

Distribution of Insects Within Riffles of Streams¹

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Abstract. Extensive quantitative sampling of aquatic insects and factors known or suspected to affect their local distribution in streams was performed in three consecutive riffles in a hardwater stream of north central Texas, USA. This study revealed a strong upstream-biased distribution pattern of lotic insects within riffles. Twelve of sixteen taxonomic categories analyzed, representing 93.4% of the total numbers, showed a distinct pattern of distribution with greater abundance toward the heads of riffles. Density of insects was statistically correlated with several physical and chemical characteristics measured including quantity of coarse particulate organic matter on the substrate, quantity of fine particulate organic matter in transport, several substrate particle size classes, current, depth, dissolved oxygen and temperature. However, none of these variables were meaningfully correlated with distance from the heads of riffles, and therefore did not sufficiently explain distribution of the insect groups. Positive rheotaxis could have significant influence on distribution of insects in riffles. The observed distribution pattern indicates that filter-feeding riffle insects compete for high quality food items produced in upstream pools, and that density of macrobenthos within these riffles may be limited by the amount of high quality food available to them rather than by space.

We incidentally observed that lotic insects were apparently more abundant near the heads of riffles in streams with distinct riffle-pool geomorphology, and decided to investigate this further. The literature is seemingly replete with studies of the effects of environmental factors on the microdistribution of invertebrates in streams and recently much emphasis has been placed on longitudinal zonation of organisms in long stretches of streams in the northern and western United States (e.g., Bruns, Minshall, Brock, Cushing, Cummins & Vannote 1982; Hawkins & Sedell 1981; Vannote, Minshall, Cummins, Sedell & Cushing 1980). However, few studies have specifically addressed whether linear distributions of macrobenthos occur within individual riffles. Mason (1976) noted that density of macrobenthos in a British Columbia stream was statistically greater in the upstream half of a riffle. Since initiation of our study, Godbout and Hynes (1982) reported a decrease in density downstream within a riffle of an Ontario stream. Godbout and Hynes (1982) suggested that the observed decrease was related to very low groundwater flow in their downstream transect.

The principal environmental factors affecting microdistribution of macrobenthos in streams are considered to be substrate particle size (Brusven & Prather 1974; Chutter 1969a; Cummins 1966; Cummins & Lauff 1969), current velocity (Chutter 1969b; Edington 1968; Madsen 1969), and availability of preferred food items (Egglishaw 1964; Wallace & Merritt 1980). Additional factors that have been shown to affect distribution include dissolved oxygen (Madsen 1968; Philipson 1954), aquatic vegetation (Lavandier & Dumas 1971; Williams & Hynes 1973), illumination (Hughes 1966a, 1966b), depth (Harker 1953), temperature (Beauchamp & Ullyot 1962; Ide 1935), substrate permeability (Cummins 1962), and interspecific interactions (Peckarsky & Dodson 1980a, 1980b; Walton 1980; Ulfstrand, Sevansson, Enckell, Hagerman & Otto 1971). These factors

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seldom if ever result in predictable distribution patterns of invertebrates but rather a patchy mosaic of the various taxa based on their specific sets of microhabitat preferences and the occurrence of the composite microhabitat suitable to them within the reach of stream. Therefore, recognition that certain taxa of macrobenthos prefer certain habitat characteristics has been of limited value to investigators attempting to design an effective but efficient quantitative sampling program for entire communities of stream benthos (see Godbout & Hynes 1980; Needham & Usinger 1956).

The primary objective of this study was to determine if a linear distributional pattern of macrobenthos actually exists within rather physically uniform stream riffles. We also wanted to know the extent to which selected environmental factors [substrate particle sizes, current, coarse particulate organic matter (CPOM), drifting fine particulate organic matter (FPOM), dissolved oxygen above and in the substrate, temperature, pH (\approx CO₂), and depth] were correlated with invertebrate distributions within these riffles. Significant correlations would suggest possible explanations for any upstream-biased distribution pattern that we might observe.

MATERIALS AND METHODS

This study was conducted on the Brazos River about 12 km below Possum Kingdom Dam in Palo Pinto County, Texas, USA. The site consisted of three successive riffles bounded by extensive pools (>2 km long). Each riffle was approximately 100 m long, 15–18 m wide with 60 m between the upstream riffle (riffle 1) and the middle riffle (riffle 2), and 412 m between riffles 2 and 3. These riffles were chosen because of their apparent uniformity in length, current, depth, and substrate particle sizes within and among riffles. Illumination was uniform due to lack of any extensive vegetative canopy. In each riffle 15 sampling sites were arranged in a 3×5 grid. The first station was located at the upstream end (head) of each riffle with the remaining four placed at 25 m intervals downstream. The three sampling sites were at equal intervals across the river at each station.

Macrobenthos were collected in March 1977, using a modified Hess sampler (0.1 m², 400 μ m mesh) and preserved in 70% ethanol. Samples were taken beginning downstream to prevent disruption of the other sample sites. Insects comprised virtually all of the macrobenthos and were identified to the lowest taxonomic category possible. To facilitate statistical analyses, taxa of low density ($<5/\text{m}^2$) were combined into a miscellaneous group, thereby including all insects in the total analyses. Substrate samples were removed to a depth of 15 cm at each station using a metal pipe (ca. 20 cm diameter) open at both ends. Percent by weight of each substrate size class was determined using the modified phi scale according to the methods suggested by Cummins (1962). Current was measured with a torpedo-type flow meter (7 cm diameter) at each sampling site within 10 cm of the substrate. Drifting FPOM and benthic CPOM were collected for analysis at each sample site. For suspended FPOM, 250 ml of water were collected from mid-depth on pre-weighed 0.45 μ m filters using a hand-operated vacuum pump. Benthic CPOM (>1 mm) was collected in the Hess samples with the benthos, hand-picked, dried and weighed. Dissolved oxygen was measured using a portable meter near the surface of the substrate and 15 cm deep in the substrate by means of a perforated pipe (ca. 5 cm diameter) driven into the substrate. Water depth was measured at each sample site. Specific conductance, pH, and temperature were measured at each site using portable meters.

Although the distributional patterns discovered were rather obvious, a stepwise multivariate multiple linear regression procedure (Draper & Smith 1966) was used to compare densities of macrobenthos at each sample location with station (1–5, distance from the heads of riffles), riffle location (1, 2, or 3, beginning upstream), current, depth, CPOM, FPOM, DO in the water, DO in the substrate and six substrate particle size classes. The stepwise procedure identified correlations between environmental variables

and benthos densities and ranked them according to their relative importance. This was followed by a general linear model statistical method to determine the prediction equations and coefficients of determination for each taxon based on the environmental parameters determined to be significantly correlated with density by the stepwise procedure. A matrix correlation was also performed among all insect groups and individual environmental parameters. Student's t-tests were used to compare simple means. The various analyses were performed using square root transformed data as appropriate and necessary to normalize the data. The significance level used was $p > 0.05$.

RESULTS AND DISCUSSION

Physical and chemical measurements confirmed preliminary observations concerning uniformity of the riffles (Fig. 1). Flow rate was relatively constant within and among riffles with mean flow varying from 22-39 cm/sec. Maximum variation in depths among the riffles was 32 cm and occurred at the 100 m stations. Riffle 3 was approximately 5 m wider and 10 cm shallower than riffles 1 and 2. Substrate particle size classes were distributed within and among riffles with no discernible patterns. Temperature of the water above the substrate was uniformly 13.5° C, but the interstitial water ranged from 12.5° to 13.5° C with the highest value at station 5 (downstream) in each riffle. Oxygen was always near saturation above the substrate (10.4-11.8 mg/l). The first riffle had significantly less hyporheic oxygen available than the other two (see Fig. 1). Specific conductance and pH were uniform throughout the study area (2700 μ mhos/cm and pH 8.5) as expected. Benthic CPOM was not statistically correlated with distance from the heads of riffles and was not significantly different among riffles. Transport FPOM was relatively constant within riffles but riffle 3 had significantly less FPOM ($p > 0.001$) than riffles 1 or 2.

Insects collectively showed significantly higher densities at the heads of riffles ($r^2 = 0.63$, $p < 0.001$; Fig. 2). Of the 16 insect taxa analyzed, 12 showed a significant upstream bias in their distribution (Table 1, Fig. 3). These taxa comprised 93.4% of the total insects collected. Insects were most abundant in riffle 2 ($\bar{x} = 8997/\text{m}^2$). Multivariate analysis indicated that CPOM showed the only significant correlation with total insect distribution ($r^2 = 0.52$, $p < 0.0002$; Table 1). This was surprising at first because the insect taxa were predominantly FPOM feeders. Most FPOM is produced from CPOM and the organisms may have settled very near the sources. Conversely, CPOM and drifting insects may tend to settle in the same places because their sizes are similar.

Choroterpes mexicanus (Ephemeroptera: Leptophlebiidae) was the most abundant species with an overall mean density of 2372/ m^2 (ca. 31% of total). Distribution of *C. mexicanus* was skewed toward the head of each riffle (Fig. 3) and directly correlated with depth (Table 1). Other taxa which exhibited the same pattern of distribution and were significantly correlated with distance from the heads of the riffles (inversely correlated with station, 'S' = distance) were *Cheumatopsyche* spp. larvae (Trichoptera), *Cheumatopsyche* spp. pupae, *Hydropsyche* spp. larvae (Trichoptera), *Heptagenia maculipennis* (Ephemeroptera), Chironomidae larvae (Diptera), *Stenelmis* spp. larvae (Coleoptera), *Stenelmis bicarinata* adults and *Neoperla clymene* (Plecoptera) (Table 1, Fig. 3). Taxa which displayed the same distributional pattern but were not statistically correlated with station were *Oecetis* sp. (Trichoptera), *Simulium* sp. (Diptera), and *Argia translata* (Odonata). *Simulium* was positively related to current and negatively related to depth, i.e., they were more abundant in shallow, swift areas. This was due to their method of feeding and is consistent with results of other studies (Maitland & Penney 1967). All the organisms with an upstream bias were collectors or predators (Merritt & Cummins 1978). The other four insect taxa shown in Figure 3 (6.6% of total numbers) were not distributed with an upstream bias in riffles. Although *Tricorythodes* sp. (Ephemeroptera) had a

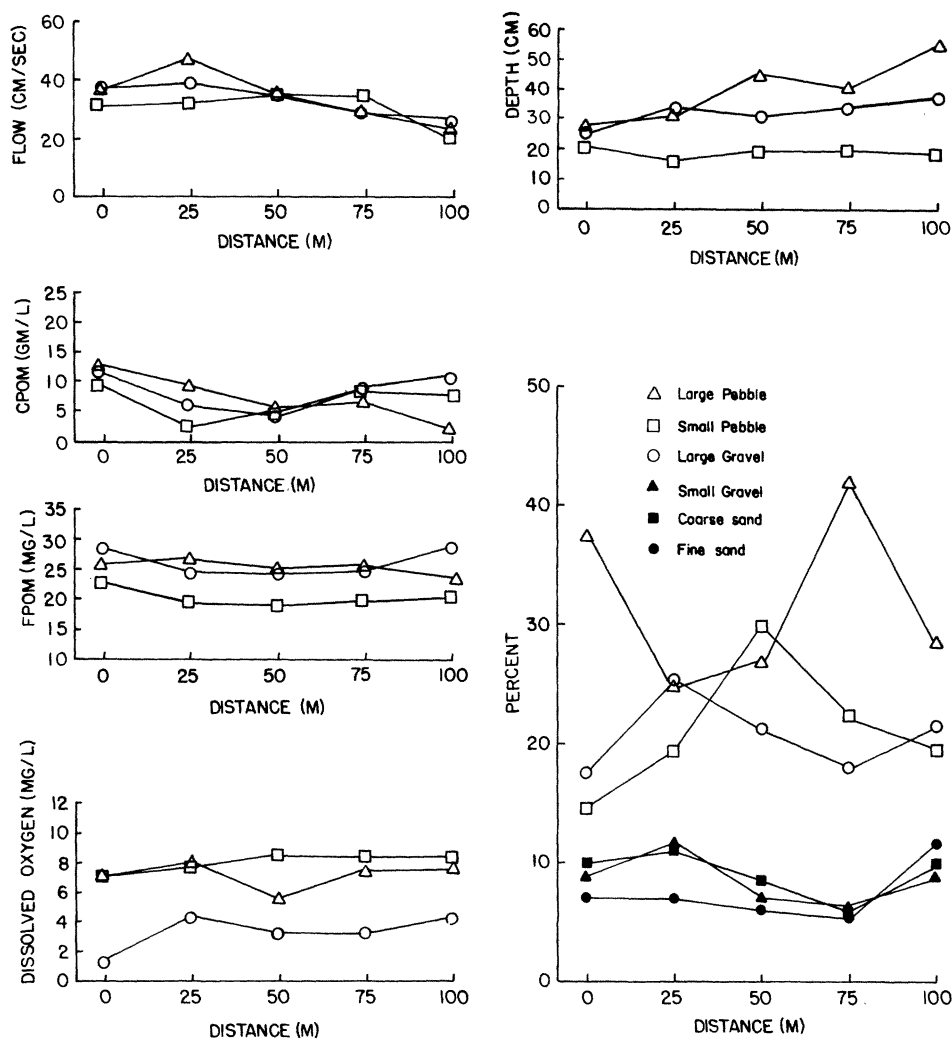


Fig. 1. Physico-chemical characteristics within three riffles of the Brazos River: Riffle 1 (○), Riffle 2 (▲), Riffle 3 (□). Symbols for substrate particle sizes are given in the figure.

reverse distribution among riffles (i.e., riffles 3 > riffle 2 > riffle 1), none of the species were statistically more numerous toward the tails of riffles. *Tricorythodes* is a collector-gatherer usually found in depositional zones of streams, or the littoral sediments of lakes. *Hydroptila* sp. is a trichopteran piercer-herbivore that was attached to *Cladophora* colonies. *Parargyractis jaliscalis* (Lepidoptera) is a scraper which may explain the negative correlation with fine sand (Table 1). The remaining taxa comprised 0.2% of the total insects and collectively even this miscellaneous group was significantly biased in distribution toward the heads of riffles.

Distribution of predators such as *N. clymene* and *A. translata* might be related to distribution of their prey. According to matrix correlation tests, *N. clymene* density was highly correlated with density of *Choroterpes* and *Tricorythodes*. *Choroterpes* is an important prey species for *N. clymene* in this reach of the Brazos, but *Tricorythodes* apparently is not eaten by them (Vaught & Stewart 1974). *Argia translata* was significantly correlated with *C. mexicanus*, *H. maculipennis*, and total insects. Results of

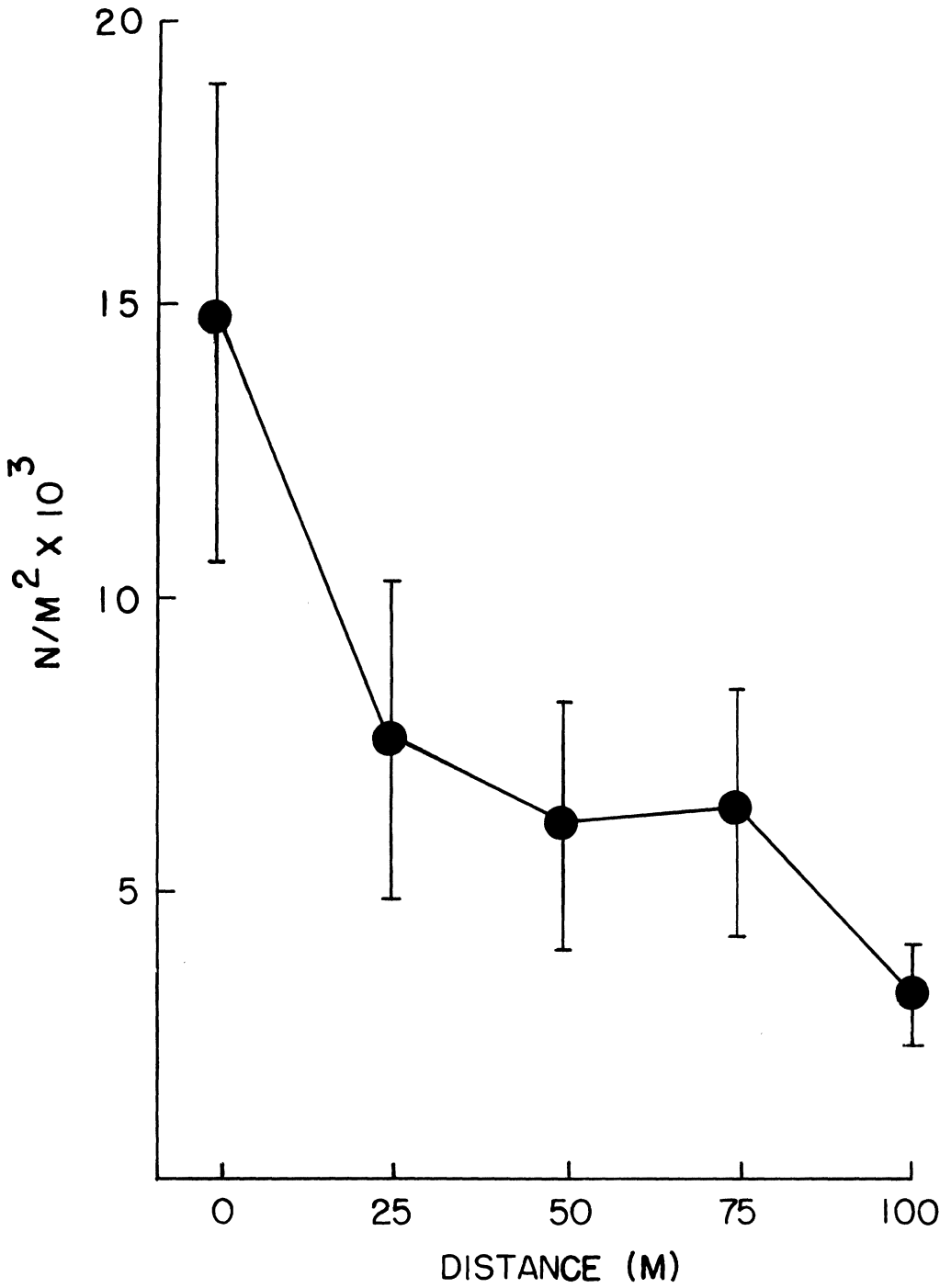


Fig. 2. Density of total insect fauna in relation to distance from the heads of riffles in the Brazos River. Vertical lines represent ± 2 standard errors of the mean.

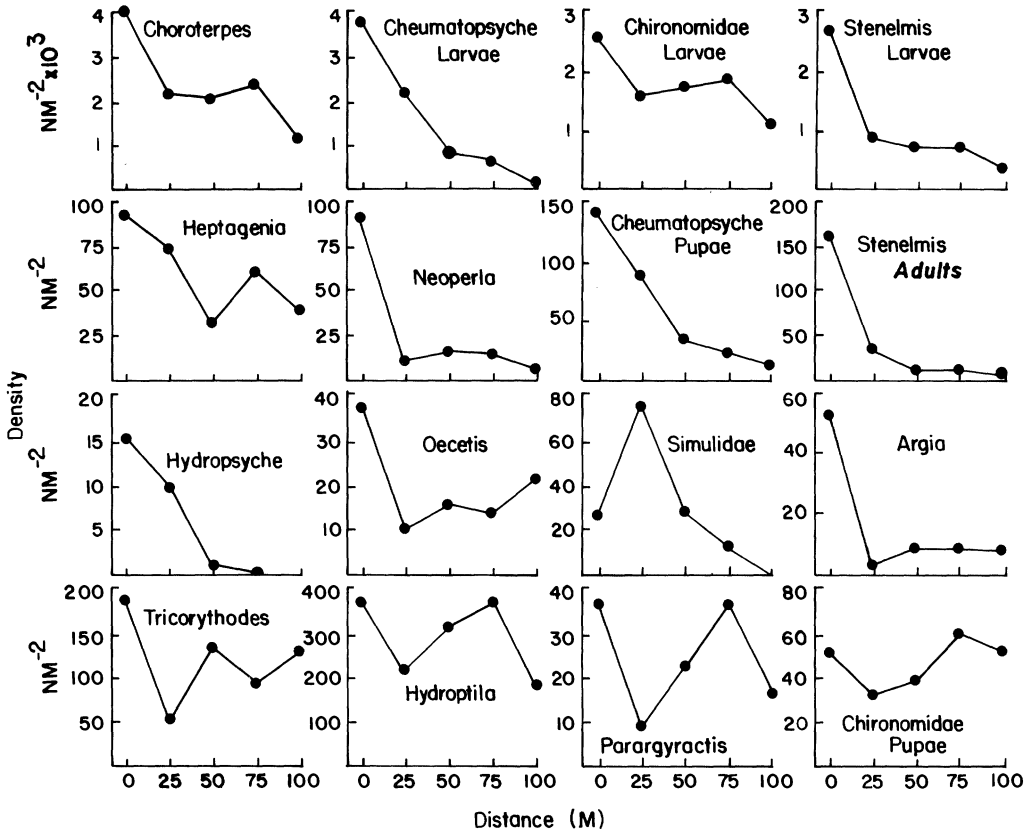


Fig. 3. Distribution of aquatic insect taxa in relation to distance from the heads of riffles in the Brazos River.

this study certainly did not indicate any large-scale spatial separation between predators and their prey as Peckarsky and Dodson (1980a) have suggested might occur due to predator-induced downstream drift of prey species.

Drift has been indicated to influence the size distribution of mayfly nymphs between riffles and pools in a Minnesota stream (Hall, Waters & Cook 1980). We considered the possibility that drift through pools with the following reassociation with the substrate in the riffle might result in the observed distribution. But it is very unlikely that riffle-adapted insects drifted through the long (>2 km) pool above the first riffle, and this riffle exhibited a particularly strong upstream-skew of macrobenthos densities.

Microhabitat characteristics that have previously been demonstrated to influence the distribution of aquatic insects in streams (substrate, current, food, etc.) were insufficient to explain the strong upstream bias in density of insects within riffles. Insect densities at the sampling sites were correlated with certain physical and chemical variables that are known to influence distribution of lotic insects. However, these variables were not themselves correlated with distance from the heads of riffles, and therefore did not completely explain the pattern of macrobenthos distribution observed. For example, total insect distribution (Fig. 2) was strongly biased toward the heads of riffles and was significantly correlated only with CPOM abundance (Table 1), but quantity of CPOM was not related to distance from the heads of riffles (Fig. 1). Additional factors apparently affect the linear distribution of insects within riffles. Quantity of FPOM was significantly lower in riffle 3 and there were significantly fewer insects in riffle 3. Filter-feeding insects

TABLE 1

Prediction equations for densities of benthic insects based on multivariate analyses.*

Density of Prediction Equations	Coeff. of Determination (r^2)	\bar{x} Density (N/m^2)
<i>Choroterpes mexicanus</i> = $15.69 - 2.10S + 0.16D$	0.26	2372
<i>Heptagenia maculipennis</i> = $11.85 - 0.32S + 0.07D - 1.06DOW + 0.84CPOM$	0.54	60
Chironomid larvae = $24.51 - 2.55R - 0.89S + 5.31CPOM - 1370.89FPOM$	0.52	1800
<i>Cheumatopsyche</i> larvae = $11.61 - 3.00S + 0.16Cur + 3.27CPOM$	0.69	1486
<i>Cheumatopsyche</i> pupae = $6.63 - 0.60R - 1.09S + 0.40D + 0.12CPOM - 0.13$	0.57	132
<i>Hydropsyche</i> = $-4.79 - 0.30R - 0.35S - 0.63DOW - 0.12SG + 0.09CS$	0.46	5
<i>Stenelmis</i> larvae = $16.22 - 2.10S + 2.93CPOM - 0.35SG$	0.46	1108
<i>Stenelmis bicarinata</i> adults = $6.15 - 1.38R - 0.59S - 0.07SP + 0.14FS$	0.57	43
<i>Neoperla clymene</i> = $5.20 - 0.59S - 0.04Cur - 0.14SG$	0.34	28
<i>Tricorythodes</i> = $1.93 + 0.64R - 0.06Cur + 2.00CPOM$	0.56	122
<i>Hydroptila</i> = $2.08 + 3.16CPOM$	0.25	300
<i>Oecetis</i> = $1.55 - 0.31R + 0.99CPOM - 0.07FS$	0.46	21
<i>Parargyactis jaliscalis</i> = $1.95 - 0.040R + 0.90CPOM - 0.10FS$	0.34	25
<i>Simulium</i> = $-0.97 + 0.10Cur - 0.03D$	0.55	30
Chironomidae pupae = $2.34 - 0.47R + 0.80CPOM$	0.29	51
<i>Argia translata</i> = $0.86 - 0.45R + 0.08SG$	0.22	18
Total Insects = $36.61 - 2.45R - 3.74S + 7.50CPOM$	0.63	7615

*Based on square root transformed densities for 0.1 m^2 , R = riffle; S = station; Cur = current; D = depth; DOW = DO in water; SP = small pebble; SG = small gravel; CS = coarse sand; FS = fine sand.

on the first two riffles may have reduced the FPOM, as there were about 3×10^6 *Cheumatopsyche* in riffle 1 and 5×10^6 in riffle 2, not including the other filter-feeders. Significant reduction in the quantity of seston within similar distances along streams has been attributed to its removal by filter-feeding insects (e.g., see Chutter 1963; Maciolek & Tunzi 1968; Oswood 1979). However, FPOM in transport was not shown to be more abundant at the heads of riffles and therefore could not explain distribution of the filter-feeding insects within riffles.

Upstream movement of lotic insects, which has been documented by several investigators (e.g., Bishop & Hynes 1969; Elliott 1971) could result in their concentration near the heads of riffles. Benthic invertebrates may consistently move upstream to counteract for downstream drift which results from dislodgement during feeding and other activities which expose them to swift currents (Ploskey & Brown 1980). Riffle-adapted invertebrates would not voluntarily enter pools, and therefore would become concentrated at the upstream ends of riffles.

There may be a higher quality of food items available to invertebrates at the heads of riffles. Plankton have been shown to be an important food for filter-feeding simuliid (Diptera) and hydropsychid (Trichoptera) larvae downstream from lakes and reservoirs where these insects often reach very high densities (Chutter 1963; Maciolek & Tunzi 1968; Oswood 1976, 1979; Ward 1975). The insects' populations decline downstream as the plankton resource diminishes resulting in distribution patterns that resemble those observed in this study within riffles. Plankton inhabiting unpounded reaches of small order (1-7) streams are generally considered to be of little consequence to the streams'

trophic dynamics (see Vannote et al. 1980). However, many streams that are not in steep mountain regions have pools in which true plankton may proliferate and provide high-quality nutrients to riffle invertebrates. Illies (1958) recognized this to be the case in many middle-European streams of the riffle-pool type. Recent studies in the first order section of the White River in Arkansas indicate that significant numbers of zooplankters are transported onto riffles even during poor habitat conditions one week following a spate (A. Brown, D. Jackson, unpubl. data).

The upstream bias in density of macroinvertebrates below pools suggests that they may be competing for high quality food items and if this is true that food is a more important resource than space in this type of stream. Suitable habitat space was relatively abundant further downstream in each riffle. This agrees with Benke and Wallace's (1980) contention that production of net-spinning caddisflies is limited in small order streams by the amount of high quality food available in the seston.

During the last decade, the river continuum concept has been developed as a general model for the structure and functioning of lotic ecosystems (Minshall et al. 1983; Vannote et al. 1980) and has proven to be extremely valuable. We believe that understanding of lotic ecosystems of distinct riffle-pool geomorphology is enhanced by an additional perspective that emphasizes the importance of sedimentation of POM and plankton production in the pools of these streams. Perhaps it would be conceptually meaningful to consider riffle-pool type streams to be a chain of unique small lakes connected by a series of short, nearly isolated segments of stream. Relatively low gradient streams with extensive pools resemble rivers with sequential epilimnion-release reservoirs. Each pool may partially reset the continuum in much the same way as described by the serial discontinuity concept of Ward and Stanford (1982).

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