

The effect of rock size upon the distribution of species of Orthocladiinae (Chironomidae: Diptera) and *Baetis intercalaris* McDunnough (Baetidae: Ephemeroptera)

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ABSTRACT. 1. Three experimental stream bed sections were established in areas of similar depth and current velocity to examine the effect of rock size upon the distribution of *Baetis intercalaris* and Orthocladiinae. Each section was composed of one rock size with the diameters (mm) of the three rock classes being 30–70, 90–140 and 160–190.

2. Colonization was measured at 2 week intervals over an 8 week period, and these data were used to calculate abundance or the number of individuals per unit area of stream bed and density or the number of individuals per unit area of rock surface.

3. Statistical analyses reveal that rock size was of secondary importance in determining Orthocladiinae abundance and density among the experimental bed sections. Rock size differences had a more pronounced effect upon *B. intercalaris* since on every sampling date both abundance and density increased with rock size.

4. Rock size differences appeared to have little effect on the response of Orthocladiinae to silt deposition, whereas the reverse was true for *B. intercalaris*.

Substrate particles are distributed non-randomly within the bed of a stream. Mean particle size decreases relatively rapidly in the first kilometres of a stream and more slowly thereafter (Leopold *et al.*, 1964). Within this longitudinal pattern the particles are further distributed between pools and riffles as a result of kinematic wave action. Thus there tends to be a greater mean particle size in riffles than in pools. This and other differences, such as depth, current velocity and dissolved oxygen, have led many investigators to compare the fauna of the two habitats (Wene, 1940; Pennak & van Gerpen, 1947; Sprules, 1947; Jones, 1948; O'Connell & Campbell, 1953; Minckley, 1963; Ward, 1975), but few studies (Needham & Usinger, 1956; Lium, 1974) have examined the distribution of

benthic fauna within either of these two macrohabitats.

The purpose of this study was to examine the effects of rock size upon the distribution of *Baetis intercalaris* and Orthocladiinae species within a riffle macrohabitat. Artificial stream bed sections of varying substrate composition were created in similar conditions of current velocity and depth, and subsequent insect colonization was observed. By varying only rock size among the beds, I could then consider this factor responsible for observed differences among the experimental beds. Though the methods of colonization were not quantified, it was assumed that, as Williams & Hynes (1976) found, colonization by drift would be of greatest importance.

Preliminary sampling indicated that *B. intercalaris* and Orthocladiinae species were the most abundant taxa within the study riffle. Although the present study did not include

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dietary analysis, both are considered to be generalist herbivores-detritivores (Chapman & Demory, 1963; Gilpin & Brusuen, 1970; Cummins, 1973, 1974). Cummins (1974) considered Baetidae and Orthocladiinae to be functionally analogous as collector-scraper feeding on both attached periphyton and deposited detritus.

In the White Clay Creek in southeastern Pennsylvania, *B. intercalaris* has multiple overlapping generations (R. L. Vannote, pers. comm.). Similarly, the subfamily Orthocladiinae is composed of both univoltine and multivoltine species which do not emerge synchronously (S. S. Roback, pers. comm.). Consequently, the inter-bed comparisons were probably not affected by temporally concentrated emergence and/or oviposition periods.

Materials and Methods

Cedar Run is a spring-fed stream with its source located in Harris Township, Centre Co., Pennsylvania (latitude $40^{\circ}47'$; longitude $77^{\circ}44'$). The drainage area is underlain with limestone and dolomite of Cambrian and Ordovician age (Butts & Moore, 1936). The stream has a gradient of 6 m/km, and its width and depth vary from 1.0 to 10.0 m and from 0.1 to 1.0 m, respectively. Preliminary measurements indicated a uniform current velocity and depth over a great part of the riffle chosen for experimentation.

Crushed limestone rocks were obtained from a local quarry and then separated by size into three classes with the ranges of the maximum diameter (mm) for the small, intermediate, and large classes being 30–70 (ϕ -5), 90–140 (ϕ -6) and 160–190 (ϕ -6), respectively. The original substrate of the experimental riffle was then manually removed to the banks, and in doing so care was taken not to remove so much of the fine material as to create trough-like depressions. Three adjacent bed sections, each 0.91×3.05 m, were then established in longitudinal positions, i.e. with their short sides perpendicular to the flow. Each bed was composed of only one size class of rocks. For the sake of brevity, each bed will be referred to in terms of the rock size class of which it is composed

(i.e. the bed composed of rocks of the small size class will be termed the small bed and so on).

The utilization of crushed quarry rocks instead of rocks from the stream itself had advantages and disadvantages. Since the quarry rocks were available in quantity in three suitable size ranges, their use eliminated the time consuming tasks of rock 'hunting' and cleaning which would have been necessary if stream rocks were used. On the other hand, the quarry rocks were more angular and possessed fewer crevices and cavities than worn stream rocks. In this preliminary study, I chose to save time; future studies will take surface texture into account.

The beds were established on 10 June 1975, and were sampled on the following dates: 19 June, 1 July, 15 July and 2 August 1975. Five samples were taken in each bed on each sampling date for a total of fifteen samples per series and sixty samples for the entire study period. Sampling sites within a bed were chosen to minimize the possibility of re-sampling an area. Since the beds were outlined by wire stretched across the stream, the position of each sample could be noted. All samples were taken at least 15 cm from the nearest boundary of the bed.

At each sampling site, I measured current velocity (pygmy current meter at $\frac{1}{2}$ depth), bed height (height of experimental rocks over compact bed) and depth (height of water above experimental rocks). None of these habitat conditions differed significantly among the beds on any sampling date ($P < 0.05$). The mean depth (cm), bed height (cm) and current velocity (cm/s) values for all sixty samples were 18.7 (SE = 3.8), 8.8 (SE = 1.8) and 66.9 (SE = 8.0), respectively. Following these measurements a cylindrical pipe (diameter 20 cm) was manoeuvred into its lowest possible position, and all rocks with over half their maximum diameters within the sampling circumference were removed. The resulting 'hole' was filled with unused rocks of the same class to prevent unusual current patterns.

After sampling, the material was taken to the laboratory where the rocks were rinsed to remove all organisms and all the residue was examined for *B. intercalaris* and Orthocladiinae. Since no water was screened or filtered, the problem of underestimating early instars due

to a large mesh size was avoided. Total rock surface area estimates were then obtained as follows. Prior to the initiation of the experiment, thirty rocks in each size class were selected for surface area determination. Aluminium foil was moulded around each rock so as to conform to its shape, and upon removal the outline of the foil was traced with a planimeter. The mean surface areas (cm^2) for a small, intermediate and large size class rock were 63 (SE = 19), 220 (SE = 33) and 607 (SE = 96). The number of rocks in a sample was then multiplied by the appropriate mean area per rock to obtain total rock area estimate.

The number of individuals per sample provided 'abundance' estimates, whereas this number divided by the total rock area in that sample provided 'density' estimates. Thus, abundance estimates represent numbers per unit area of the stream bed, i.e. the area of the sampling device, and density estimates represent numbers per unit area of rock surface area. Both abundance and density data were subjected to two statistical analyses. The main effects of rock size and time (sampling date) were tested using a two-way ANOVA after a logarithmic transformation of the data. Such an analysis isolates the importance of rock size differences in affecting organism distribution over the entire study period. To test for significant differences in distribution patterns on a single date, a Duncan's multiple range test (after Steel & Torrie, 1960) was used for the inter-bed comparison of means. The two-way ANOVA permitted analysis of rock size effects over all four sampling dates,

while the multiple range test examined these effects among rocks with equal exposure time for colonization.

Results

The abundance patterns of *B.intercalaris* and Orthoclaadiinae species are presented in Table 1. The two-way ANOVA revealed a significant interaction ($F = 6.02$; $P < 0.001$) between rock size and date for *B.intercalaris*. For Orthoclaadiinae larvae the interaction component was insignificant ($F = 2.24$; $0.01 < P < 0.05$), and testing the main effects revealed the effect of rock size to be insignificant ($F = 1.89$; $0.25 < P < 0.10$) while that of date was significant ($F = 38.6$; $P < 0.001$). Thus the effect of rock size in determining *B.intercalaris* distribution was dependent upon time, and for Orthoclaadiinae sampling date alone accounted for a significant amount of the variation.

The results of the multiple range test show that on all sampling dates the large bed supported significantly more *B.intercalaris* than did the small bed (Table 1). However, on only one date, 15 June, was the abundance of the large bed significantly greater than that of the intermediate bed and on only two dates, 15 July and 2 August, was *B.intercalaris* significantly more abundant in the intermediate bed than in the small bed. The intermediate bed apparently represented a habitat similar enough to both the large and small beds so as to preclude significant differences in *B.intercalaris* abundance between it and either extreme. With respect to Orthoclaadiinae

TABLE 1. Log number of *Baetis intercalaris* and Orthoclaadiinae per sample (abundance) for each experimental bed on each sampling date. Numbers in parentheses represent one standard deviation of the mean ($n = 5$).

Rock size	15 June	1 July	15 July	2 August
<i>Baetis intercalaris</i>				
Large	1.66 (0.24) ^{a*}	2.58 (0.15) ^a	2.52 (0.18) ^a	2.97 (0.23) ^a
Intermediate	1.07 (0.26) ^b	2.48 (0.08) ^{a, b}	2.51 (0.06) ^a	2.06 (0.14) ^a
Small	0.52 (0.32) ^b	2.33 (0.07) ^b	2.23 (0.07) ^b	1.56 (0.11) ^b
Orthoclaadiinae				
Large	1.25 (0.24) ^a	2.71 (0.16) ^a	2.18 (0.24) ^a	2.05 (0.33) ^a
Intermediate	1.93 (0.15) ^a	2.68 (0.14) ^a	2.09 (0.20) ^a	2.16 (0.10) ^a
Small	1.60 (0.17) ^a	2.54 (0.07) ^b	2.23 (0.17) ^a	2.07 (0.12) ^a

* Means within each taxon/sampling date followed by the same letter are not significantly different by the Duncan multiple range test ($P = 0.05$).

TABLE 2. Log number of *Baetis intercalaris* and Orthocladiinae per 100 cm² of rock surface area (density) for each experimental bed on each sampling date. Numbers in parentheses represent one standard deviation of the mean ($n = 5$).

Rock size	15 June	1 July	15 July	2 August
<i>Baetis intercalaris</i>				
Large	0.20 (0.24) ^{a*}	1.37 (0.09) ^a	1.34 (0.20) ^a	1.47 (0.15) ^a
Intermediate	0.39 (0.23) ^a	1.21 (0.12) ^b	1.20 (0.06) ^b	0.75 (0.12) ^a
Small	0.00 (0.00) ^c	0.79 (0.12) ^c	0.65 (0.21) ^c	0.04 (0.05) ^c
Orthocladiinae				
Large	0.19 (0.21) ^a	1.53 (0.13) ^a	0.99 (0.29) ^a	1.06 (0.19) ^a
Intermediate	0.65 (0.16) ^a	1.41 (0.29) ^a	0.80 (0.17) ^a	0.85 (0.10) ^a
Small	0.09 (0.14) ^a	0.99 (0.08) ^b	0.65 (0.25) ^a	0.49 (0.15) ^a

* Means within each taxon/sampling date followed by the same letter are not significantly different by the Duncan multiple range test ($P = 0.05$).

distribution, on three of the four sampling dates, abundance did not differ significantly among the three beds (Table 1). On 1 July the large and intermediate beds both had significantly more larvae than the small bed but did not differ significantly from each other.

The density patterns of *Baetis intercalaris* and Orthocladiinae are presented in Table 2. The two-way ANOVA revealed a significant interaction between rock size and date for both *B. intercalaris* ($F = 13.4$; $P < 0.001$) and Orthocladiinae ($F = 3.75$; $P < 0.01$). Thus for both taxa the effect of rock size in determining density was dependent on time.

The results of the multiple range test for density parallel those of abundance. On all sampling dates the densities of *B. intercalaris* in both the large and intermediate beds were greater than those in the small bed (Table 2). However, on only two dates, 1 July and 15 July, was the observed density of the large bed significantly greater than that of the intermediate bed. With respect to Orthocladiinae distribution, on three of the four sampling dates density did not differ significantly among the three beds. On 1 July the large and intermediate beds both had significantly greater density than the small bed but did not differ significantly from each other.

Discussion

The present findings indicate that, in conditions of uniform current velocity and depth, the effect of rock size upon benthic insect

distribution varies among different taxa. More specifically, neither statistical treatment revealed Orthocladiinae abundance to be greatly affected by rock size differences. The distribution patterns of *B. intercalaris* were less clear due to a significant interactive effect, yet the multiple range test revealed a consistent trend of increasing abundance with rock size on any one date.

The finding that the interactive effect varied in the level of significance between the two taxa may suggest different responses to silt deposition in the three beds. Although only qualitative observations were made, silt deposition was clearly far greater in either the small or intermediate bed than in the large bed. For *B. intercalaris* the effect of rock size may have varied with time as the differences in deposition patterns became more pronounced among the beds. Evidence is provided by the abundance data which show that in the small and intermediate beds the 2 August values represented only 16% and 37% of their peak abundances respectively. This trend was not nearly as dramatic in the large bed as the 2 August value represented 83% of the peak abundance. The significant interaction effect, may have been due to (1) silt deposition being a time dependent process and (2) its effects being markedly different among the sized rocks.

The lack of a significant interaction effect for the Orthocladiinae may indicate a more uniform effect of increased silting among the experimental beds. Despite the apparent greater sedimentation with decreasing rock

size, the three beds exhibited similar decreases in abundance as the 2 August values in the large, intermediate and small beds were 26%, 30% and 35% of their peak abundances respectively. The non-significant interaction effect and the ability of time alone to account for a significant amount of the variation, may have been due to (1) silt deposition being a time-dependent process and (2) its effects being markedly similar among different sized rocks.

The finding that for any one sampling date *B. intercalaris* abundance increased with increasing rock size agrees with those of Allan (1975) for *Baetis bicaudatus* Dodds, *Epeorus longimanus* (Eaton) and *Ephemerella coloradensis* Dodds and Cummins & Lauff (1969) for *Perlesta placida* (Hagen) and *Stenelmis crenata* Say. Cummins & Lauff (1969) also report that selection of larger substrate particles by *P. placida* became more pronounced with increased silt deposition. Their hypothesis that silting rendered the smaller substrate particles unsuitable, parallels the aforementioned findings regarding *B. intercalaris* distribution and observed silt deposition. The apparent secondary importance of rock size in affecting Orthocladiinae distribution agrees with the results of Cummins & Lauff (1969) for *Tipula caloptera* Loew, *Sialis vagans* Ross, *Caenis latipennis* Banks and *Helicopsyche borealis* Hagen.

Regarding density estimates, the results indicate that, for any one date, the number of *B. intercalaris* per unit area of rock surface increased with increasing rock size but that no significant differences in Orthocladiinae density existed among the beds. The significant interaction effect found for both taxa in the two-way ANOVA is not surprising, given (1) the dependence of silting upon time and (2) the dependence of density estimates upon a parameter, i.e. total rock surface area per sample, that is determined by the size of the individual rocks within a sample. In the only other study presenting comparable data, Lium (1974) found that total insect numbers per cm² of rock area increased with rock size from 22 to 64 mm and then decreased as rock size increased to 256 mm. To account for this trend, Lium (1974) suggested that above a certain rock size total insect density may decline because there are proportionately

fewer available suitable microhabitat sites per unit area of rock. Neither the data for *B. intercalaris* nor Orthocladiinae larvae exhibit this trend, yet further conjecture regarding the validity of Lium's hypothesis is beyond the scope of this report and awaits definition of the preferred microhabitat sites of every taxon under investigation.

Since no dietary analyses were performed, the distribution pattern noted should not be interpreted in the light of potential competitive interactions. Neither do the present findings elucidate the exact nature by which rock size affected the distribution of the taxa studied. That is, the observed responses cannot be ascribed strictly to rock size since an important factor such as food availability was not monitored. However, if, as seems likely, food availability is itself dependent upon the hydrodynamics of current flow over and among rocks of varying size, then the value of rock size as a means predicting the distribution of benthic organisms becomes obvious. The present study must be viewed as an attempt to define this predictive capacity rather than as an attempt to explain it.

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