PATCH-SPECIFIC VARIATION IN DRIFT DENSITY OF *BAETIS*

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ABSTRACT

We examined spatial variation in daytime drift density of *Baetis* larvae collected from 42 habitat patches in Clearwater Creek, southwest Washington, USA. Drift density ranged between 22 and 525 100 m^{-3}. Variation in drift density appeared to be inversely related to current velocity, although only weakly. Drift density showed no relationship with substrate size, time of day (daylight hours only), length of sampling interval, or size of substrate patch sampled. Although significant variation in drift density can occur within relatively short reaches of stream the mechanisms promoting observed variation are not well understood.

INTRODUCTION

Drift of aquatic invertebrates is a ubiquitous phenomenon in streams. Significant variation in drift density occurs among stream reaches, within reaches, and over time. Stream ecologists are interested in such variation for several reasons. For example, 1) drift is a method of dispersal and thereby affects colonization dynamics of stream insects (Sheldon 1984), 2) drift may be an indicator of the toxic effects of pollutants (Wiederholm 1984), and 3) drift may influence the abundance and distribution of drift feeding fish species (Waters 1969). Factors associated with variation in the magnitude of drift include current, light and substrate (e.g. Holt and Waters 1966, Corkum *et al.* 1977, Walton *et al.* 1977, Ciborowski 1982, review by Statzner *et al.* 1984). However, for most species, the relative and interactive effects of different factors are poorly understood.

Most stream ecosystems are mosaics of different habitat patches that differ in water velocity, water depth, substrate composition, food types, patch size and other features. Patchiness occurs at several spatial scales, and benthic distributions of stream invertebrates are strongly affected by such environmental heterogeneity (Hynes 1970, reviews in Resh and Rosenberg 1984). Because drift depends on benthic sources of animals, some of the observed spatial variation in magnitude of drift may be influenced by environmental patchiness.

The purpose of this study was to:

1. assess the magnitude of variation in drift density of *Baetis* among habitat patches, and
2. determine how much of the observed variation was associated with patch character.

We studied *Baetis* because it occurs in many stream ecosystems and a variety of factors are known to influence its benthic distribution (Minshall and Minshall 1977, Gore and Judy 1981).

STUDY AREA

Our study was conducted in Clearwater Creek approximately 15 km northeast of the Mt St Helens crater in southwestern Washington (Fig. 1).

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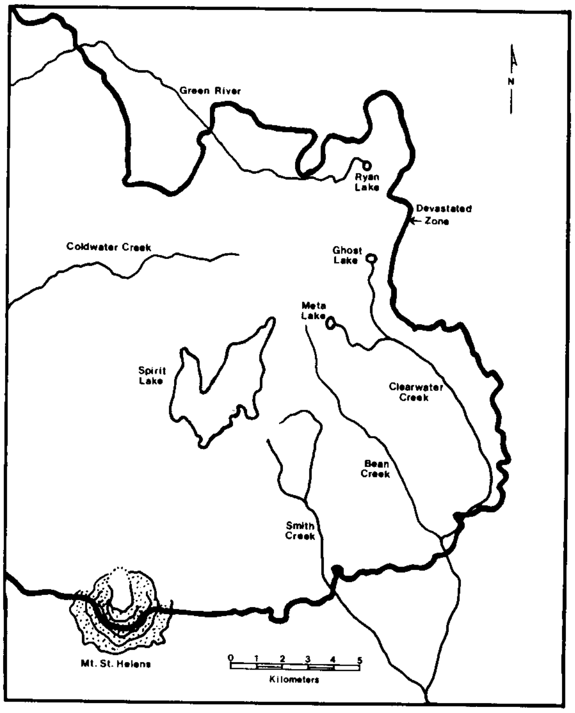

Fig. 1. Map of the study area showing Clearwater Creek in relation to Mt St Helens and the area devastated by the May 1980 eruption.

Elevation of the stream is *ca.* 750 m. In May of 1980 the Clearwater basin was catastrophically disturbed by the eruption of Mt St Helens. Primary disturbance to the stream included heavy tephra deposition, channel scour and blown down timber. Six years after the eruption riparian vegetation is scarce and the stream canopy is open with little shading. In 1985 stream temperatures (°C) ranged between a winter low of 2° and a summer high of 18°. Mean summer water temperature was 12°.

METHODS

We characterized habitat patches by dominant particle size of inorganic substrates (Fig. 2). Particle sizes were assigned to six categories: sand (< 1 cm), gravel (1–2 cm), pebble (2–4 cm), rubble (4–8 cm), cobble (8–16 cm), and boulder (16 + cm). Forty-two patches were selected for sampling: seven of each substrate type. Length of each habitat patch was used as a measure of patch size.

A 250 μm mesh drift net was set at the downstream end of each habitat patch. Nets were cone shaped, had a mouth area of 177 cm^2 and were 1 m long. Nets were secured to metal stakes driven into the stream bed so that the bottom edge of each net was approximately 5 cm above the substrate. Nets were completely submerged. Upon setting the net, current speed at the mouth of the net was measured with a Montedoro Whitney Inc. flow meter (model PVM-2A). In general, nets were left in place for 0.5–2.0 hours. Current speed was measured again immediately prior to removing the net from the stream. Samples were preserved in ethanol for later sorting.

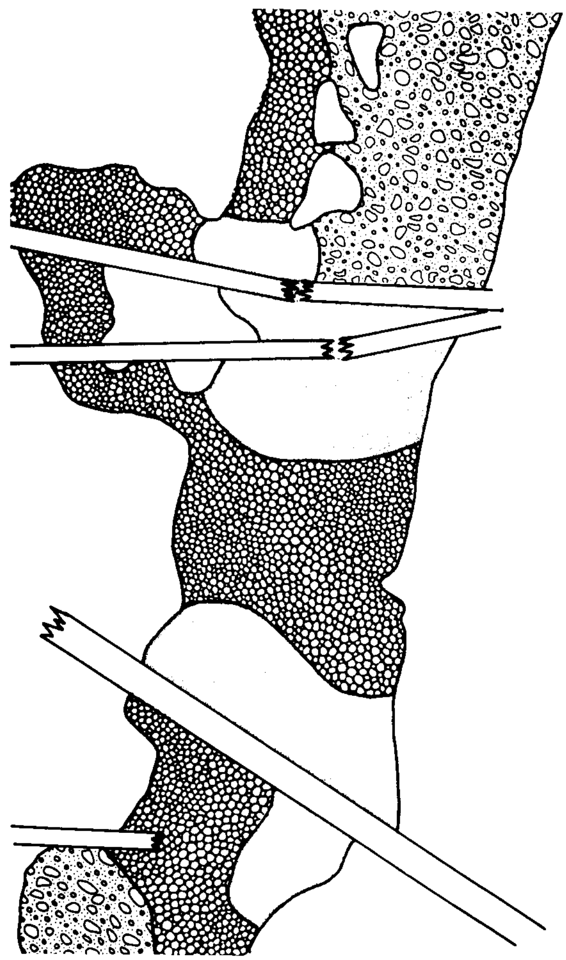

Fig. 2. Example of the mosaic of patches that occur in Clearwater Creek. The patches shown are characterized based on dominant substrate type.

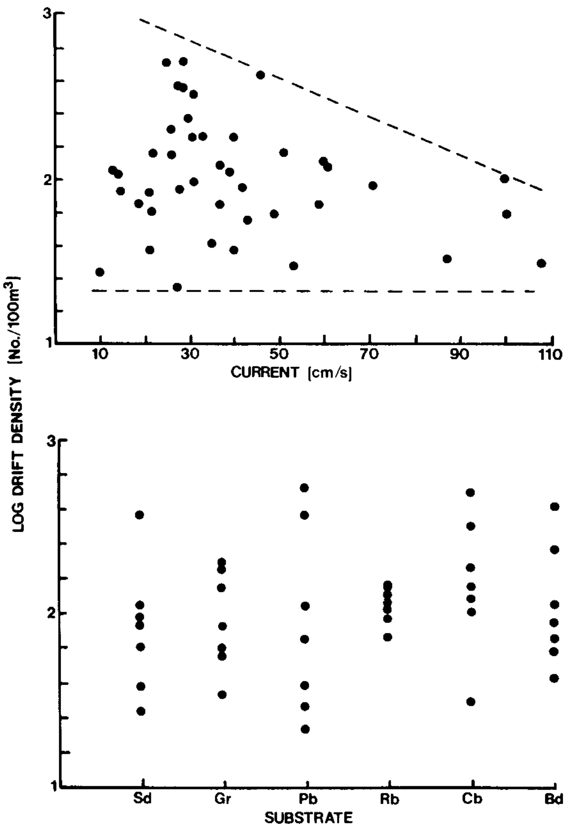

Fig. 3. Relationships between $\log_{10}$ drift density and both current speed and substrate type. The dashed lines on top of the graph illustrate our interpretation of how upper and lower ranges of drift density varied with current speed. Substrates are: sand (Sd), gravel (Gr), pebble (Pb), rubble (Rb), cobble (Cb) and boulder (Bd).

All drift samples were taken during daylight hours (1030–1700 hr) to minimize variation associated with diel differences in drift activity. Even though other studies have shown that drift density of *Baetis* does not vary significantly during daylight hours (e.g. Holt and Waters 1966, Waters 1969, 1972), we recorded time of day that each sample was taken to check for temporal differences. All samples were taken between 5 and 12 August, 1986.

Drift density was calculated for each sample as:

$$\text{sample drift density} = \frac{\text{numbers per net-hour}}{\text{m}^3 \text{ filtered per net-hour}} \times 100$$

as described by Allan and Russek (1985). This equation provides an estimate of the number of animals drifting per 100 m^3 of water. It is a measure of concentration of animals in the water column and not a measure of drift rate.

Correlation and visual analysis of graphs were used to evaluate whether drift density varied with substrate type, current speed, patch size, and time of day. One way analysis of variance (ANOVA) and analysis of covariance (ANCOVA) were also used to assess effect of substrate type and other factors on drift density. All data were transformed (log x) prior to statistical analyses.

RESULTS

We observed two species of *Baetis* in our samples (*B. tricaudatus* and *B. bicaudatus*). Among all samples, drift density of *Baetis* varied by almost 24 fold (range = 22–525 100 m^{-3}). Mean density was 142 100 m^{-3}. The coefficient of variation ($s/x \times 100$) around the mean for nontransformed data was 90. Lower and upper 95% confidence intervals were 103 and 182 100 m^{-3} respectively. Based on these confidence intervals, about a two fold difference would be expected between high and low observations.

No single factor accounted for a large proportion of the observed variation in *Baetis* drift density. Of the factors studied, only current speed appeared to show a relationship with drift of *Baetis* (Fig. 3). However a simple linear or curvilinear relationship was not apparent ($r = -0.024$, P = NS). Part of the reason that a simple linear correlation failed to detect a relationship between drift density and current was that substrate and current varied in such a way that the effects of each on drift were obscured. An analysis of covariance revealed that the regression coefficient of drift density on current speed was significant when adjusted for substrate (pooled correlation coefficient = −0.39, $P < 0.02$). Even so, assuming a linear model, current speed explained < 15% of the variation in drift density. Also, it is possible that the observed negative correlation may be spurious due to the restricted number of observations at higher current velocities.

Drift density was not directly related to any of the other variables measured. Simple ANOVA indicated that means for each substrate type were not significantly different from one another ($F = 0.53$, $P < 0.97$). A wide range of drift density values were observed for all substrate sizes (Fig. 3). Furthermore, no significant substrate effects were observed when means were adjusted for effects of current, time of day, length of the sampling period and patch size (ANCOVA). ANCOVA also showed that drift density was not related to length of habitat patches ($r = 0.04$), time of day that samples were taken ($r = 0.12$) or length of time nets were in the water ($r = -0.21$).

DISCUSSION

Few studies have described the magnitude of variation in drift density among replicate samples (Allan and Russek 1985). In this study, replicate samples taken over several days from 42 locations on Clearwater Creek allowed us to: 1) assess magnitude of variation in drift density and 2) evaluate potential cause of variation among replicates. Although Clearwater Creek was catastrophically disturbed in 1980, mean drift density of *Baetis* was equal to or greater than that noted in other studies. Minshall and Winger (1968) observed that daytime drift densities of *Baetis* sp. were 130-270 100 m^{-3} under normal conditions of flow. Lemkuhl and Anderson (1972) noted that mean drift density of *Baetis tricaudatus* in a heavily shaded Oregon stream ranged between ca. 135-340 100 m^{-3} during summer months. The range of sample drift densities (ca. 10–500 100 m^{-3}) of *B. bicaudatus* observed by Allan and Russek (1985) in a Rocky Mountain stream was almost identical to that which we observed (22-525 100 m^{-3}) for the two species we studied. Our data and the study by Allan and Russek (1985) show that large differences in drift density can occur among locations on the same stretch of stream.

Consideration of the range of observed drift densities probably exaggerates the real ecological significance of variation among locations. Estimates of confidence intervals are more meaningful, because they specify the magnitude of variation expected at a certain level of probability. Based on 95% confidence intervals, the magnitude of difference that would be expected among sample locations on Clearwater Creek is about two fold.

In our analyses, we assumed that most drifting *Baetis* were derived from the habitat patch directly upstream from the drift net. If this is not true, it will be difficult or impossible to associate variation in drift density to environmental differences among patches. We have no direct data bearing on this question. Waters (1965) estimated that *Baetis* drifted 50–60 m day^{-1}, a distance greater than the size of most patches in our study. However this value is high compared to other drift studies. For example, Townsend and Hildrew (1976) found that most invertebrates drifted < 2 m. Elliott (1967) and McLay (1970) found most drift to originate within 10 m of the drift net. Also, because daylight suppresses *Baetis* drift (Holt and Waters 1966), detached individuals probably re-attach as soon as possible thereby minimizing distance travelled.

Although benthic distributions of aquatic insects are often related to variation in the benthic environment (e.g. Cummins and Lauff 1969, Williams 1978, Tolkamp 1980), relationships between drift and the environment are poorly understood. Several studies have shown that the benthic abundance of *Baetis* varies with either substrate type or current speed (Lemkuhl and Anderson 1972, Minshall and Minshall 1977, Gore 1978, Gore and Judy 1981, Culp *et al.* 1983). Most species of *Baetis* apparently prefer relatively coarse substrates and moderate to rapid current. We might therefore expect patch-specific differences in drift density to exist and that drift density will vary in some fashion as a function of benthic density. However, it is difficult to predict *a priori* the specific relationship between benthic density and drift density. The most simple prediction is that drift density from a patch is proportional to benthic density within that patch.

Our data suggest that, of the factors examined, current speed was most likely to influence drift density of *Baetis*. Although the nonuniform distribution of samples across current speeds limits strong statistical inferences, we offer the following tentative interpretation of our results. Instead of describing a simple linear response, current speed seemed to limit the range of drift densities possible. Inspection of the scatter plot of log drift density vs current speed suggests that at slow flows a wide range of drift densities occurred. With increasing current speed the highest observed drift density decreased in magnitude. Flow rate, therefore, may limit the maximum drift density possible. At any particular current speed significant variation may occur, presumably associated with other factors. This interpretation agrees in general with data of both Corkum *et al.* (1977) and Ciborowski *et al.* (1977) who observed that drift of *Baetis* and *Ephemerella,* respectively, decreased with increasing current speed.

Patch-specific variation in drift is virtually unexplored in natural stream ecosystems. Our data suggests that one patch-specific attribute of the benthic environment (current speed) may be associated with local variation in drift variation of *Baetis.* We suspect that the differences among patches in other characteristics may be associated with much of the observed variation that was not explained. For example we did not determine whether drift density varied with either food abundance or benthic density in this system, although other studies have indicated that both are probably important (e.g. Kohler 1985). Also, we do not know to what extent factors interact and thereby modify direct effects of single factors. These questions should be fruitful areas of future research.

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