UTILIZATION OF COARSE WOODY DEBRIS BY EPHEMEROPTERA IN THREE OZARK STREAMS OF ARKANSAS

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ABSTRACT—Collections of ephemeropteran nymphs were made from both coarse woody debris (CWD) and benthic habitats from the White River, Illinois River, and Clear Creek of northwestern Arkansas, from February 1991 through February 1992. Two-way analysis of variance comparing the density of mayflies between habitat types, and among seasons yielded significant main effects only with habitat type. There was no two-way interaction. Mayflies were significantly more abundant in benthic habitats than on CWD. Of at least 35 species of mayflies, 11 were collected in significantly greater densities from benthic habitats, and only two from CWD. Degree of decay was an important factor in determining the abundance of species on CWD. Species with a preference were more abundant either on wood with loose bark remaining, or well decayed wood containing many interstitial spaces. The volume of biofilm on CWD was a factor in determining the abundance of only one species.

Coarse woody debris (CWD) has been shown to influence fluvial processes and channel form (Keller and Swanson, 1979), to store large quantities of organic matter, and to physically increase stream heterogeneity (Trotter, 1990). The utilization of woody debris as habitat by aquatic insects has only recently received attention (Nilsen and Larimore, 1973; Anderson et al., 1978; Dudley and Anderson, 1982; Pereira et al., 1982; Benke et al., 1984; Smock et al., 1985).

While some aquatic insect species are obligated to living on woody debris because they feed on wood fibers, Dudley and Anderson (1982) and Pereira et al. (1982) collected only one species of mayfly (*Cinygma integrum* Eaton) that they considered to be closely associated with wood. Those two studies indicated that all genera of Ephemeroptera collected from snags contained traces of wood fibers in their digestive tracts. However, the presence of wood was attributed to mayfly feeding by scraping, and wood fiber ingestion was secondary to Aufwuchs consumption; therefore, all associations of ephemeropterans, other than *C. integrum,* were listed as facultative (Dudley and Anderson, 1982).

Many mayfly species colonize woody debris facultatively, as substrate. Three investigations conducted in southeastern blackwater streams reported greater densities of mayflies from snags than from benthic habitats (Benke et al., 1984; Smock et al., 1985; Jacobi and Benke, 1991). The primary reason given for higher snag abundances was that the sand and mud benthic substrates were too unstable to support high densities of most species of large insects (Benke et al., 1984). However, the burrowing species *Dolania americana* Edmunds and Traver (Berner and Pescador, 1988) and *Hexagenia bilineata* (Say) (Fremling, 1960) have been collected in high densities in streams with sand and mud bottoms.

While recent investigations of wood debris have increased our knowledge concerning the use of these habitats by aquatic insects, there are still many questions that remain unanswered about these habitats. The primary objectives of this study were: (1) to determine if mayflies colonized CWD in the same densities that they colonized benthic habitats; (2) to determine if season affected the utilization of either habitat type; (3) to determine the species level differences of mayflies inhabiting both types of substrate; (4) to determine if microhabitat factors associated with the degree of decay and the volume of biofilm affect Ephemeroptera densities on CWD.

MATERIALS AND METHODS—Ephemeroptera nymphs were collected monthly from the White River, Illinois River, and Clear Creek, from February 1991

TABLE 1—Methods for evaluating the degree of decay of woody debris, modified from Robison and Beschta (1990).

Decay class	Bark	Twigs	Texture	Shape	Wood color
I	Intact	Present	Intact	Round	Original
II	Beginning to loosen	Absent	Intact	Round	Original
III	Some loose bark remaining	Absent	Smooth, some surface abrasion	Round	Center original, edges dark
IV	Absent	Absent	Some holes and openings	Round to oval	Dark
V	Absent	Absent	Many holes and openings	Irregular	Dark

through February 1992. Three sample sites were established in each order of first through third order reaches of the White River, second through fourth order reaches of the Illinois River, and first through third order reaches of Clear Creek. Collections were made from both coarse woody debris (CWD) and benthic habitats at all sample sites.

Coarse woody debris in this study included submerged snags, logs, chunks of wood resulting from the breakdown of larger snags and logs, and large branches—after the definitions by Harmon et al. (1986), and Robison and Beschta (1990). Each piece of CWD was evaluated, and placed into one of five categories designating its degree of decay (Table 1). Volumetric measurements of biofilm were also taken from each piece of CWD. Sampling was done by scraping all the biofilm from three 5-cm^2 areas, and measuring their volume, by water displacement, in ml in a 10-ml graduated cylinder. Mean volumes of biofilm per piece of CWD were then converted to ml/cm^2. Categories of biofilm density were: light, less than 0.2 ml/cm^2; moderate, between 0.2 ml/cm^2 and 0.8 ml/cm^2; heavy, greater than 0.8 ml/cm^2. Biofilm included any plant or animal material growing on the CWD (Hax and Golladay, 1983).

Coarse woody debris samples were taken by placing a mesh bag (243 μm mesh size) over the wood so that no insects could escape as the wood was removed from the water, cutting the wood with a bow saw, if necessary, and removing it from the water. Coarse woody debris samples were taken in quantities sufficient to equal approximately 1.5 m^2 per site per month. Visible insects were removed from the log and mesh bag at stream side and preserved in 70% ethanol. The logs were later washed into a bucket to remove any additional mayflies, which were sorted by pouring the water through a standard sieve series, then sorting remaining insects from an enamel pan. The wood was then placed in a five-gallon bucket to dry for five days, and any remaining mayflies were collected as they left the drying wood. Mayfly nymphs were then identified and enumerated. The surface area of each piece of CWD was calculated from a conversion factor derived from the weight of plastic food wrap used to cover them (Doeg and Lake, 1981; O'Connor, 1991). Densities of mayflies per square meter were calculated using this information.

In addition to snag samples, 10 benthic samples were taken at each site during each month. Benthic samples were taken using a Surber sampler (243 μm mesh size), and all samples were preserved in the field in 95% ethanol and later sorted, stored in 70% ethanol, identified, and counted in the laboratory. Surface area of each benthic sample was estimated from the measurements of substrate particle size at each site. Plastic wrap (Doeg and Lake, 1981) was used to cover individual stones of different size classes, and surface area was calculated from a conversion factor of the weight of plastic wrap and total mass of each size class of stones (Shelly, 1979; Reice, 1980).

Substrate particle size was measured by first collecting three samples from the top 10 cm of substrate at each sampling site. Each sample was sorted into phi size classes, -6 through 3, and weighed to the nearest 0.01 g according to the methods outlined by Briggs (1981). Water temperature was measured weekly, and the monthly mean was calculated. Dissolved oxygen was measured during each sampling period using a YSI Model 54 oxygen meter. Flow rate was measured using the orange floatation method during each sampling period.

Two-way analysis of variance (ANOVA) was performed on mayfly density to determine interactions among habitat type (benthic vs. CWD), and season (spring, summer, fall, winter). The Student-Newman-Keuls (SNK) multiple-range test was used to compare mayfly density where significance was detected.

One-way ANOVAs were performed on individual mayfly species to determine if there was a significant difference in density between CWD and benthic hab-

TABLE 2—Mean annual density/m^2 ($\pm SE$) of the most commonly collected Ephemeroptera nymphs on benthic substrates and coarse woody debris (CWD) (one-way ANOVA results, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

Taxon	Benthic	CWD
Acentrella carolina (Banks)	50 ± 18	22 ± 9
Acerpenna pygmaea (Hagen)	19 ± 6	3 ± 1
Baetis frondalis McDunnough	12 ± 2***	2 ± 1
B. propinquus (Walsh)	9 ± 3	7 ± 3
Isonychia rufa McDunnough	42 ± 10***	1 ± <1
Leucrocuta hebe (McDunnough)	28 ± 8**	0 ± 0
Stenacron interpunctatum (Say)	12 ± 2***	2 ± 1
Stenonema femoratum (Say)	16 ± 3	13 ± 3
S. mediopunctatum (McDunnough)	111 ± 18***	13 ± 3
S. pulchellum (Walsh)	22 ± 4***	6 ± 2
S. terminatum (Walsh)	45 ± 13*	13 ± 4
S. integrum (McDunnough)	10 ± 3**	0 ± 0
Ephemerella spp.	1 ± 1	6 ± 2*
Eurylophella temporalis (McDunnough)	1 ± 1	10 ± 2**
Tricorythodes atratus (McDunnough)	10 ± 5	5 ± 2
Caenis anceps Traver	151 ± 56**	5 ± 2
C. hilaris (Say)	14 ± 4*	1 ± 1
C. latipennis Banks	8 ± 1	17 ± 8
Leptophlebia cupida (Say)	8 ± 1	6 ± 2
Ephemera simulans (Walker)	57 ± 15***	0 ± 0
Ephoron album (Say)	415 ± 132**	0 ± 0

itats. Two-way ANOVAs were conducted with the eight most abundant mayfly species collected from CWD to determine if factors associated with the degree of decay, and/or the volume of biofilm growing on the CWD influenced their density. The alpha level of significance for all statistical tests was 0.05.

RESULTS—At least 35 species of Ephemeroptera were collected from both habitat types combined. One-way ANOVAs revealed 13 species that were collected in significantly different densities from CWD and benthic habitats (Table 2). Of these, 11 were collected in greater densities from benthic habitats, and two were collected in greater densities from CWD (Table 2). One species, *Stenonema exiguum* Traver, was collected only from CWD, but was collected in low densities.

Two-way ANOVA comparing habitat type, and season revealed significant main effects differences only between habitat types ($F = 28.18$, $P = 0.0001$). Student-Newman-Keuls analysis (SNK) showed that benthic habitats supported significantly greater densities of Ephemeroptera nymphs than did CWD ($P < 0.01$). Mean annual mayfly density in benthic habitats was 562 ± 102/m^2, and mean annual density on CWD was 97 ± 9/cm^2. The greatest seasonal density of mayflies occurred during the summer (492 ± 208/m^2), followed by spring (337 ± 128/m^2), fall (307 ± 138/m^2), and winter (181 ± 33/m^2). None of these differences were significant ($F = 2.12, P = 0.1382$). Two-way interactions between habitat type and season ($F = 2.71$, $P = 0.0798$) were not significant.

Two-way ANOVAs comparing densities of species collected from CWD among different degrees of decay and different volumes of biofilm revealed four taxa that were influenced by degree of decay, and one that was influenced by biofilm volume (Table 3). Three species were not affected by these factors (Table 3). *Ephemerella* sp. nymphs were collected in the greatest densities from wood in decay classes III and V, followed by wood in classes II and IV, and were least abundant on wood in class I (SNK $P < 0.05$). *Eurylophella temporalis* density was most influenced by biofilm volume, and it was collected in its greatest densities from wood with heavy, followed by moderate, and then light biofilm volumes (SNK $P < 0.01$). There was a two-way interaction between decay and biofilm and the density of *E. temporalis,* indicating that *E. temporalis* preferred wood in decay stages III and V with heavy volumes of biofilm. The three species of *Stenonema* that we examined all showed a preference for decay class. *Stenonema femoratum* was most abundant on class III wood, followed by wood in classes II, IV, and V, and least abundant on wood in Class I (SNK $P < 0.05$). *Stenonema mediopunctatum* had its greatest densities on wood in classes II, III, and V and was least abundant on wood in classes I and IV (SNK $P < 0.05$). *Stenonema terminatum* was most abundant on wood in class V, followed by wood in classes II, III, and IV, and least abundant on wood in class I (SNK $P < 0.05$).

Mean substrate particle size was −5.7 phi in the White River, −5.2 phi in the Illinois River, and −5.5 phi in Clear Creek. Overall, substrate particle size ranged from −6.1 phi to −4.5 phi which is classified as cobbles to coarse gravel using the Wentworth grade (Briggs, 1981). Overall mean size was −5.5 phi which is classified as coarse gravel.

TABLE 3—Results of two-way ANOVAs testing the effects of the degree of wood decay and the volume of biofilm on the density of Ephemeroptera nymphs (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

	F ratio		
Taxon	Decay	Biofilm	Decay/biofilm
Acentrella carolina	2.20	1.09	0.50
Caenis latipennis	0.67	0.46	0.01
Ephemerella spp.	9.02**	3.66	1.80
E. temporalis	2.23	4.04*	3.41*
Stenonema femoratum	4.73**	2.28	0.96
S. mediopunctatum	3.76**	0.75	1.46
S. terminatum	2.73*	0.91	1.55

DISCUSSION—Our results showing greater densities of mayflies in benthic habitats over CWD were different from those reported from studies in southeastern blackwater streams, where mayfly abundance and production was much higher on wood than in benthic habitats (Benke et al., 1984; Smock et al., 1985; Jacobi and Benke, 1991). Probably the most significant factor causing higher abundances on snags in blackwater streams versus Ozark Streams is the substrate. Blackwater streams have primarily a sand or mud bottom which is very unstable (Benke et al., 1984; Smock et al., 1985). Ozark streams, on the other hand, have a much more stable coarse gravel to cobble substrate. The larger substrate in Ozark streams allows ephemeropteran nymphs to inhabit more of the stream benthos rather than relying on wood habitats for substrate.

Comparisons between benthic and snag abundances at the family level were provided by Jacobi and Benke (1991) for the Ogeechee River, Georgia. They collected all families of ephemeropterans (Baetidae, Heptageniidae, Tricorythidae, Ephemerellidae, Oligoneuriidae, and Caenidae—in descending order of abundance) in greater densities from snags than from benthic habitats. In contrast, we found significantly greater abundances of Baetidae, Heptageniidae, Tricorythidae, Isonychiidae, and Caenidae (also Leptophlebiidae, Potamanthidae, Ephemeridae, and Polymitarcyidae) in benthic habitats rather than on wood debris. The only family we found to have greater densities on snags was Ephemerellidae.

Other investigations, such as those in the Pacific northwest (Anderson et al., 1978; Dudley and Anderson, 1982; Pereira et al., 1982) do not provide enough information on species densities to allow comparisons with our investigation. However, we collected species from all families reported by Dudley and Anderson (1982) and Pereira et al. (1982) except Siphlonuridae. Additionally, we collected species representing the families Isonychiidae, Tricorythidae, and Caenidae which those investigators did not collect from wood.

Although the majority of mayflies in Ozark streams preferred benthic habitats to CWD some exploited both habitat types, and those that did appeared to use wood only facultatively, as substrate, which agrees with the findings of Dudley and Anderson (1982). We collected one species, *S. exiguum*, only from snag habitats; however, it was collected in densities too low to draw definite conclusions about its affinity for woody debris.

Mayfly species collected from CWD that showed a preference for decay stage were generally collected in greater densities from wood in stages II, III, and V decay. All species with a preference were collected in their lowest densities from wood in decay class I. Stages II, III, and V provide mayflies with either loose bark (classes II and III), or with interstitial spaces (class V) in which to conceal themselves. Decay stage IV provides some interstitial space, but usually much less than stage V wood. Mayflies that were collected from class I wood were usually found near the points of branch attachment. Dudley and Anderson (1982) found greater densities of insects on well-conditioned wood that contained interstitial space, and concluded that well-conditioned wood provided protection from predators and the abiotic environment. O'Connor (1991) found that grooved wood was more heavily colonized by some invertebrate species groups than was smooth wood.

Nilsen and Larimore (1973) found that logs with more surface texture accumulated more Aufwuchs, and were more heavily colonized by invertebrates. Hax and Golladay (1993) found that increased biofilm development was correlated with macroinvertebrate density on wood substrates. During our study, *E. temporalis* was the only species that showed a preference for wood with heavy volumes of biofilm. All specimens of *E. temporalis* that we collected were themselves covered with large amounts of biofilm. This selection for heavy volumes of biofilm could be used to conceal them from predators. Another possibility is that some component of the biofilm may provide a source of food for *E. temporalis*.

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