Substrate Associations and Longitudinal Distributions in Species of Ephemerellidae (Ephemeroptera: Insecta) from Western Oregon[1]

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Abstract. Substrate associations and longitudinal distributions are described for 12 species of Ephemerellidae. Habitat specialization seems to have been a major means of adaptive radiation within this family. All species showed restrictive use of available habitats: sand-gravel, cobble, boulder, or moss. Patterns of longitudinal distribution may be, in part, a consequence of the specificity that species show for different substrates.

Mayflies in the family Ephemerellidae are often important and conspicuous members of stream communities. Eighty species in eight genera are currently recognized in North America. Thirty-two species occur in the western United States and Canada, 24 of which occur in Oregon. Although the taxonomy of species in this family has been well studied (Allen 1980; Edmunds et al. 1976), relatively little quantitative information exists by which to compare ecological differences among species.

The purpose of this study was to 1) describe patterns of habitat use among 12 species occurring in a single drainage basin and 2) examine whether habitat use may explain, in part, distribution patterns along a river continuum.

STUDY SITES AND METHODS

All sampling sites were located in streams draining the western Cascade Mountains (Fig. 1). Animals were collected at eight sites during April and June 1979 and February 1980. Sites were located along a longitudinal gradient extending from the headwaters of Mack Creek to the McKenzie River, a seventh order stream (Table 1). Dominant habitats changed gradually with location along this continuum. Bedrock and moss were most abundant at the headwater site, cobble and rubble at intermediate sites, and sand and gravel at the largest river site (Table 1).

At each site I collected from different habitats classified by substrate type. Classification of habitats based on substrate type alone clearly ignores other variables that may influence distributions. Substrate was chosen as the basis for classification for these reasons: 1) habitat patches were easily and quickly classified in the field, 2) others (e.g., Tolkamp 1980) have shown substrate to be a major factor affecting local abundance, and 3) other important factors (e.g., current) are often strongly correlated with substrate type.

Habitat classes used in this study were not chosen to reflect all the subtle differences in physical conditions that might be important to a specific species (i.e., microhabitats).
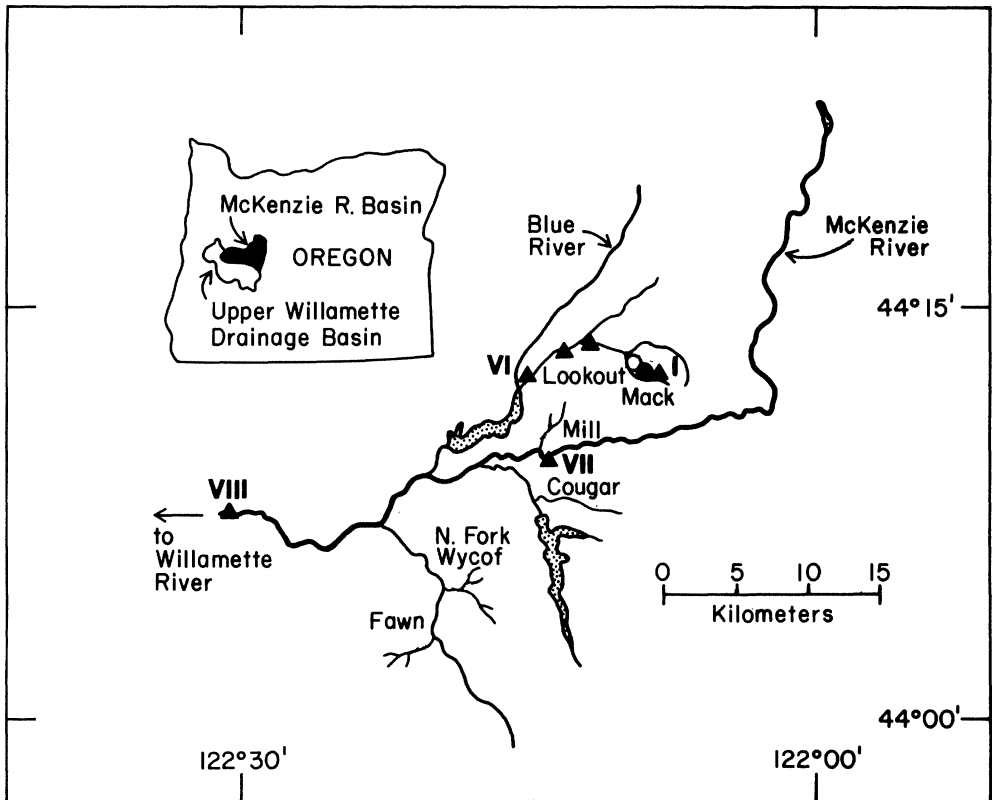
Fig. 1. Location of the study sites. See Table 1 for site descriptions.

TABLE 1

Physical characteristics of sites on the longitudinal gradient from headwaters to the McKenzie River.

Name of Stream	Mack	Mack	Mack	Lookout	Lookout	Lookout	McKenzie	McKenzie
Sampling Station	I	II	III	IV	V	VI	VII	VIII
Order	2	3	4	4	5	5	7	7
Elevation (m)	915	760	730	549	435	420	365	260
Gradient (%)	45	10	5	5	3	3	0.6	0.2
Bank-full width (m)	3	12	20	20	24	18	40	50-60
Dominant Substrates*	BR,M	B,C	B,C	B,C,G	B,C,G,S	G,S	C,G,S,M	G,S
Canopy	coniferous	coniferous	open	open	open	open	open	open

*BR = bedrock; B = boulder; C = cobble; G = gravel; S = sand; M = moss.

Measurement of such differences and collection of animals from many different microhabitats were outside the scope of this study. Rather, I chose to sample from a few distinctly different habitats that spanned the range of substrate types occurring at each site. As a result of such a classification, species with subtle difference in habitat use (e.g., upstream vs. downstream side of cobble) would appear similar in their substrate preferences. On the other hand, observed variation among species in use of substrate classes defined here should reflect distinct differences in habitat preferences. Because I was most interested in describing the extent of adaptive radiation in habitat use among these species, I emphasized sampling that would distinguish major differences among species rather than subtle ones. I used the following substrate classes when sampling:

1) Tops of boulders and bedrock (B),
2) Areas of cobble and rubble of approximately fist sized (ca. 10 cm) stones (C),
3) Areas of gravel and sand with stones <20 mm in diameter (G),
4) Growths of filamentous and sheetlike algae attached to boulders and cobbles (usually *Prasiola* or *Vaucheria*), and
5) Patches of moss (M).

Mosses consisted of *Fontinalis* sp. in the McKenzie River and a mixture of species at other sites.

Samples were collected with a standard D-frame kicknet (mesh = 0.5 mm). A D-frame net was used rather than standard 'quantitative' samplers (e.g., Surber, Hess) because of the difficulty in sampling heterogeneous habitats with such devices. Rigid frames could not be placed effectively over many habitat types (e.g., tops of boulders in rapid current). Conversely, the D-frame net could quickly be positioned to minimize open space between the bottom of the net and the substrate. Approximately 0.1 m^2 of substrate was then disturbed by hand to wash animals into the net. Efficiency of sampling was almost certainly affected by lack of side panels, but this was probably less important of a sampling bias than the positioning problems encountered with other samplers.

Habitats were sampled roughly in proportion to their occurrence at each site. Between 5 and 22 samples were taken at each site on each date depending on stream size and diversity of habitats. After a sample was taken, it was placed in a white enamel pan with water. Ephemerellid mayflies were removed and placed into labeled vials containing 80% ethanol. Individuals were later identified and counted in the laboratory.

Data from the raw samples were treated in the following manner. For each site the total number of individuals in each species observed over all three dates was noted and the mean density of each species calculated (habitats pooled). Similar calculations were made for each habitat (sites pooled). Based on these data the percent of total individuals within a species occurring at each site and in each habitat was calculated. These data are presented in Tables 2 and 3. Because I found very few individuals of Ephemerellidae associated with algae, I have deleted that habitat from the following comparisons. Also, abundances at Site VI (Lookout Creek) were always extremely low. Because data from this station are so anomalous compared with the rest, I have excluded these data from comparisons as well.

RESULTS

The 12 species considered in this report are *Caudatella cascadia* Allen and Edmunds, *C. hystrix* Traver, *C. heterocaudata* McDunnough, *C. edmundsi* Allen, *Serratella teresa* Traver, *S. tibialis* McDunnough, *Drunella pelosa* Mayo, *D. doddsi* Needham, *D. coloradensis* Dodds, *D. spinifera* Needham, *Ephemerella infrequens* McDunnough, and *Attenella delantala* Mayo.

Most of the species collected showed well-defined distributions with most individuals occurring at only one or two sites (Fig. 2, Table 2). Among sites, a longitudinal progression of species occurred. Species that were abundant in the headwaters were usually not found at the river sites and vice-versa. Approximately one-half of the species were most abundant in intermediate (III-V) sized streams. Three species (*C. edmundsi, S. teresa,* and *S. tibialis*) were only observed at one site. Two species were broadly distributed over most sites (*D. doddsi* and *E. infrequens*). Other species were intermediate in their distribution among sites.

Each species also showed rather restricted distribution among different habitats (Table 3). Three species were commonly found in gravel/sand, nine in cobble, three on tops of
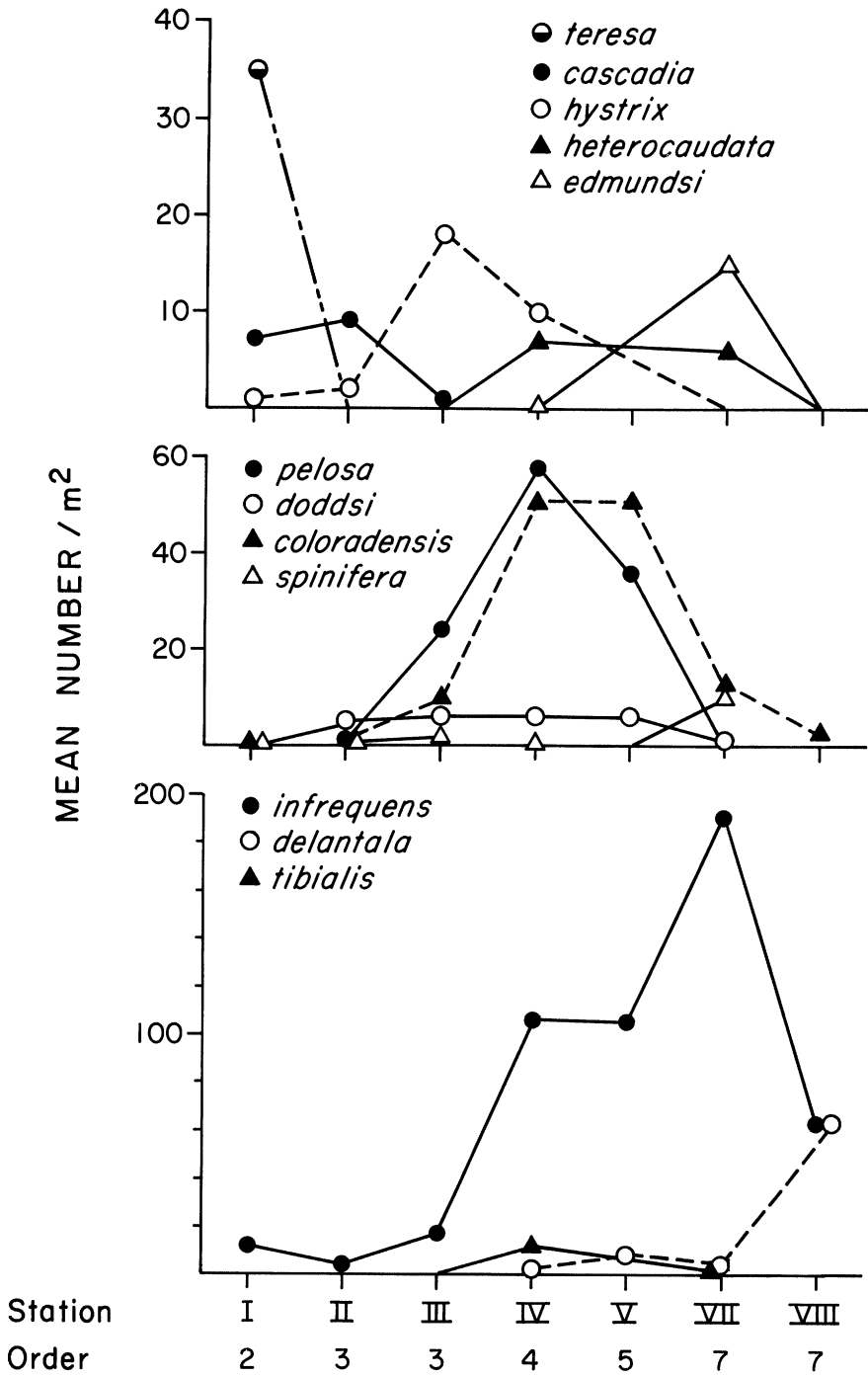
Fig. 2. Mean densities of the 12 species at each of the sampling stations.

TABLE II

Distribution of species of Ephemerellidae among transect stations. Data are percent of total numbers observed over all stations and sampling dates. Values rounded to nearest percent. Species ranked in order of upstream to downstream abundance.

Species	Total Individuals	Station						
		I	II	III	IV	V	VII	VIII
Serratella teresa	75	100	0	0	0	0	0	0
Caudatella cascadia	29	41	53	6	0	0	0	0
Caudatella hystrix	84	3	6	58	32	0	0	0
Serratella tibialis	52	0	0	0	100	0	0	0
Drunella doddsi	88	0	21	25	25	25	4	0
Drunella pelosa	351	0	1	20	49	30	0	0
Drunella coloradensis	149	0	1	11	38	38	10	2
Caudatella heterocaudata	52	0	0	0	34	33	33	0
Ephemerella infrequens	968	2	1	3	21	21	38	13
Drunella spinifera	41	0	6	12	6	0	75	0
Caudatella edmundsi	611	0	0	0	0	0	100	0
Attenella delantela	86	0	0	0	1	11	4	84
Number of species with ≥ 10% of individuals at a site		2	2	5	7	6	5	2

boulders, and five in moss. I arbitrarily considered a species to be common in a habitat if ≥ 10 percent of its total numbers was observed in that habitat. Inspection of Table 3 shows that species were generally associated with one or two of the habitat classes examined. No species showed abundances greater than 10 percent of total density in three or four habitats.

DISCUSSION

Zonation of stream faunas along longitudinal gradients is well documented (see reviews by Hawkes 1975, Illies & Botosaneanu 1963, Williams 1981). Species of most taxa invariably show restricted ranges along gradients, a phenomenon also true for Ephemerellidae (see also Allan 1975a,b; Ward & Berner 1980). The mechanisms determining these patterns are not always obvious, although among the speculations and hypotheses advanced include the effects of temperature (Dodds & Hisaw 1925; Ide 1935), food (Wiggins & MacKay 1978), substrate (discussed in Hynes 1970 and Maitland 1966), and competition (Allan 1975b; Beauchamp & Ullyot 1932).

Similarly, the spatial distributions of species over smaller scales (i.e., within a reach) are known to vary among species. These patterns have often been linked to species-specific preferences for different substrate types (Cummins & Lauff 1969; de March 1976; Linduska 1942; Rabeni & Minshall 1977; Williams 1980; Williams & Mundie 1978; Wise & Molles 1979; and reviews by Hynes 1970, Williams 1981). Other factors, however, are often correlated with substrate characteristics (e.g., current, depth, food), so it is often difficult if not impossible to isolate the role of substrate alone.

If habitat is a key factor determining the distributions of stream benthos, pattern at small scales should provide insights into pattern at larger scales. The 12 species considered here show a pattern of gradual species replacement along the longitudinal gradient of stream size (Table 2) as observed for many other taxa. If substrate specificity was an important factor influencing this pattern, substrate availability and species abundance at a site should be correlated. Data in Table 3 show this to generally be the case. With a few exceptions (see below), species restricted to moss were most abundant at upstream sites where moss was a major habitat. Species using sand-gravel habitats were most abundant

TABLE III

Percent habitat use by species of Ephemerellidae. Data as in Table II except that comparisons are among habitats. Habitats ranked from left to right in order of upstream to downstream dominance. Species ranked in order of upstream to downstream dominance.

| Species | Habitat | | | |
	Moss	Top of Boulder	Cobble	Sand-Gravel
Serratella teresa	85	0	14	1
Caudatella cascadia	46	54	0	0
Caudatella hystrix	22	72	6	0
Serratella tibialis	0	0	90	10
Drunella doddsi	0	2	89	9
Drunella pelosa	2	66	32	0
Drunella coloradensis	2	9	81	8
Caudatella heterocaudata	0	9	91	0
Ephemerella infrequens	2	1	40	51
Drunella spinifera	54	0	40	7
Caudatella edmundsi	100	0	0	0
Attenella delantala	0	0	70	30
Number of species with ≥10% of individuals in a habitat	5	3	9	3

at downstream sites where these substrates are most important. The two major exceptions to this trend actually support the contention that habitat is a key factor influencing distributions. *Caudatella edmundsi* and *Drunella spinifera* are both most abundant at a downstream site. These two species were collected most often in mats of the moss *Fontinalis* (*C. edmundsi* was found in no other habitats). This moss was common (not abundant) in the McKenzie River. Other mosses were abundant at the headwater site, but few patches of moss were observed at intermediate size reaches.

The pattern for intermediate size reaches to have more species than either upper or lower reaches agrees with predictions by Vannote et al. (1980) but may be a consequence of the dominance of cobble substrates in intermediate reaches rather than temperature. Cobble substrates had almost twice as many common species than any other habitat. The reason for this is probably that cobble substrates are complex habitats and share traits in common with most of the other habitat types. For example, the tops of cobbles are often sufficiently large to provide habitat similar to tops of boulders. Also, moss occasionally occurs on cobbles, sand and gravel deposit in the interstitial spaces around cobbles, and interstitial spaces provide a unique habitat.

Although species abundance and habitat availability appear to be correlated, cause and effect is clearly not demonstrated and it is not possible from these data to test habitat and temperature hypotheses. Only experimental evidence can distinguish with certainty the effect of habitat on distributions. However, sufficient correlative and comparative data exists for these species and others by which to hypothesize that habitat may be a key factor. Ranking of mean pairwise overlap in resource use among these same species shows that habitat is most important in separating species, time of year (temperature?) intermediate and food least important ($\bar{x} = 0.40$, 0.54, and 0.76 respectively, Hawkins 1982 and in prep.).

Restricted use of available habitats may in fact be the rule among stream invertebrates. In a far more extensive analysis of organism - substrate relationships of stream invertebrates, Tolkamp (1980) demonstrated that each of 84 taxa he encountered was overrepresented in one or more of seven habitat classes, that is, some habitats were

preferred over others. Exactly half of these taxa were strongly associated with only one of the habitats. Only 12 were overrepresented in three or more classes. The results of Tolkamp (1980) and this study are in apparent contrast to those of Williams (1980) who noted that only six of 23 taxa showed strong substrate associations. Habitat classes in Williams' study, however, were more subtle (particle size range = 3.5-64 mm) than those used by either Tolkamp (1980) or myself. As I did, Tolkamp (1980) examined distribution of species among all major habitats within a reach. Clearly, the extent to which habitat classes represent different environmental conditions must be considered and not just number of classes.

Although species may generally exhibit strong habitat specificity, the ecological and evolutionary basis for such specialization is not clear. Specificity is probably a consequence of numerous processes. Among these are: 1) differential foraging ability among habitats, 2) differential competitive ability among habitats, and 3) differential susceptability to mortality (e.g., predation) among habitats. Distinguishing between the numerous proximate factors that may influence habitat selection is difficult and determining the role of different ultimate (i.e., evolutionary) factors is almost impossible. Neither can proximate and adaptive responses to habitat always be cleanly separated from the effects of other factors. Ecological responses to multiple factors are often interactive and confounding in nature, whereas evolutionary responses are usually integrated. For example, a morphological trait may serve more than one function. Nonetheless, in our efforts to understand both the phylogeny of related species and patterns of community diversity, it is often both necessary and useful to first consider important factors separately. These ephemerellid mayflies show sufficiently strong substrate associations to suspect that adaptive radiation in the use of different habitats may be the basis for much of the taxonomic and ecological diversity observed in this family.

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