# Recolonization of Denuded Stream Bottom Areas by Drift

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where the bottom substrate is inorganic, and in the course of taking the sample the stones and gravel are returned, it is possible that the invertebrates will recolonize the area more quickly if some means of rapid dispersal exists.

The high drift rates that have been observed for certain stream invertebrates (Müller, 1954; Waters, 1962) may provide such a rapid dispersal; Leonard (1942) and Müller (1954) have described the rapid colonization of newly excavated stream beds by drifting invertebrates. Sampling is often done in stream riffles where rooted plants are absent and the bottom is composed of stones and gravel. Thus it was postulated, in an ecological study of invertebrates that I conducted on a small stream riffle, that bottom samples could be taken frequently yet safely from the riffle, since the species of principal interest were by far the dominant ones and were also subject to a high drift.

The objective of the present study was to test this postulate by comparing the rate of recolonization of denuded areas with the drift rate at various times of the year, and to determine the minimum time interval necessary between successive bottom samplings to avoid effects of previous samples on the bottom fauna.

The study was conducted in Valley Creek, a small trout stream in east-central Minnesota. Two species of stream invertebrates were involved: *Baetis vagans* McDunnough, a small, free-swimming mayfly, and the scud, *Gammarus limnaeus* Smith. These two species were by far the dominant macroinvertebrates in Valley Creek riffles, *Baetis* in numbers and *Gammarus* in weight.

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### INTRODUCTION

In a program of sampling bottom fauna periodically, it is essential that successive samples are not taken from the locations of previous ones when the effects of such disturbances are still present. This is a particularly vexing problem in a small area such as a single stream riffle. Either the previous locations must be carefully avoided, or the assumption must be made that populations have returned to normal. When samples are taken from areas that include rooted plants, and the plants are serving as substrates for the invertebrates or otherwise fulfill a significant ecological function for invertebrates, it appears obvious that the populations will not return to preexisting levels and structure at least until the plants themselves return. But

### METHODS

The basic device used for all of the following experiments consisted of a permanent track anchored flush on the stream bottom and a frame placed on the track for sampling (Figure 1). The track outlined six identical square areas of 0.0625 square meter. It was principally constructed of angle iron with a strip of sheet metal welded on the bottom to project down into the stream gravel. The sampling frame was constructed of iron rods and
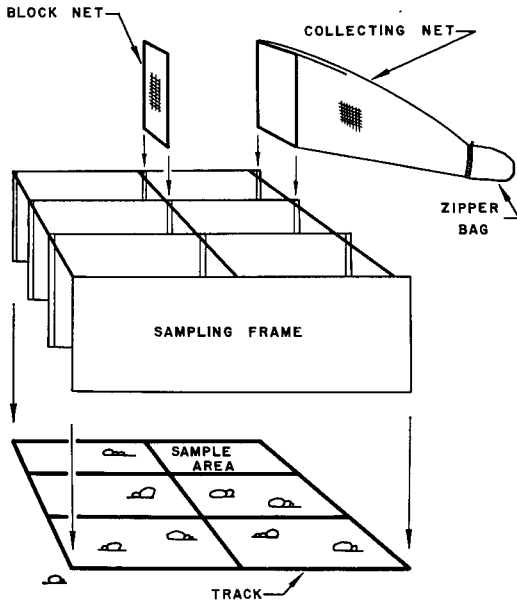
FIGURE 1.—Stream bottom track and sampling device used in recolonization experiments.

sheets of hardboard (masonite). The track was placed in a stream riffle several months prior to any sampling in order to allow ample time for the invertebrate populations to return to normal conditions following the disturbance of installing the track. The sampling operation consisted of fastening the frame to the track with special bolts, and placing the blocking net and collecting net at the upstream and downstream ends, respectively, of a sample area. The nets were constructed of Nitex with a mesh size of 471 microns. The bottom sample was taken by agitating the bottom materials in the usual manner so that the organisms drifted back into the collecting net; the zipper bag could be removed at intervals and replaced with an empty bag so that, by repeated sampling on the same area, checks could be made on the effectiveness of the procedure. Recolonization was measured by taking two successive bottom samples from a sample area separated by an experimental time interval; the first sample denuded the area and the second sample measured the quantity that had returned. "Percent recolonization" was computed for each bottom area as 100 times the ratio of the population density in the latter sample to that in the original

sample. On those occasions when data on drift rate were required, the collecting net was left in place at the downstream end of a selected area for the desired time interval; "drift rate" was computed as the quantity (wet weight) of organisms accumulated in the collecting net per unit time.

The work consisted of three experiments: (1) the long-term relationship between percent recolonization and time, conducted in two different periods of the year between which drift rates were widely different, (2) the relationship between percent recolonization and accumulated drift in short time periods through a single 24-hour period, and (3) the relationship between percent recolonization in one day and the daily drift rate, over a full year. The methods for each of these experiments are included in the following specific sections.

## LONG-TERM RECOLONIZATION

The procedure for this experiment was as follows: Bottom samples were collected from all six sampling areas on one date, then a single area was sampled on each of six later dates. This procedure was followed once during autumn when drift rates were high and once during midwinter when drift rates were low. In autumn the original six bottom areas were sampled on October 10, 1961, and the six later samples were collected over a period of 13 days; in the winter the original six samples were collected on December 27, 1961, and the later six over a period of 30 days. The results suggested that *Baetis* population density returned to 100 percent in about 4 days in autumn, and in 10 days in winter; *Gammarus* population density returned to about 100 percent in 1 day in autumn and in 4 days in winter. However, the degree of variation could not be measured since there was only one bottom area sampled per date, and normal phenological effects were apparent over these lengths of time. For example, the population densities of both *Baetis* and *Gammarus* normally increase during the winter due to growth, but *Baetis* decreases sharply in autumn due to emergence. Therefore, these results are suggestive only.
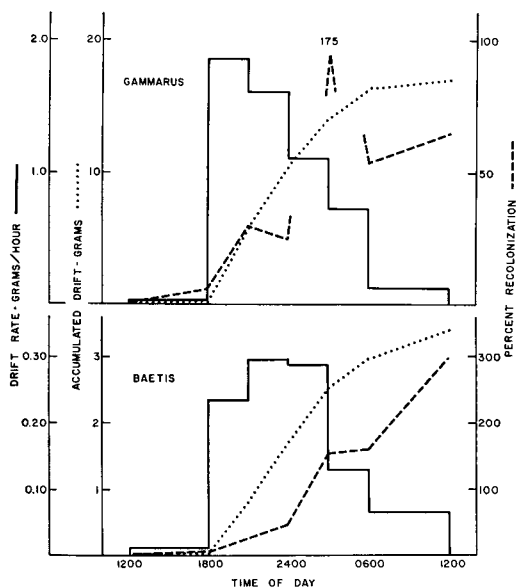
FIGURE 2.—Drift rate, accumulated drift, and rate of recolonization in experimental areas during a 24-hour period.

### RECOLONIZATION-DRIFT WITHIN 24 HOURS

In this experiment, the six bottom areas were sampled at a specific time on a day in summer when drift rates were normally high, then the same areas were sampled successively during the following 24 hours. Six drift samples were obtained with the collecting net set at the downstream end of one of the sample areas (as in Figure 1) during the intervals between bottom samples. The results suggested strongly that the drift of these organisms was the mechanism by which such denuded areas were recolonized, since the increase in percent recolonization was very nearly parallel to the accumulated drift, for both species (Figure 2). The 175 percent recolonization of *Gammarus* at 0300 (Figure 2) appeared to be the result of extreme variation often found among bottom samples. Again, the results suffer from a lack of a measure of variation, but with the exception of this single point (the 0300 sample), variation did not affect the appearance of a strong relationship between accumulated drift and percent recolonization. The diurnal changes in drift rates, represented in Figure 2 by the block histograms, were typical for these two species (Waters, 1962).
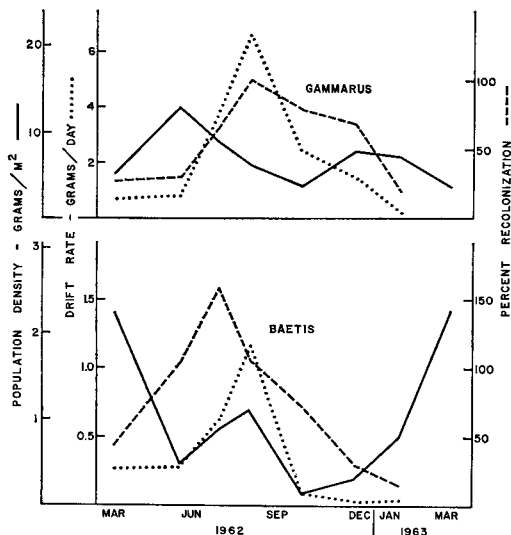


FIGURE 3.—Seasonal changes in population density, drift rate, and rate of recolonization in experimental areas.

The recolonization of *Baetis* far exceeded 100 percent during this 24-hour period, while that of *Gammarus* did not reach 100 percent (with the exception of the anomalous 0300 sample). This result has been often observed (in following and unpublished data) and suggests that since *Gammarus* does not often immediately fill the space in a denuded area, *Baetis* recolonizes well above its original density in space left unoccupied by *Gammarus*. The two species apparently adjust to both their original densities, probably in 1 or 2 more days. This factor might also be important in the case of space left unoccupied by nondrifting organisms removed in bottom sampling, resulting in atypically high rates of recolonization by drifting species. In the present case, however, *Baetis* and *Gammarus* together composed virtually the entire biomass of macroinvertebrates in the riffle.

### DAILY RECOLONIZATION-DRIFT

In this experiment, the six areas were sampled at a given time on the first day, the collecting net was left in place (as in Figure 1) for 24 hours, and then all six areas were sampled at the same time on the second day. This procedure was repeated eight times over a period of approximately 1 year, from March
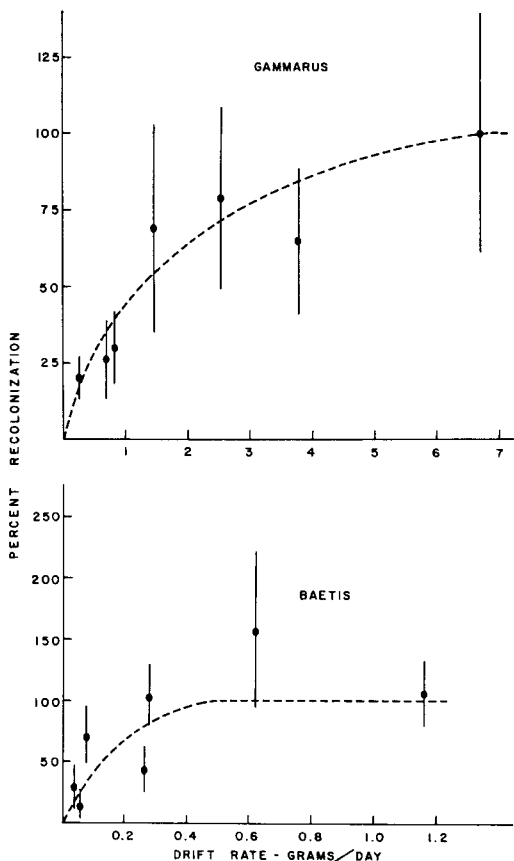
FIGURE 4.—Drift rate and rate of recolonization in experimental areas. Solid points are means, vertical lines represent two standard errors on each side of means. Dashed line is hypothetical relationship.

1962 to March 1963, among which times the drift rates varied widely. Mean percent recolonization was computed as the arithmetic mean of the six percentages, which allowed a measure of variation in percent recolonization. Standard error was computed using the method for obtaining variance of percentages given by Hansen, Hurwitz, and Madow (1953). Since my interest in mean percent recolonization was on the basis of stream bottom area, and since all areas were identical in size, I considered the arithmetic mean more appropriate than a mean weighted according to density of the organisms, which incidentally was not highly variable among the six areas.

The results for both species indicated that the seasonal changes in drift rate and percent recolonization were approximately parallel,

while neither drift rate nor percent recolonization was as closely related to population density as they were to each other (Figure 3). The quantity of organisms drifting over the denuded sampling areas was at all times ample to provide the source of organisms recolonizing the areas. The ratio of daily drift to mean original population density per sampling area ranged from about 1 in midwinter to about 18 in summer. Again, drift was indicated as the mechanism effecting rapid recolonization.

When percent recolonization was plotted against drift rate (Figure 4, where the dashed lines represent the hypothetical relationships), there appeared a direct relationship up to the point where recolonization was 100 percent, and beyond this point recolonization remained at 100 percent no matter how high drift rate became (at least for *Baetis*; higher drift rates were not recorded for *Gammarus*), suggesting that the original population density was equivalent to the carrying capacity.

### DISCUSSION

The downstream drifting of some stream invertebrates is a mechanism fully sufficient to return disturbed populations to normal or capacity levels in a short time. In the present case of dominant organisms exhibiting high drift rates, such as *Baetis* and *Gammarus*, bottom populations were returned to normal conditions in a day or two, at least during summer months when drift rates were high. However, the failure of an abundant organism to recolonize quickly may permit another organism to recolonize to above original levels, at least temporarily, as was the case with *Baetis* when *Gammarus* did not quickly return to normal levels. In July, *Gammarus* drift rate was moderately high (3.8 grams per day) and mean percent recolonization was only 65 percent; at this time *Baetis* recolonization was about 160 percent. In August, with *Gammarus* drift even higher (6.7 grams per day), recolonization was 100 percent, and at this time *Baetis* recolonization was also about 100 percent. Apparently when *Gammarus* failed to fill the capacity of the bottom area, *Baetis* recolonized—when its drift rate was sufficient —to above preexisting levels, occupying the

additional space unfilled by *Gammarus*; but when *Gammarus* recolonization was essentially complete, *Baetis* recolonization held at 100 percent also. These relationships would probably be more obvious in the case of an abundant, nondrifting organism whose previously occupied space might be quickly occupied at high levels of density by drifting organisms.

From Figure 4 it appears that a drift of about 0.4 gram would result in the return of *Baetis* to normal population density; thus at the lowest daily drift rates observed (0.04 gram per day), a 10-day interval would be sufficient, which agrees closely with the results from the long-term study. In the case of *Gammarus*, 100 percent recolonization occurred after a drift of about 7 grams (Figure 4); with the lowest drift rates of about 0.5 gram per day, a 14-day interval would be sufficient for a return to normal densities. Furthermore, it is likely that the sum of successive days with low drift would result in greater recolonization than 1 day with an equivalent high drift, because the lower drift rates are more efficient in effecting recolonization; *i.e.*, lower drift rates result in a higher percent recolonization per unit drift than do higher drift rates. I therefore selected a frequency of bottom sampling of 2 weeks in my other studies, during which time it was reasonably certain that *Baetis* and *Gammarus* populations would return to normal.

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