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THE DISTRIBUTIONAL ECOLOGY AND DIVERSITY OF BENTHIC INSECTS IN CEMENT CREEK, COLORADO[1]

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Abstract. Distributional patterns and species diversity of benthic insects in an alpine stream in Gunnison County, Colorado, USA were investigated on several levels of spatial scale, from faunal replacement over 1,000 vertical m to microdistribution within the stony substratum. Ecotones including zonation in terrestrial vegetation and in trout distribution did not appear to affect faunal replacement. Competition among congeners accounted for 7–30% of the cases, while in the majority of species, faunal replacement appeared to be associated with gradual changes in the physical gradient. Trout zonation may affect total numbers of insects, however, as the trout-free headwaters had two to six times higher insect densities.

Microdistribution was investigated by measures of species and substratum patterning in a series of microhabitats (0.093 m^2) at a series of sites (separated by 75–150 vertical m), and by field colonization experiments with various substratum choices. I hypothesize that increased substratum complexity leads to greater species richness based on several lines of evidence: (1) different species showed different substratum preferences, (2) colonization of mixed substrata generally resulted in greater mean species richness than did colonization of a single substratum type, and (3) both species diversity and substratum complexity were greatest at the within-microhabitat level. However, substratum composition showed little variation along the elevational gradient and did not appear to be a cause of faunal replacement.

The several scales of investigation were complementary, as congeners exhibiting sharp mutual exclusion in vertical distribution had similar microhabitat preferences, while other congeners showed less exclusion and differed in microhabitat preferences. Most of species diversity as measured by H' was found within habitats rather than between habitats while species richness depended equally upon within-habitat variation (owing to rare species) and between-habitat variation (owing to faunal replacement).

Key words: Colorado; competition; distribution; insects, aquatic, benthic; niche breadth; species diversity.

INTRODUCTION

Streams exhibit longitudinal zonation in such factors as temperature, current, substratum, and biota. As a result, studies of zonation have been common in stream biology, including the construction of various classification schemes (see Macan 1961, Hynes 1970 for reviews). Maitland (1966) argued that a variety of physical and chemical factors may be influential in limiting species range, with different species showing unique responses. As an alternative explanation several studies have implicated competition in faunal replacement (Beauchamp and Ullyot 1932, Maitland and Penney 1967). Over a stream's course several terrestrial vegetation zones may be encountered and Dodds and Hishaw (1925) argued that faunal replacement is accelerated at ecotones. Clearly a number of complex processes is indicated.

The study of ecological distributions has proceeded in a statistical and descriptive fashion; only recently have there emerged explicit models attempting to relate underlying dynamic processes to observed patterns. First, large-scale geographic distributions were examined as extinction-immigration equilibria (MacArthur and Wilson 1967). Later developments have included gradient analysis of faunal replacement on the scale of ecological range (Terborgh 1971) and microhabitat patches explained as equilibriar islands (Horn and MacArthur 1972). This study attempts to apply the above principles to an analysis of the distributional ecology of benthic stream invertebrates. Streams offer unique advantages: a pronounced elevational gradient, a stony-bottom microhabitat structure which may be measured and manipulated, and complex distribution patterns on the scale of 0.1 m^2 up to that of species' range. I analyze the roles of ecotones, competition and the physical-chemical gradient in determining faunal replacement, following the approach of Terborgh (1971). Microdistribution patterns are measured and habitat preferences evaluated from colonization experiments utilizing various manipulations of the stony substratum. Finally, I attempt to relate macrodistribution and microdistribution in the context of within-habitat and between-habitat diversity (MacArthur 1965) and demonstrate how each scale of investigation may aid in understanding the other.

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The study area

Cement Creek, Gunnison County, Colorado, is a tributary of the East River watershed. Originating in snowmelt at 3,600 m, Cement Creek receives no major tributaries and increases gradually in size without appearing to change in stream type as it flows towards its confluence with East River at 2,602 m. Vegetation along its valley may be divided into three broad zones (following Langenheim 1962): (1) upland herb above timberline at 3,475 m, composed of tall grasses, sedges and erect forbs, (2) Spruce-fir coniferous forest from 3,475 m to about 3,200 m, composed primarily of Engelman spruce (*Picea engelmanni*) and subalpine fir (*Abies lasiocarpa*), and (3) an aspen community type below 3,200 m. This latter community type is dominated by aspen (*Populus tremuloides*) but includes Engelman spruce and a generally greater plant diversity, added in the form of lodgepole pine (*Pinus contorta*), blue spruce (*Picea pungens*) and Douglas fir (*Pseudotsuga menziesii*), with regions of sagebrush (*Artemesia tridentata*) and fescue grasslands interspersed below 3,000 m. The boundary between zones 2 and 3 is not particularly distinct, in part because aspen seems to form a fairly stable zone between 2,900 m and 3,200 m, and is an early succession species colonizing burn and slide areas within the spruce-fir zone (Langenheim 1962). Scrub willows (*Salix* spp.) are the predominant riverbank vegetation throughout, except for upland herbs in the higher reaches of zone 1. The headwaters and upper two-thirds of Cement Creek lie in Gunnison National Forest and receive relatively little disturbance from occasional individuals and range cattle. Below 3,000 m more human use is evident including some residences and a public campsite at 2,800 m. In general, Cement Creek meets the necessary criteria of a uniform gradient, passing through distinct vegetation zones, relatively undisturbed by human use.

METHODS

Collecting techniques

Pilot studies were conducted in July 1972 and more detailed studies from 15 June to 15 August 1973. Sampling sites were chosen at intervals of ≈ 75 vertical m of elevation, and some additional areas were sampled occasionally. Both the fauna and the substratum were collected in a manner which allowed within- and between-microhabitat comparisons. At each site I collected 12 Surber samples 0.093 m^2 in area (Surber 1937) positioned as a 3 × 4 grid across the stream. The mesh size of 0.5 mm probably was adequate to retain most Ephemeroptera, Plecoptera, Trichoptera and Coleoptera during the period of sampling, but not Diptera which were excluded from the present analysis. Each sample was preserved separately in 70% alcohol. I also collected a kick sample obtained by thoroughly agitating the substratum directly in front of a rectangular net 44 cm long, 22 cm high and with a mesh size of 0.65 mm. Six individual kick samples were combined for a single collection at each site. The substratum was sampled at approximately 50% of the sites along the gradient in a 3 × 4 grid corresponding to the 12 Surber samples. A Surber frame was held in place while I removed all larger substrata (> 2 mm diam) corresponding to the surface region agitated in sampling the fauna. Each substratum sample was individually sorted through a series of Tyler sieves (2 mm–64 mm) according to numbers and volume in each category (Cummins 1962).

Sample size

Needham and Usinger (1957), Chutter (1972) and others have stressed the large number of samples (ca. 200) required to estimate numbers of invertebrates within ≈ 10% of the mean with 95% confidence; however, only a small number of samples will collect most of the commoner species (Leonard 1939, Hynes 1970). Some increase in statistical precision may be obtainable through the use of more sophisticated samplers (e.g., Mundie 1971). Chutter's (1972) studies and my own data agree that 12 Surber samples give an estimate of total numbers which falls within ± 30% of the mean with 95% confidence. Higher precision can be obtained only at greatly increased cost in sample size and for questions based on comparisons rather than absolute numbers, 12 samples were judged adequate.

An estimate of the number of species (species richness) present at a site was obtained by combining data from the 12 Surber samples, kick sample, and colonization experiments described below. The results were plotted against elevation and if a species was found to be absent from one site only, out of an otherwise unbroken string of observations, I assumed that it was present in the general area of that site but not collected in the sample. Rare species found only at scattered sites and in low numbers were not included in this manner. Species diversity (H') was calculated from Surber sample collections only. Although the number of species present was underestimated by 12 such samples, the diversity index H' was adequately estimated as it responds more to patterns in relative abundance than to species richness.

Habitat colonization

To determine substratum preference of different species, four size categories were chosen corresponding to substratum diameters > 64 mm, 32–64 mm, 16–32 mm, and 8–16 mm. On the phi scale (-$\log_2$: Krumbein 1936, Cummins 1962) these correspond to -6, -5, -4 and -3 respectively. Together these sizes constitute the predominant surface assemblage of the substratum in Cement Creek, and since current was sufficient to remove smaller sizes from the 22 cm × 30 cm enameled pans utilized to study colonization, these were the only practical categories for manipulation. Field experiments were conducted using four replicates of each of the four substrata arranged in a 4 × 4 latin square design to correct for possible variation along or across the stream bottom. A second 4 × 4 latin square was placed a few meters downstream from the first to provide further replication. The two sets of 16 pans were placed in 15–30 cm deep water on a given afternoon and retrieved the following morning. An analysis of variance testing the null hypothesis of no substratum preference was performed on the average result of the two. Experiments were conducted between 9 July and 22 July 1973 at sites 1 (2,602 m), 5 (2,725 m), 7 (2,820 m), 10 (2,990 m), 12 (3,140 m), and 14+ (3,440 m).

A second set of experiments was conducted to determine changes in habitat colonization over longer time. Three replicates were set at site 10 (2,990 m) on 22 July 1973 and destructively sampled on following days 2, 5 and 10. The design was reduced to a 3 × 3 latin square to provide sufficient colonization pans. As the one-day habitat colonization studies had indicated a general preference for larger size categories among all colonizers, only substratum categories > 64 mm, 32–64 mm and 16–32 mm were employed.

A third set of experiments was conducted to ascertain the effect of mixing substratum categories to increase habitat complexity. Substratum sizes > 64 mm, 32–64 mm, 16–32 mm and 8–16 mm were arranged into the six possible two-way combinations, four possible three-way combinations and the four-way combination. The various sizes were combined in approximately equal amounts by volume. Two replicates of the 11 pans of substrata were placed at site 12 (3,140 m) on 28 July 1973 and two replicates at site 5 (2,725 m) on 29 July 1973. They were retrieved the following day.

Trout distribution

Electrofishing of 160-m stretches of Cement Creek was conducted at each of six sites on 9 August 1973, with the cooperation of the Colorado State Division of Wildlife. This technique probably underestimated total numbers as it is less effective with the youngest age class (McFadden 1961), and fish attracted to the submerged anode and temporarily stunned must be scooped by net from rapidly flowing water. However, species distributions and minimum abundances may be determined. All fish were measured and weighed. Stomach contents were preserved in 70% alcohol.

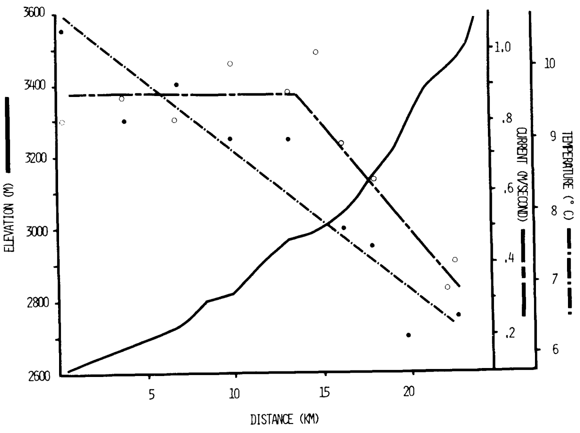

FIG. 1. Physical description of the Cement Creek gradient from snowmelt to its confluence with East River. Current is the average of three readings in the region of max flow 1–3 August 1973. Temperature is the average of max and min values over a 48-h period 1–4 July 1973.

RESULTS AND DISCUSSION

Physical gradient

Cement Creek exhibits a typical concave profile (Leopold et al. 1964) with prominent meadows at 2,800 m, 2,980 m, and 3,450 m (Fig. 1). Temperature appears to vary linearly (Fig. 1, $r^2 = 0.91$). Above 3,000 m, current flow decreases linearly with elevation, whereas in the lower reaches of Cement Creek there is considerable variation and no clear trend.

Faunal replacement

Faunal replacement patterns appeared to be constant as range and relative abundance data showed little variation between the 2 years of observation. The analysis is based on 37 species of Ephemeroptera, Plecoptera, Trichoptera and Coleoptera. Diptera were excluded because of taxonomic difficulties but were represented by the Tipulidae, Simuliidae and especially the Chironomidae. The restricted sampling period (June through August) is obviously a limitation of the present study. As an alpine stream, Cement Creek may show a lesser degree of seasonal variation in species composition than do lowland streams, but further work is necessary to clarify this point.

Several trends are discernable along the stream elevational gradient. Species richness decreased with

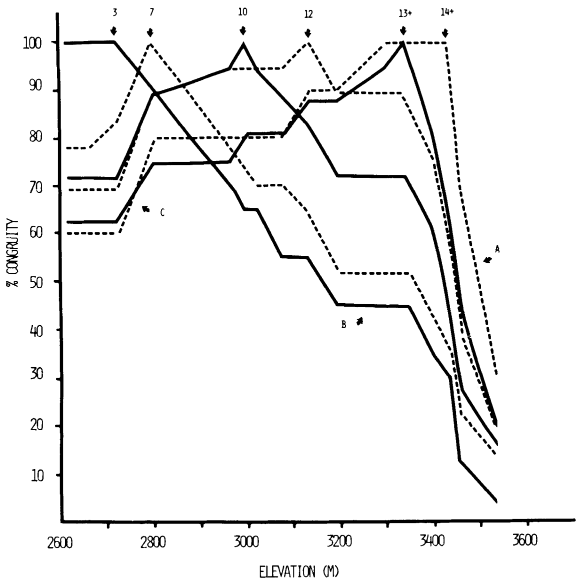

FIG. 2. Faunal congruity curves representing the degree of faunal replacement along the gradient. Each site is taken in turn as a reference point and the similarity of faunal lists at all other sites is expressed as a percentage of the faunal list at the reference site. Only 6 of the 16 possible curves are shown. See text for discussion.

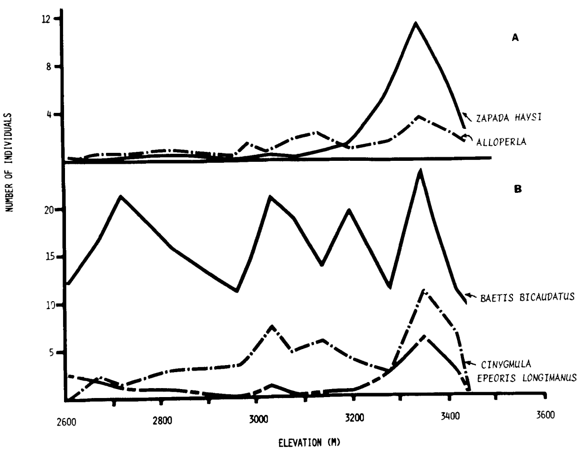

FIG. 3. (A) Numbers of 2 species of Plecoptera (*Alloperla, Zapada haysi*) and (B) 3 species of Ephemeroptera (*Baetis bicaudatus, Cinygmula, Epeoris longimanus*) per Surber sample, based on mean of 12 samples.

increased elevation (Table 1). Some species were quite broad, others restricted in their altitudinal ranges. Parenthetically, Table 1 also demonstrates that 12 Surber samples fail to provide an accurate estimate of species richness.

Faunal congruity is a measure of the similarity of sites progressively further apart along the gradient (Fig. 2). Each site was taken in turn as a reference point, and the similarity of faunal lists at all other sites was expressed as a percentage of the faunal list at the reference site. Only 6 of the possible 16 faunal congruity curves are shown, as the trends were consistent. Sharp slopes represent zones of rapid faunal change, while plateaus represent zones of no faunal change. A sharp decline in faunal congruity occurred at elevations above 3,350 m (arrow A in Fig. 2). This is due in part to a loss of species at the upper terminus, and in part to rapid replacement of species with narrow ranges. No such downstream decline occurred, as a number of species occurring at upper elevations extended the entire range, while many of the species occurring at lower elevations did not extend to the upstream terminus. In general, the pattern of faunal replacement was

TABLE 1. Species diversity of Cement Creek sites based on several sampling techniques, and substratum particle size diversity

		Species diversity				Substratum diversity	
Site	Elevation (m)	Species richness (total)	Species richness (Surber only)	*H'*	Species richness (Surber & Kick)	MDϕ	*J'*
1	2,610	20	12	0.993	20	-7.3	0.430
3	2,670	21	12	1.065	21		
5	2,725	20	12	0.962	17	-7.26	0.448
7	2,820	25	20	1.759	25	-6.23	0.501
9	2,970	21	11	1.306	20		
10	2,990	18	15	1.576	15		
11	3,030	20	16	1.623	19	-6.94	0.452
11+	3,075	20	16	1.676	17		
12	3,140	17	14	1.761	16		
12+	3,200	16	11	1.715	14	-7.52	0.396
13	3,290	16	14	1.983	15		
13+	3,350	18	13	1.931	16	-7.12	0.415
14	3,410	14	12	1.806	14	-7.39	0.406
14+	3,440	12	10	1.596	12	-4.77	0.733
15	3,460	7	----		7		
15+	3,535	3	----		3		

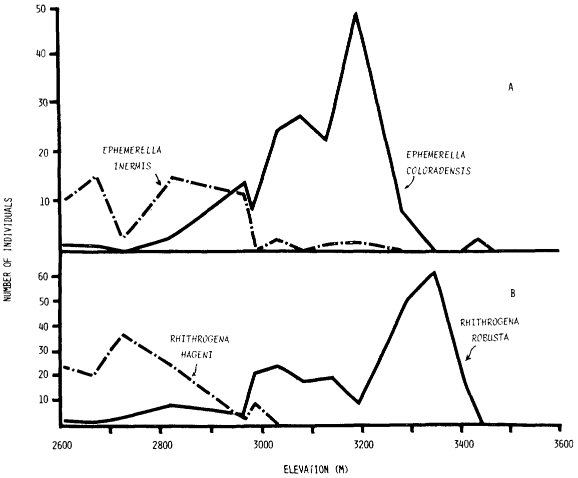

FIG. 4. (A) Numbers of 2 species of *Ephemerella* and (B) 2 species of *Rhithrogena* from 12 Surber samples and kick samples combined.

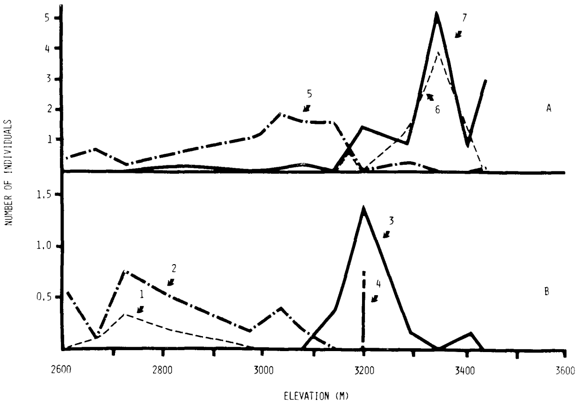

FIG. 5. Numbers of 7 species of *Rhyacophila* per Surber sample based on mean of 12 samples. (B): 1 = *R. angelita*, 2 = *R. acropedes*, 3 = *R. hyalinata*, 4 = *R. verrula*; (A) 5 = *R. valuma*, 6 = *R. coloradensis*, 7 = *R. alberta*.

gradual, with downstream additions of species. A region of no apparent faunal change exists between 3,200 and 3,350 m (arrow B) and below 2,700 m. The lower plateau was separated by a fairly sharp zone of faunal change (arrow C) which correlates well with a canyon region at about 2,775 m, but the plateau above 3,200 m has no ready explanation.

Abundances of some individual species are given in Figs. 3–5. Species abundance curves often showed an upstream peak with a long downstream tail (e.g., *Rhithrogena robusta*, Fig. 4B; *Zapada haysi*, Fig. 3A). Some species were more evenly distributed (e.g., *Rhyacophila valuma*, Fig. 5A).

Three groups of congeners occurred and were inspected for possible competitive limits to ranges. *Rhithrogena hageni* and *R. robusta* display a sharp, mutual truncation in numbers at about 2,950 m (Fig. 4B). The downstream tail of *R. robusta* obscures any marked distributional boundary, and it may often be true in streams that altitudinal replacements show greater overlap of the upstream congener into the downstream congener's range than the reverse, due to drift and downstream colonization. *Ephemerella coloradensis* and *E. inermis* show a less pronounced truncation (Fig. 4A), and *E. inermis* maintains a presence, although rare, well up into *E. coloradensis*' distributional peak. Two other species of *Ephemerella* differ in size and in habitat (Table 2). The genus *Rhyacophila* is represented by seven species, one of which (*R. verrula*) is herbivorous and hence not expected to compete for food with its six carnivorous congeners (Table 2). Although peak abundances are altitudinally displaced in some of these six species (*R. alberta* and *R. valuma*), others overlap (*R. alberta* and *R. coloradensis*, Fig. 5), and again no strong inference may be drawn concerning competitive limits to ranges. Of 27 species (13 of them congeners) observed in sufficient abundance to apply these criteria, only one pair, *Rhithrogena hageni* and *R. robusta*, clearly was consistent with the argument that competition limits species ranges.

Terborgh (1971) has recently introduced a set of three graphical models which attribute faunal replacement to either ecotones, competition or gradual changes in the physical-chemical gradient. The degree to which these models represent truly independent processes is questionable. Certainly they are a convenient summarization of conflicting views in the literature regarding distributions of stream invertebrates (Dodds and Hishaw 1925, Beauchamp and Ullyot 1932, Maitland 1966).

The ecotone model predicts rapid faunal change coincident with an independently recognized ecotone. Vegetational zonation exhibited transitions at 3,200 m and 3,475 m. Above 3,200 m faunal congruity shows a plateau (Fig. 2, arrow B) and below 3,200 m rather steady change. The upper vegetation discontinuity, between spruce-fir and upland herb, is too close to the upstream terminus to be unambiguously interpreted. The results do not indicate that ecotones between vegetational zones are important in faunal replacement in Cement Creek, although turbulent canyon regions may have a small effect. This conclusion is unchanged by assuming that the influence of these ecotones is displaced a moderate distance (≈ 100 vertical m) downstream.

The competition model predicts sharp truncation in numbers at the boundary between ranges of congeneric species. Out of a total of 13 congeners, only one pair, *Rhithrogena hageni* and *R. robusta*

TABLE 2. Cement Creek fauna of period 15 June to 15 August, 1972 and 1973. Size range includes all instars encountered during the study period. Feeding habits are given by family except where additional information shows a species to differ from familial trend. Diptera not included

Species	Size range (mm)	Feeding habits	Source†
EPHEMEROPTERA			
Baetidae		detritivore: fine particle deposit feeder;	
Baetis bicaudatus	2.5–7.0	herbivore: mineral and organic scraper	2, 3, 4, 5
Ephemerellidae		detritivore: fine particle deposit feeder;	
Ephemerella coloradensis	3.0–7.5	herbivore: mineral scraper	2, 3, 4, 5
E. doddsi	6.5–13.5		
E. grandis	12.5–14.5		
E. inermis	5.0–10.0		
Heptageniidae		detritivore: fine particle deposit feeder;	
Cinygmula sp.	3.0–7.5	herbivore: mineral and organic scraper	2, 3, 4, 5
Epeoris longimanus	1.5–6.0		
Rhithrogena hageni	7.0–10.0		
R. robusta	7.5–13.5		
Leptophlebiidae		detritivore: fine particle deposit feeding	
Paraleptophlebia vaciva	5.5–8.5	herbivore: organic scraper	2, 3, 4, 5
Siphlonuridae		herbivore-detritivore: suspension feeding	2, 4
Ameletus velox	7.0–12.0		
PLECOPTERA			
Chloroperlidae		carnivore, maybe polyphagous	2, 6
Alloperla spp.	2.0–7.0		
Leuctrinae		presumed to be herbivore-detritivore	
Paraleuctra sp.	5.5–7.0		
Nemouridae		presumed to be herbivore-detritivore	
Malenka flexura	5.5–7.0		
Podmosta sp.	5.0–7.0		
Zapada haysi	2.0–5.5		
Perlidae		carnivore, may be polyphagous	2, 6
Hesperoperla pacifica	7.0–16.0		
Perlodidae		carnivore, may be polyphagous	6
Isoperla ebria	13.0–16.0		
Kogotus modestus	8.0–14.5		
Megarcys signata	21.0–26.0		
TRICHOPTERA			
Brachycentridae		herbivore-detritivore; suspension feeding	2, 3
Brachycentrus sp.	5.0–8.5	may switch to carnivory in later instars	1
Micrasema sp.	4.0–8.0		
Hydropsychidae		omnivore: suspension feeding; carnivore	1, 3
Arctopsyche grandis	16.0–30.0		
Parapsyche sp.	8.0–16.0		
Lepidostomatidae		detritivore: large particle chewer and miner	2, 3, 9
Lepidostoma sp.	9.5–10.5		
Limnephilidae		detritivore: large particle chewer and miner	1, 2, 3, 9
Ecclisomyia conspersa (?)	10.0–13.0		
Limnephilid genus D	5.0–7.0		
Neothremma alicia	6.0–7.0		
Oligophlebodes sp.	5.0–8.0		
Rhyacophilidae		carnivore	1, 3, 7, 8
Rhyacophila acropedes	4.0–16.0		
R. alberta	3.5–15.5		
R. angelita	3.5–10.0		
R. coloradensis	7.5–13.0		
R. hyalinata	7.5–13.5		
R. valuma	5.0–12.5		
R. verrula	3.5–10.5	herbivore	7
COLEOPTERA			
Elmidae		presumed to be herbivore-detritivore	
Heterlimnius sp.	2.5–6.5		

† Sources: 1 = Balduf 1939, 2 = Chapman and Demory 1963, 3 = Cummins 1973, 4 = Gilpin and Brusven 1970, 5 = Muttkowski and Smith 1929, 6 = Richardson 1962, 7 = Smith 1968, 8 = Thut 1969, 9 = Winterbourn 1970.

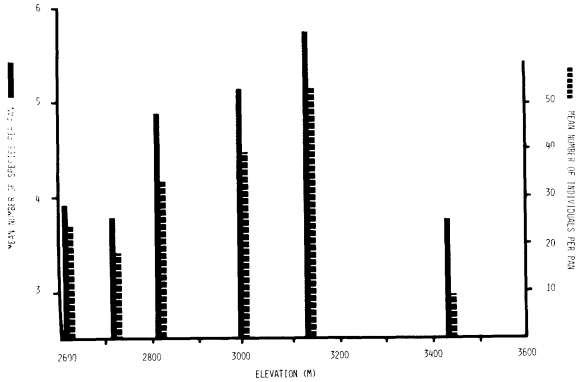

FIG. 6. Mean number of individuals and mean number of species colonizing 20 cm × 25 cm pans of substrata. Data are pooled over 4 substratum sizes used: 8–16 mm, 16–32 mm, 32–64 mm, > 64 mm.

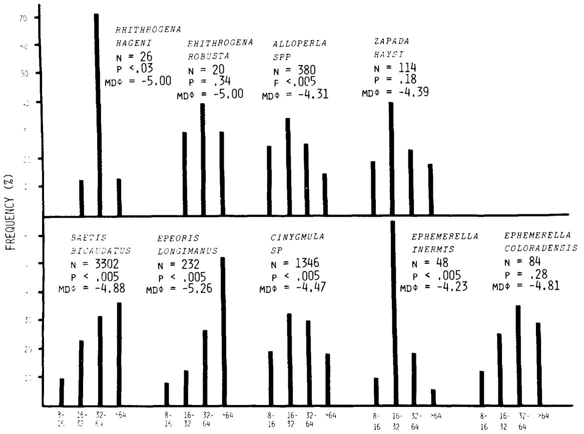

FIG. 7. Habitat preferences of nine species of insects over substratum sizes 8–16 mm, 16–32 mm, 32–64 mm, > 64 mm. N = number of observations, P = probability of obtaining that distribution by chance, MDϕ = midpoint of substratum distribution by volume of particles.

(Fig. 4), showed such a sharp truncation, and some additional pairs were weakly implicated (*Ephemerella coloradensis* and *E. inermis*, Fig. 4; up to four species of *Rhyacophila*, Fig. 5). Unlike Terborgh (1971), I did not find reduced species range accompanying exclusion by competition. It appears that the upstream member of the pair has a long downstream "tail" to its distribution, predictable from the unidirectional colonization forced by drift.

The gradient model is essentially a residual model into which are placed all species not assigned to ecotones or competition. In Cement Creek, 19–25 species out of 27, or 70–93% of the total, were assigned to the gradient model, and the remaining 7–30% were given a competitive explanation. None appear determined by ecotones. This is in sharp contrast with Terborgh's (1971) analysis of the avifauna of the Peruvian Andes, where somewhat < 20% of the 410 species examined were assigned to the ecotone model, about one-third to the competition model, and the remaining half to the gradient model. My results are similar to Illies (1953) who constructed faunal congruity curves for invertebrates in the Fulda River of southern Germany, revealing gradual transition and the absence of ecotones.

Substratum habitat

Colonization and habitat preferences.—Colonizing events were sufficiently frequent during a 24-h period to provide detailed habitat preference information on seven species of Ephemeroptera and two species of Plecoptera. A total of 31 species was observed at least once. The mean number of individuals and mean number of species colonizing a single pan of substratum both increased with elevation until the highest site tested, where a sharp decline occurred (Fig. 6). A breakdown by site and by substratum particle size indicated a consistent trend towards a preference for larger substrata, in numbers of individuals and species. The mean number of species colonizing a particular substratum size was compared to the total number of species collected as colonizers in that substratum size during the 24-h period at a particular site. This index is 100% when the four replicates of a given substratum size have identical species lists. It varied between 40% and 70% with the smallest substratum size generally showing the lowest values, and did not exhibit any trend with elevation.

Habitat selection by individual species was generally quite distinct. Results are expressed as frequency histograms (Fig. 7) along with a probability level derived from a latin square analysis of variance and substratum size preference based on the median particle size selected on the phi scale. No significant row or column effects were observed. Substratum size preferences were similar at each of the six elevations tested (Table 3), although *Cinygmula* sp. showed a tendency toward smaller substrata in the sites where it was an abundant colonizer (Site Nos. 7, 10, 12) compared to where it was rare (Site Nos. 1, 5, 14+). In general, for all species, preferences varied somewhat from site to site but not in any discernible direction.

Colonization patterns were observed over a 10-day period in sequentially harvested replicates. Comparable one-day results were derived by selecting observations for the three larger substratum sizes from the total observations at site 10 (2,990 m) where the longer term experiments were performed. Over 10 days the mean number of individuals per pan

TABLE 3. Substratum preferences based on colonization of 22 cm × 30 cm enameled pans filled with substrata in one of the sizes: 8–16 mm, 16–32 mm, 32–64 mm, > 64 mm. Experiments were conducted at 6 elevations. N = number of colonizing individuals, p = probability of obtaining that distribution by chance, MDϕ = median particle size selected, in phi units

Species		Sites					
		1 (2,610 m)	5 (2,725 m)	7 (2,820 m)	10 (2,990 m)	12 (3,140 m)	14+ (3,440 m)
Baetis bicaudatus	N	660	408	662	588	902	82
	p	<0.05	<0.01	<0.02	<0.02	<0.02	<0.005
	MDϕ	-4.76	-5.21	-4.97	-4.65	-4.91	-5.16
Epeoris longimanus	N	16	44	68	48	56	----
	p	<0.01	<0.02	<0.29	<0.005	<0.005	----
	MDϕ	-5.12	-5.42	-4.83	-5.39	-5.50	----
Cinygmula sp.	N	10	64	168	440	542	116
	p	0.86	0.18	0.07	<0.005	<0.005	<0.01
	MDϕ	-4.71	-4.89	-4.38	-4.38	-4.44	-4.90
Ephemerella inermis	N	7	13	10	16	2	----
	p		0.09	----	<0.05	----	----
	MDϕ		-4.15	----	-4.12	----	----
E. coloradensis	N	----	----	1	33	50	----
	p		----	----	0.82	0.32	----
	MDϕ		----	----	-4.63	-4.92	----
Rhithrogena hageni	N	4	5	16	----	----	----
	p	----	----	----	----	----	----
	MDϕ	----	----	----	----	----	----
R. robusta	N	----	----	----	----	20	----
	p		----	----	----	0.34	----
	MDϕ	----	----	----	----	-5.0	----
Zapada haysi	N	4	12	14	14	24	46
	p	----	0.11	0.94	0.97	0.11	0.30
	MDϕ	----	-4.53	-4.60	-4.36	-4.46	-4.32
Alloperla spp.	N	30	24	74	132	78	42
	p	0.86	0.56	0.11	0.18	0.07	0.33
	MDϕ	-4.43	-4.76	-4.16	-4.38	-4.15	-4.38

increased from 43 to 75 and species richness increased from 5.25 to 7.75 species per pan (Fig. 8). The percent similarity of replicates increased from initial values near 65% to day 10 values between 70% and 80%, indicating an increased similarity among replicates within a substratum category. An examination of substratum preference for individual species over the 10-day period revealed no obvious shifts (Table 4), although it may be questioned whether replication was sufficient to overcome natural scatter. The overall increase in density (Fig. 8) may be divided into two broad trends: an initial abundance of the rapidly colonizing *Baetis bicaudatus* followed by a pronounced decline in its abundance, and a concomitant increase in the rest of the community (Table 4). Whether *B. bicaudatus* is responding to a high level of intraspecific competition or to a form of diffuse competition (MacArthur 1972) remains unknown. However, the results definitely suggest some increase in biotic interactions.

TABLE 4. Mean number of individuals per colonization pan ($\bar{x}$) and substratum size preferred (MDϕ) over 10 days of colonization at one site, using substratum sizes 16–32 mm, 32–64 mm, $>$ 64 mm

Species		Day			
		1	2	5	10
Baetis bicauduatus	$\bar{x}$	23.5	37.3	6.2	13.8
	MDϕ	-4.96	-4.87	-5.16	-4.74
Epeoris longimanus	$\bar{x}$	1.4	3.3	0.4	2.3
	MDϕ	-5.45	-5.31	-5.50	-5.33
Cinygmula sp.	$\bar{x}$	13.8	15.11	25.3	28.2
	MDϕ	-4.81	-4.63	-5.01	-4.67
Ephemerella inermis	$\bar{x}$	0.5	0.6	3.3	2.9
	MDϕ	-4.39	-4.00	-4.50	-4.20
Ephemerella coloradensis	$\bar{x}$	1.0	2.2	2.0	4.0
	MDϕ	-4.93	-4.80	-5.06	-4.76
Zapada haysi	$\bar{x}$	0.5	0.9	2.0	5.6
	MDϕ	-4.90	-5.00	-4.88	-4.40
Alloperla spp.	$\bar{x}$	3.7	5.0	15.3	15.7
	MDϕ	-4.82	-4.71	-4.63	-4.35

Colonization patterns indicated that well over 50% of numbers of individuals and of species establish in virgin substrata within 24 h. A gradual increase continues, however, and although some workers claim complete recovery in 4–10 days (Waters 1964), Coleman and Hynes (1970) recorded increases for 28 days. Some of the conflict

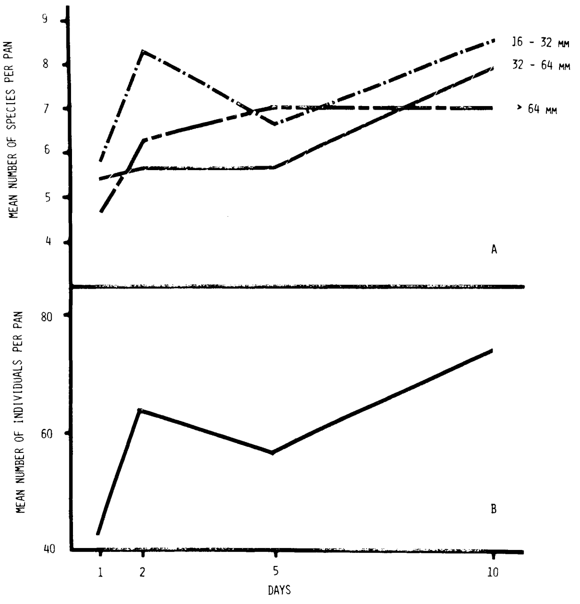

FIG. 8. Colonization over a 10-day period. (A) mean number of species per pan, (B) mean number of individuals per pan based on substratum sizes 16–32 mm, 32–64 mm, and > 64 mm combined.

is resolved by recognizing that species differ in colonization rates. I observed very rapid colonization among most Ephemeroptera and very slow colonization among most Trichoptera.

Species diversity and habitat complexity.—Colonization experiments and field measurements were used to determine the effect of complexity in the physical habitat on the species diversity of an assemblage.

1) Experimental mixing: Mixtures of substrata provided 11 combinations of 2–4 particle sizes to determine if more species would colonize complex experimental habitats than simple ones. In each case the mean number of species was higher in mixed substrata than for a single substratum category (Table 5). At site 12, the mean number of species increased continuously with more diverse substratum mixtures, whereas at site 5 the experiments showed no such regularity. Vagaries in the geometry and interstitial packing of particles are one possible cause of these differences. Combining substratum categories posed a problem in replication since each point for one substratum type represents the average of 32 observations, while there were 12 observations on 2 substratum types, 8 observations on 3 substratum types and only 2 observations on the 4 substrata mixture.

TABLE 5. The mean number of species (and range) colonizing 22 cm × 30 cm enameled pans containing one to four substratum particle sizes. Experiments conducted over a 24-h period beginning 28 July at site 12 and 29 July 1973 at site 5. The mean number of species colonizing one substratum particle size over all sizes and all sites was 4.81

	Number of substratum categories			
	1	2	3	4
Site 5	3.83(1–6)	4.68(2–7)	4.64(3–6)	4.01(2–6)
Site 12	5.70(2–10)	5.92(5–7)	5.88(4–8)	6.50(6–7)

TABLE 6. Components of diversity of faunal collection, Cement Creek, 1973. The niche breadth of each species is partitioned into site and microhabitat components. Total species diversity (H' species) is partitioned into between site (BSC), between microhabitat (BMC) and within microhabitat (WMC) components

Species	Total niche breadth	Site niche breadth	Microhabitat niche breadth
Baetis bicaudatus	4.900	2.600	2.300
Epeoris longimanus	3.979	2.117	1.862
Cinygmula spp.	4.549	2.377	2.172
Rhithrogena hageni	3.093	1.422	1.671
R. robusta	3.776	2.065	1.711
Ephemerella inermis	2.302	1.639	0.663
E. coloradensis	3.593	1.802	1.791
E. doddsi	3.066	1.747	1.318
E. grandis	0.451	0.451	0.000
Paraleptophlebia vaciva	0.636	0.000	0.636
Zapada haysi	3.608	1.577	2.031
Malenka flexura	0.693	0.000	0.693
Alloperla spp.	4.213	2.315	1.898
Podmosta sp.	0.693	0.693	0.000
Paraleuctra sp.	2.398	1.720	0.678
Megarcys signata	3.031	1.964	1.067
Kogotus modestus	2.675	1.811	0.864
Rhyacophila acropedes	3.025	1.891	1.135
R. alberta	3.339	1.506	1.833
R. angelita	1.550	0.956	0.594
R. coloradensis	3.090	1.025	2.065
R. hyalinata	2.694	1.234	1.460
R. valuma	4.014	2.125	1.889
R. verrula	1.677	0.000	1.677
Arctopsyche grandis	1.040	1.040	0.000
Parapsyche sp.	2.095	0.824	1.271
Heterliminus sp.	3.996	2.170	1.825
H' Species	BSC	BMC	WMC
1.897	0.266	0.228	1.404
	(14%)	(12%)	(74%)

Inspection of various mixtures of substratum type indicated that knowledge of the average number of colonizing species for single substratum types did not lead to knowledge of the average number colonizing a particular mixture. In other words, the colonization result on a mix of substratum particles $\phi = -3$ and $\phi = -5$ was not obvious from an understanding of colonization on each particle size alone.

2) Habitat complexity: Substratum complexity (H' of the seven particle sizes > 2 mm) was fairly consistent over the sites measured (Table 2), and observations suggested that this was true for the entire creek. In each set of 12 Surber samples,

TABLE 7. Components of diversity of substratum measures, Cement Creek, 1973. Substratum niche breadth measures the distribution of particular substratum sizes across microhabitats and sites, while H' substrata measures the total diversity of substratum categories analogous to species diversity

Substratum (mm)	Total niche breadth	Site niche breadth	Microhabitat niche breadth
>256	3.647	1.847	1.799
64–256	4.238	1.925	2.313
32–64	4.443	2.065	2.379
16–32	4.403	2.024	2.379
8–16	4.339	1.994	2.379
4–8	4.258	1.972	2.286
2–4	4.188	1.962	2.226
H' Substrata	BSC	BMC	WMC
0.906	0.058(6%)	0.279(31%)	0.569(63%)

smaller substrata were numerically far more abundant while larger substrata accounted for most of the volume. Median particle size, the midpoint of a cumulative % composition curve, usually ranged from -6.2 to -7.5 on the phi scale reflecting the presence of substrata in the pebble, cobble, boulder categories of 32–256 mm in diameter (Cummins 1962).

3) Partitioning diversity: Measurements were made of species diversity at 12 microhabitats (= 0.1 m^2 Surber samples) within each of 14 sites, and of substratum particle size distribution at 12 microhabitats within 8 of these 14 sites to examine how observed total diversity partitioned into within-habitat and between-habitat components. The details of this approach are considered elsewhere (Allan 1975); briefly, diversity is calculated as $-\sum p_i \log p_i$ where p_i is the proportion of observations that occur in category i. The proportion of total individuals that occur in species i would lead to a species diversity measure while the proportion of individuals of a particular species which occur in microhabitat i would lead to a niche breadth measure.

This analysis was conducted with the 27 species collected in an altitudinal series of Surber samples. Some rare species known to be present could not be included in this statistical approach, an omission which will lead to patchiness being underestimated. Site niche breadth was greater than microhabitat niche breadth in 18 cases, indicating that numbers collected in most species were more predictable from site to site than from microhabitat to microhabitat (Table 6). In the nine cases where microhabitat niche breadth was greater than site niche breadth, the species generally was localized in its elevational range but abundant within that range. *Zapada haysi* was the only abundant, widely distributed species for which microhabitat niche breadth exceeded site niche breadth.

A breakdown of average species diversity reveals that the within-microhabitat component (WMC) was quite high, hence most of the information about species abundance distributions was contained within the average microhabitat. The between-microhabitat (BMC) and between-sites (BSC) contributions were small and similar. Thus most of diversity, which is a property of an assemblage, was accounted for by the number of species and their relative abundances at the within-microhabitat level. For a particular species, however, abundances were relatively more variable from microhabitat to microhabitat than from site to site.

This analysis was repeated on the seven substratum particle sizes measured (Table 7). For particular substrata only slightly greater diversity occurs over microhabitats than over sites, and as sites offer fewer categories (12 vs. 8, respectively) and hence a lower possible maximum value, we may infer that the uncertainty of encountering a particular substratum size was about the same across microhabitats and across sites. A breakdown of average substratum diversity reveals that within-microhabitat (WMC) diversity is a large component, as is between-microhabitat (BMC) diversity. Much of the physical complexity of the substratum is contained in any given 0.1 m^2 patch, other 0.1 m^2 neighboring patches differ somewhat, and sites differ hardly at all.

A comparison of the substratum and faunal analyses reveals that in both, within-microhabitat variation is the major component. However, faunal diversity shows a distinct between-site effect while substratum does not. Hence longitudinal zonation is a faunal characteristic and not a substratum characteristic.

Microhabitats exhibit considerable similarity in species diversity and substratum complexity, while varying somewhat more in actual species composition. Since drift results in each microhabitat patch gaining immigrants and losing emigrants rather continuously with standing crop not greatly depleted (Waters 1964, 1969), the particular species present at any time may be highly variable.

The role of habitat.—Substratum appears to be one of the most basic aspects of habitat in a stream, reflecting or determining current, refuges, food distribution, etc. Various investigations have examined species preferences for particular substrata (Percival and Whitehead 1929, Linduska 1942, Cummins and Lauff 1969), and distinct selection often emerges. Substratum diversity is related to stream bed material and current, although not always in an obvious way (Leopold et al. 1964). The relation of current speed to diameter of object moved is predictable (Nielsen 1950); the current speeds of Cement Creek (Fig. 1) should remove particles less than 11 mm diameter

TABLE 8. Distribution of trout in Cement Creek, 1973. N = number captured by electro-fishing a 160-m stretch, L = length in cm ± 1 SD, W = weight in g ± 1 SD

	Elevation (m)					
Species	2,670	2,820	2,990	3,250	3,300	3,410
Salmo clarki						
N		—	—	7		—
L				23.8 ± 6.6		
W				185.7 ± 75.5		
Salvelinus fontinalis						
N	—	6	14	13	—	—
L		15.2 ± 4.6	15.7 ± 5.6	23.7 ± 6.6		
W		47.5 ± 42.8	76.8 ± 64.3	206.9 ± 121.3		
Salmo trutta						
N	36	18	2	—	—	—
L	17.4 ± 4.4	15.5 ± 6.6	26.4 ± 10.4			
W	66.9 ± 50.4	74.7 ± 80.9	237.5 ± 194.5			
Salmo gairdneri						
N	1					
L	229					
W	120					

or roughly $\phi = -2$ to -3. The smallest particle size successfully tested in colonization pans was $\phi = -3$, while the smaller $\phi = -2$ particles were scoured away.

A positive relationship between substratum diversity and species richness was suggested by several lines of evidence. Studies of individual species preferences revealed distinct differences. Hence, the more types of substrata the more types of species are expected. Colonization of mixed substrata always resulted in higher mean species richness than did colonization of a single substratum type, although no simple and clear additivity of individual effects was evidenced.

On the other hand, habitat complexity and species diversity showed no correlation over eight Cement Creek sites (Table 2). This is hardly surprising in light of the extreme similarity of sites in substratum composition (Table 7, BSC term). It may be that within a stream of fairly constant substratum type, minor variations have little effect on local species richness, although another stream of generally lower habitat complexity may contain fewer species. Indeed, Pianka's (1967) correlations of lizard species richness on plant complexity hold primarily only between systems.

Distribution of fish

Cement Creek contains breeding populations of three salmonids (*Salmo clarki, S. trutta* and *Salvelinus fontinalis*), and a fourth (*Salmo gairdneri*) is stocked several times each summer but does not appear to maintain a breeding population. These trout show distinct zonation. The upper limit for all fish lies at approximately 3,250 m, and beaver ponds at this point may serve to sharpen the boundary. The three salmonids were encountered in the order *S. clarki, S. fontinalis, S. trutta* proceeding towards lower elevations (Table 8). Some overlap occurred, apparently due to the extension upstream of larger individuals. Those *S. trutta* which extended up into the range of *S. fontinalis* were more than double the weight of *S. trutta* individuals in its central range (Table 8). Similarly, those uppermost *S. fontinalis* that overlap the range of *S. clarki* were also the largest individuals observed.

I inspected the gut contents of 42 trout and found an average of 65 prey items per trout with individual stomachs containing up to 100 items. Typically 80–100% of the prey were aquatic, with most species of larvae and nymphs observed at least occasionally. The data do not allow any statement about prey selection; indeed the most common insects (*Baetis bicaudatus, Cinygmula, Epeoris longimanus, Rhyacophila* spp.) appeared to be the most common prey. One striking observation concerning trout is the coincidence of the upper limit to trout (Table 8) and the peak abundance zone of insects (Figure 9).

The coincidence of an upper, trout-free region with a two-fold to six-fold increase in invertebrate densities implicates fish predation as a strong determinant of abundances of nymphs and larvae. Coupled with expectations of headwater depletion owing to downstream drift (Müller 1954, Waters 1964, 1969), this result is quite dramatic. It implies a headwater reservoir of high abundances and low predation which, through drift, may supply colonizers to downstream regions. Müller (1954) proposed the existence of a colonization cycle consisting of upstream adult migration to offset downstream

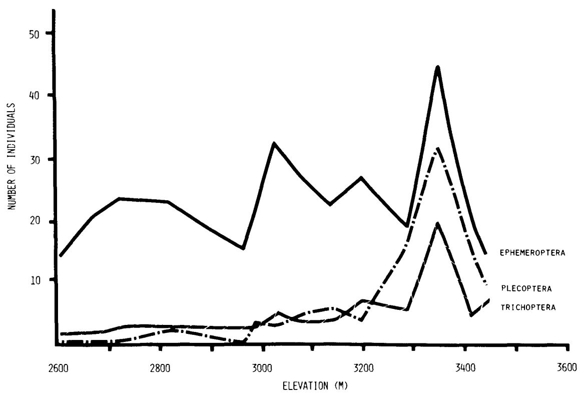

FIG. 9. Total numbers of Ephemeroptera, Plecoptera and Trichoptera per Surber sample based on mean of 12 samples.

immature drift; supporting evidence is by no means conclusive (Hynes 1970). Pearson and Kramer (1972) suggested that headwaters suffer lower scouring from anchor ice and hence are preferred for egg deposition. A third alternative implicated by this study is higher headwater survivorship owing to reduced vertebrate predation. As a result the headwaters may serve as a predator-free reservoir delivering a periodic downstream allotment of potential prey items and colonizers.

The presence in Cement Creek of four species of trout, three of which have established breeding populations, raises interesting questions of interspecific competition among the salmonids. The cutthroat trout (*Salmo clarki*) was once the sole headwater species in Colorado (Vincent and Miller 1969). Rainbow trout (*Salmo gairdneri*) were introduced in Colorado in 1882 (MacCrimmon 1971), brown trout (*Salmo trutta*) in 1894, and brook trout (*Salvelinus fontinalis*) in 1909 (Beckman 1963). Total standing crop of trout above the yearling age class, probably underestimated by electrofishing (Table 8), compares closely with brook trout standing crops in Lawrence Creek, Wisconsin (McFadden 1961) and Hunt Creek, Michigan (McFadden et al. 1967).

Distributions typically reveal rainbows and browns at lower elevations, brooks at upper elevations, occasionally cutthroat trout in the headwaters, and broad overlap (Vincent and Miller 1969). Behavioral differences among salmonids including variation in cover preference (Chapman and Bjornn 1969), feeding times (Elliott 1970, Jenkins et al. 1970), food preference (Bryan and Larkin 1972), water depth preference (Griffith 1972), etc. help explain overlap.

However, zonation among Cement Creek salmonids is reasonably distinct (Table 8), and for several reasons I believe the areas of overlap are transitional and temporary. Surveys of a number of Colorado streams show that brook trout often have replaced cutthroat trout in headwaters (Vincent and Miller 1969). Brook trout fry emerge from the gravel before cutthroat owing to earlier spawning, and throughout life maintain a consistent 20 mm size advantage and are dominant over cutthroat of the same age (Griffith 1972). Generally, it appears that aggressive rank is proportional to size in salmonids both intraspecifically and interspecifically (Jenkins 1969, Griffith 1972). Brook trout found at the upper elevational limit were larger than those at lower elevations, and all cutthroat trout were uniformly large. This suggests little recruitment to the cutthroat population in Cement Creek and its possible demise. The upper limit of brown trout also consisted of substantially larger individuals (Table 8). Brown trout may be simultaneously forcing upwards the lower limit of brook trout, since water temperatures at this lower limit were suitable for optional brook trout growth (McCormick et al. 1972). Rainbow trout are hatchery fish stocked and rapidly caught and probably play little role in stream dynamics.

Although the distribution of different trout species constitutes an interesting problem in its own right, the critical distinction from the standpoint of the invertebrate fauna appears to be trout *versus* no trout. Whether trout feed primarily from drift or the benthos has been contested (Waters 1969). Young trout may rely somewhat more on drift and older fish somewhat more on benthos (Elliott 1970). In Cement Creek, trout consume substantial numbers of drifting species (mostly Ephemeroptera) and non-drifting species (mostly *Rhyacophila*). Possibly trout zonation played some role in limiting the ranges of particular invertebrates, as the abundances of several species of *Rhyacophila* changed sharply coincident with the trout-no trout boundary (Fig. 5). However, the principle effect of the boundary was in total numbers of insects (Fig. 9), suggesting greater control over numerical abundances than over which species are present.

Integration of scale

I have attempted to ask questions concerning the number of invertebrate species in an alpine stream on various levels of scale, from faunal replacement along 1,000 vertical m to patchiness among similar 0.1 m^2 samples. The data help explain why there are as many species as observed (i.e., the lower limit on species richness for a particular season, taxon, etc.), but not why we do not find more. As the majority of species in this study appeared to respond to subtle gradient changes, it is possible that the fauna of Cement Creek is characterized by a low level of biotic interactions. Of the 37 species observed in Cement Creek during 1972 or 1973 gross feeding differences are sufficient to separate out roughly 14 carnivores from 23 herbivore-detritivores (Table 2). Sizes of individuals collected during the summer months indicate that within some families of a particular feeding type, sizes were staggered. This is especially clear in the Hydropsychidae and Perlodidae. Relatively few congeneric species were similar in size and feeding habits, and in some cases (mentioned above) elevational displacement occurred. Hence, only a very few species remain as a puzzle to competitive theory, and some of these have been shown to select different microhabitats (the abundant *Cinygmula* and *Epeoris longimanus*, Fig. 7). Finally, most species are so rare that 3–6 equally abundant species would yield a diversity index (H') equivalent to observed distributions with up to 20 species.

Studies of competition which employ distributional boundaries as evidence assume niche requirements so similar that coexistence is impossible. As food specialization seems less likely within a group of stream organisms than does habitat specialization (Hynes 1970), substratum preference should be a good index of microhabitat requirements. Hence it is satisfying that congeners showing sharp mutual exclusion (*Rhithrogena*) have highly similar microhabitat preferences while congeners showing weaker mutual exclusion (*Ephemerella*) have more disparate microhabitat preferences. The two levels of investigation are reinforcing.

Measures of species diversity usually fail to distinguish within- and between-habitat diversity (MacArthur 1965). Partitioned species diversity revealed that microhabitats are quite similar in species richness and relative abundance while varying substantially in which species are present. Any site contains rather more than half of the total species co-occurring in Cement Creek during the summer, and any microhabitat contains slightly more than half of the species at a site (see also Patrick 1968). Hence, species richness shows roughly equal dependence on within-habitat variation (owing to rare species) and between-habitat variation (owing to faunal replacement). If we combine the diversity associated within 0.1 m^2 patches (WMC) and between 0.1 m^2 patches (BMC) as an estimate of total within-microhabitat diversity, clearly only a small portion of the information contained in H' is associated with the between-site scale of investigation.

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