.

			Surface					
Taxa	Site	Day/Night	1	2	3	4	5	6
Baetis spp	1	D	0.0060 (0.0112)	0.0320 (0.0187)	0.0277 (0.0055)	0.1069 (0.0681)	0.0954 (0.0360)	0.0028 (0.0026)
		N	0.0292 (0.0137)	0.1075 (0.0466)	— —	0.0055 (0.0060)	0.0453 (0.0024)	0.0015 (0.0021)
	2	D	0.1077 (0.0260)	0.2823 (0.1107)	0.0792 (0.0603)	0.1301 (0.1551)	0.4661 (0.1663)	0.0401 (0.0632)
		N	0.2741 (0.1038)	0.9121 (0.0567)	0.0664 0.0254)	0.1457 (0.1096)	0.7929 (0.0503)	0.0463 (0.0186)
	3	D	0.1077 (0.0028)	0.2347 (0.0979)	0.0216 (0.0254)	0.1052 (0.1157)	0.2032 (0.0803)	0.0173 (0.0148)
		N	0.2144 (0.1665)	0.3981 (0.2178)	0.0193 (0.0188)	0.0554 (0.0415)	0.2258 (0.1029)	0.0140 (0.0120)
Epeorus longimanus	1	D	—	—	—	0.0265 (0.0155)	0.0167 (0.0066)	—
		N	—	—	—	—	—	—
	2	D	—	—	—	—	—	—
		N	—	—	—	—	—	—
	3	D	0.0029 (0.0013)	0.0045 (0.0045)	— —	0.0094 (0.0033)	0.0938 (0.0045)	— —
		N	—	0.0105 (0.0082)	— —	— —	0.0823 (0.0457)	— —
Ephemerella infrequens	1	D	0.0006 (0.0011)	0.0045 (0.0036)	— —	0.0072 (0.0033)	0.3313 (0.1678)	0.0110 (0.0036)
		N	—	—	—	—	0.0677 (0.0258)	0.0048 (0.0024)
	2	D	0.0281 (0.0171)	0.0265 (0.0137)	— —	0.0027 (0.0033)	0.0784 (0.0254)	0.0042 (0.0073)
		N	0.0091 (0.0130)	0.0860 (0.0379)	— —	— —	0.0572 (0.0032)	0.0185 (0.0096)
	3	D	0.0366 (0.0315)	0.1281 (0.0718)	— —	0.0470 (0.0653)	0.0915 (0.0379)	0.0110 (0.0129)
		N	0.0876 (0.0773)	0.0961 (0.1432)	— —	0.0055 (0.0011)	0.1434 (0.0320)	0.0125 (0.0016)
Drunella grandis	1	D	—	—	—	—	0.0018 (0.0009)	0.0003 (0.0005)
		N	—	—	—	—	0.0016 (0.0011)	—
	2	D	0.0048 (0.0038)	0.0169 (0.0082)	—	—	0.0075 (0.0027)	—
		N	—	0.0100 (0.0137)	—	—	—	—
	3	D	0.0057 (0.0059)	0.0173 (0.0100)	—	0.0083 (0.0072)	0.0114 (0.0082)	0.0026 (0.0017)
		N	0.0098 (0.0102)	0.0183 (0.0064)	—	—	0.0235 (0.0199)	0.0014 (0.0026)
Paraleptophlebia heteronea	1	D	—	—	—	—	0.0496 (0.0327)	0.0057 (0.0029)
		N	—	—	—	—	0.0528 (0.0409)	—
	2	D	0.0084 (0.0050)	0.0192 (0.0082)	—	—	0.00075 (0.0011)	—
		N	0.0018 (0.0020)	0.0164 (0.0096)	—	—	0.0070 (0.0043)	—
	3	D	—	—	—	—	—	—
		N	—	—	—	—	—	—
Siphlonurus occidentalis	1	D	0.0001 (0.0025)	0.0402 (0.024)	—	—	0.0267 (0.0192)	0.0033 (0.0019)
		N	0.0022 (0.0027	0.0091 (0.0022)	—	—	0.0308 (0.0279)	—
	2	D	—	—	—	—	—	—
		N	—	—	—	—	—	—
	3	D	—	0.0128 (0.0100)	—	—	0.0842 (0.0443)	0.0048 (0.0033)
		N	—	0.0059 (0.0096)	—	—	0.1304 (0.0354)	0.0030 (0.0052)

TABLE 1. (*continued*)

Taxa	Site	Day/Night	Surface 1	2	3	4	5	6
Amphiremura banksi	1	D	—	—	—	—	0.0016 (0.0025)	—
		N	—	—	—	—	0.0020 (0.0041)	—
	2	D	—	—	—	—	0.0016) (0.0013)	0.0003 (0.0005)
		N	—	—	—	—	—	—
	3	D	—	—	—	—	0.0059 (0.0043)	0.0021 (0.0010)
		N	—	—	—	—	0.0073 (0.0045)	0.0009 (0.0013)
Taenionema spp.	1	D	—	0.0013 (0.0022)	—	—	0.0132 (0.0102)	0.0014 (0.0005)
		N	0.0040 (0.0011)	0.0059 (0.0059)	—	—	0.0068 (0.0137)	0.0003 (0.0005)
	2	D	—	—	—	—	0.057 (0.0020)	—
		N	—	—	—	—	—	—
	3	D	—	—	—	—	—	—
Glossosoma spp.	1	D	0.0064 (0.0022)	0.0045 (0.0036)	0.0016 (0.0033)	0.0016 (0.0044)	0.0077 (0.0041)	0.0013 (0.0006)
		N	—	0.0013 (0.0022)	—	—	0.00098 (0.0050)	—
	2	D	—	—	—	—	—	—
		N	—	—	—	—	—	—
	3	D	0.1233 (0.1070)	0.3011 (0.2778)	0.0188 (0.0182)	0.0947 (0.1019)	0.0125 (0.0082)	0.0014 (0.0017)
		N	0.0922 (0.0784)	0.2897 (0.1070)	—	0.0808 (0.0858)	0.3105 (0.1528)	0.0251 (0.0279)
Lepidostoma ormeum	1	D	—	—	—	—	—	—
		N	—	—	—	—	—	—
	2	D	—	—	—	—	—	—
		N	—	—	—	—	—	—
	3	D	0.0004 (0.009)	0.0137 (0.0157)	—	—	0.0739 (0.0324)	0.0035 (0.0026)
		N	0.0006 (0.0013)	0.0045 (0.0064)	—	—	0.0221 (0.0098)	—
Rhyacophila spp.	1	D	—	—	—	—	0.0118 (0.0025)	0.0014 (0.0009)
		N	—	—	—	—	0.0086 (0.0048)	—
	2	D	0.0038 (0.0048)	0.0032 (0.0027)	—	—	0.0082 (0.0027)	—
		N	—	0.0050 (0.0086)	—	—	0.0089 (0.0050)	—
	3	D	—	—	—	—	0.0096 (0.0070)	0.0025 (0.0012)
	N	—	—	—	—	—	0.0130 (0.0144)	—
Polycelis coronata	1	D	—	—	—	—	0.0052 (0.0027)	0.0016 (0.0012)
		N	—	—	—	—	0.0089 (0.0045)	0.0010 (0.0008)
	2	D	—	—	—	—	0.0018 (0.0006)	0.0011 (0.0009)
		N	—	—	—	—	0.0070 (0.0061)	—
	3	D	—	0.0068 (0.0086)	—	0.0072 (0.0066)	0.02006 (0.1498)	0.0163 (0.0141)
		N	0.0040 (0.0048)	0.0022 (0.0045)	—	—	0.1709 (0.0274)	0.0072 (0.0056)

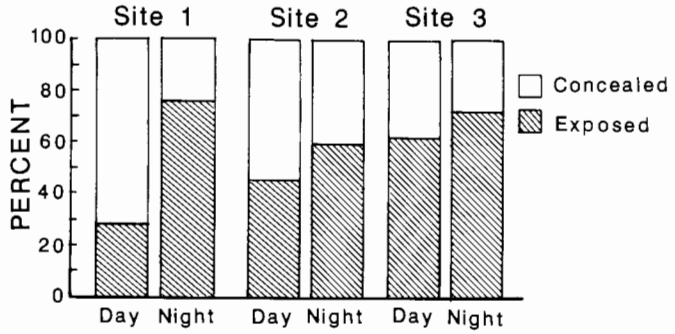

FIG. 2. Percent of *Baetis* spp., based on density estimates, utilizing exposed ("top" and "side" surfaces) versus concealed ("bottom" surface and interstices) micro-habitat space during the day and at night.

Nematoda primarily comprised the non-Insecta on "bottom" surfaces and in the interstices (Table 1).

Diel Epibenthic Movements (Objective 2)

The relationship between drift periodicity and benthic diel migration remains unclear. In some investigations, increased densities on the upper surfaces of stones at night appeared to correspond with periods of peak drift (Elliott 1968; Campbell 1980; Bailey 1981; Casey 1987; Wilzbach et al. 1988), whereas other studies demonstrated either greater densities during the day (Graesser and Lake 1984; Statzner and Mogel 1985; Allan et al. 1986) or no difference between day and night density estimates (Clifford 1972; Kovalak 1979; Kohler 1983). With respect to the total macroinvertebrate assemblage, this study demonstrated that there were no significant ($P = 0.87$) density differences on the upper surfaces of stones at night compared with the day. Similarly, the "Diel" main effect was not significant ($P = 0.21$) when data for *Baetis* spp., a common member of the drift, were analyzed separately. However, the "Diel" × "Site" interaction term ($P = 0.07$) suggested that there were significant differences in the density of *Baetis* spp. on exposed surfaces during the night compared with the day at one or more sites. At Site 1, there was a 47% increase in the density of *Baetis* spp. on exposed surfaces at night compared with the day (Fig. 2 and Table 1). Also, a majority of *Baetis* spp. occurred on concealed surfaces during the day and exposed surfaces at night. The density of *Baetis* spp. on exposed surfaces at Site 1 did not correspond to periods of peak drift; therefore, both active and passive mechanisms could explain drift periodicity at this site. Although *Baetis* spp. utilized a greater proportion of exposed surfaces at night compared with the day at Sites 2 and 3, this trend was not significant (Fig. 2). The abundance of filamentous algae downstream from the dam increased habitat heterogeneity and probably diminished prey detection by fish, providing refugia from predators and the current, on upper substrate surfaces making them more similar to concealed bottom surfaces. Therefore, *Baetis* spp. at Sites 2 and 3 may utilize upper and lower surfaces with equal frequency without experiencing increased predation on current-related dislodgement which are typically associated with upper, exposed surfaces.

A review of the literature indicated no relationship between the methods used to detect a response and the diel movement of mayflies from concealed to exposed surfaces. Half of the six studies demonstrating an increase in density on upper substrate surfaces during the night used a substrate sampling technique (Elliott 1968; Campbell 1980, Site 1 of this study), whereas, the other half used observational methods (Bailey 1981 and 1982; Wilzbach et al. 1988; Casey 1987). One out of three studies demonstrating a decrease in density on exposed surfaces during the night used a substrate-sampling technique (Graesser and Lake 1984). The remaining two used observational methods (Statzner and Mogel 1985; Allan et al. 1986). Three out of four studies indicating no difference in density between exposed and concealed surfaces from day to night used a substrate sampling technique (Clifford 1972; Kovalak 1979; Sites 2 and 3 of this study), while, one used observational methods (Kohler 1983). It appears that response differences may be attributable to natural biological variation and not necessarily methodological biases.

Substrate sampling techniques, compared with observational methods, provide information on the distribution of organisms across all substrate surfaces and are equally accurate during the day or at night. Viewing box observational methods do not disturb the substrate but can only record data from upper surfaces and often require a bright red light for night observations (Casey 1987). Although some mayflies responded similarly during the daylight hours to artificial white light, red light, and no artificial light (Casey 1987), aquatic insects may be able to detect and avoid red light (Harker 1953), especially bright sources of red light at night. The nighttime response of aquatic insects to various intensities of red light should be tested against observations using infrared light. Night observations, however, have been accomplished using dim sources of red light (e.g. Allan et al. 1986) and ambient light intensifiers (Statzner and Mogel 1985). Poor visual acuity may be a problem with both methods, but especially when using light intensifiers. Most night observations can be best accomplished using video cameras (e.g. Peckarsky and Wilcox 1989) with infrared capabilities. Recent technology (fiber optics with infrared enhancement) has allowed relatively undisturbed observations over small portions of the bottom surface where interstitial openings are sufficiently large (Wilzbach et al. 1988). At present, fiber optics has been used primarily in laboratory experiments (Wilzbach et al. 1988). Each method has advantages and disadvantages which must be considered with respect to site-specific environmental conditions, and the hypothesis being tested.

Baetis Body Size/Diel Relationship (Objective 3)

Smaller sized *Baetis* spp. (0.01–0.1 mg) at Site 1 utilized a greater proportion of exposed surfaces (day and night) compared with larger *Baetis* spp. (Fig. 3). This trend, however, was not observed at either Sites 2 or 3. The large-sized *Baetis* spp. (0.45–>1.0 mg) at site 1 also utilized a significantly ($P<0.05$) greater proportion of exposed surfaces during the night compared with the day (Fig. 3). This pattern was not evident for large-sized *Baetis* spp. at Sites 2 and 3. The growth of abundant filamentous algae at both sites below the dam likely provided cover for *Baetis* spp. utilizing exposed surfaces. Therefore, the risk of predation from visual predators was reduced and nymphs did not use exposed surfaces more frequently during the night compared with the day. Therefore, only data from Site 1 supports the hypothesis that the density of large nymphs on exposed surfaces should increase at night to reduce predation from visually feeding predators (i.e. trout). Although Casey's (1987) data did not support this hypothesis, he was working in a small second order stream with "no fish presently in the study area." All three sites in this study support abundant populations of (*Oncorhynchus mykiss*) (Richardson), *Salmo trutta* (Linnaeus) and *Salvelinus fontinalis* (Mitchell). It appears, therefore, that

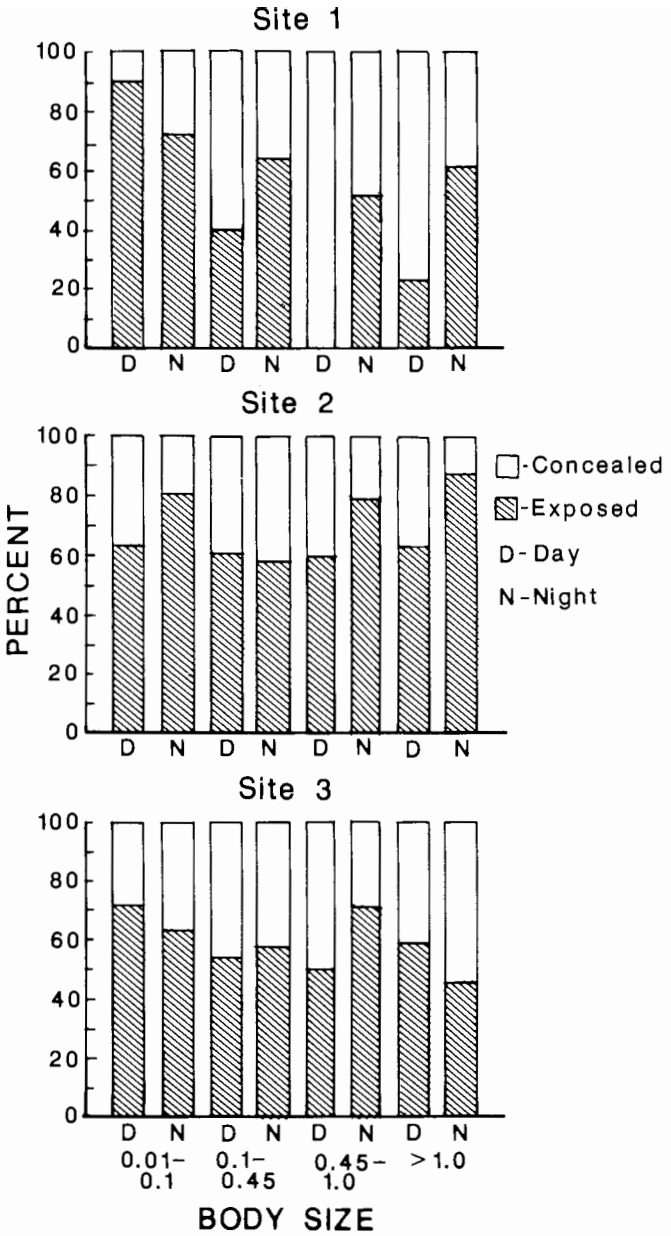

FIG. 3. Percent density of four *Baetis* spp. body size categories utilizing exposed ("top" and "side" surfaces) versus concealed ("bottom" surface and interstices) micro-habitat space during the day and at night. Size categories represent milligrams of dry weight biomass.

where the risk of predation is high (e.g. Site 1 where upper substrate surfaces are not covered with filamentous algae and moss), larger nymphs may become increasingly more nocturnal in their use of exposed substrate surfaces.

Summary and Conclusions

Stream regulation indirectly influenced macroinvertebrate microhabitat utilization in the upper Colorado River. Constant flow conditions (daily and seasonally) reduce the influence of scouring and increases bed substrate stability allowing abundant growths of periphyton to cover upper substrate surfaces, thereby providing prey refugia and altering microcurrent flow conditions across exposed substrate surfaces. Several of the larger sized mayfly species (e.g. *Drunella grandis*) as well as other typically cryptic macroinvertebrate taxa were able to use upper substrate surfaces because of the periphyton cover. Although the total macroinvertebrate fauna did not shift from concealed to exposed substrate surfaces on a diel basis, *Baetis* spp. density at Site 1 on exposed surfaces significantly increased at night due to the behavior of the larger size classes. This pattern corresponds with periods of peak drift densities and is therefore consistent with both passive and active explanations for drift periodicity in streams. Furthermore, the movement of large bodied *Baetis* spp. onto exposed substrate surfaces during the night at Site 1 supports previous discussions concerning fish predation and the proportionately greater number of large-sized *Baetis* spp. in the drift (Allan 1978). Periphyton growth on upper substrate surfaces at sites downstream from the dam provided predator and current refugia allowing *Baetis* spp. to utilize bottom and upper surfaces with roughly equal frequency during the day and night.

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