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Biological interactions as determinants of distributions of benthic invertebrates within the substrate of stony streams

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Abstract

Stainless steel screen cages were buried in the substrate of Otter Creek, Wisconsin, during spring 1976 and 1977 and the East River, Colorado, during summer 1977 and stocked with known densities of benthos. Cages were retrieved after 3 days of colonization and attrition from a given direction and species densities and distributions compared to those initially present. With increasing initial benthic density, the net change in numbers of invertebrates per cage decreased linearly, the net immigration decreased linearly, and the net emigration increased linearly. Benthic invertebrates preferred low density areas of substrate to high density areas of comparable physical-chemical quality. Theoretical equilibrium cage densities indicated that given a consistent habitat, a consistent number and assemblage of benthic invertebrates will colonize. The most abundant species in both streams were categorized according to their observed immigration patterns as density-dependent or density-independent species; overall trends showed that most species were density-dependent.

Studies of benthic distributions within stream substrates have followed two general approaches. One involves sampling the benthos with surface techniques (*see* Cummins 1962) or core sampling devices (Williams and Hynes 1974) and concurrently measuring parameters that are considered important determinants of the distributions. The other is an experimental approach by which stream habitats are manipulated so that the effects of particular factors can be measured individually. The former approach is more conventional and yields results on population fluctuations. The latter is more effective in measuring the relative importance of different factors in determining the distribution of species; it is more difficult, yet more likely to yield conclusive data (Woodin 1974). Recent studies have emphasized the importance of biological interactions as determinants of stream distributions (Fox 1977; Friberg et al. 1977; Hildrew and Townsend 1976) and suggest that experimental procedures such as caging rocks and altering species composition in cages are useful techniques by which to examine the effects of predation and competition on benthic distribution patterns. The cages described here provide such a technique.

My purpose is to show the effect of varying the initial benthic density in experimenial cages on the colonization (immigration) and attrition rates (emigration) in interstitial habitats. Habitat choice probably involves more than preference for physical and chemical conditions such as substrate, current, temperature, and dissolved oxygen. By keeping these factors constant and varying only benthic density, I tested the following hypothesis: Benthic invertebrates are attracted to substrates that are uncolonized or undercolonized and will migrate from those habitats which are at greater than equilibrium density or overcolonized in favor of open habitat of the same or similar physical, chemical quality.

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Study sites

Otter Creek—The primary research was done in Otter Creek, Sauk County, Wisconsin. The creek originates from springs in an unglaciated area of the Baraboo Range at 400 m and enters agricultural land (at 275 m) through which it

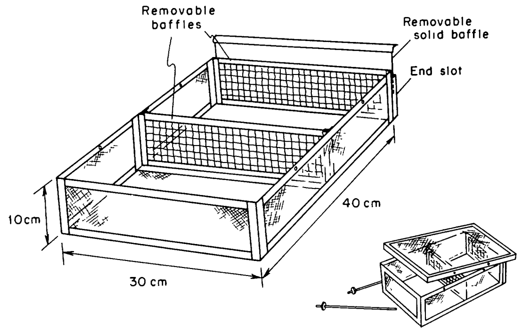

Fig. 1. Two views of cage.

flows until emptying into the Wisconsin River. The experimental section of the stream (at 300 m) has very soft water, low nutrients, and high dissolved oxygen. It descends over quartzite rocks through a thick, mixed coniferous-deciduous forest that contributes a considerable input of allochthonous detritus. The stony substrate is heterogeneous with many rocks protruding through the water surface; flow is turbulent in places. The stream has a maximum depth of 1.5 m in largest pools and a minimum depth of 0.10 m in riffles. It ranges from <1 m wide to 4 or 5 m at the largest pools. It does not freeze during winter but does have intermittent ice cover. I chose Otter Creek because it is reasonably close to the University of Wisconsin, the substrate is suitable for burial of cages, the diverse fauna includes many large species of insect predators, and tourist traffic is relatively scarce.

East River—The East River in Gunnison County, Colorado, has summer benthic populations showing activity levels comparable to those in Otter Creek during very active spring, early summer, and late fall periods. It originates from snowmelt at Emerald Lake (3,400 m) and flows south through the site of Rocky Mountain Biological Lab (RMBL) at Gothic (3,200 m). The East River intersects with the Slate River below Crested Butte (2,800 m) and continues south to Almont after which point it merges with the Taylor River to become the Gunnison River. It is also a soft water, low nutrient, high dissolved oxygen stream. It flows through a gradient of subalpine spruce-fir-aspen forests to montane meadow landscape. Much of the river is bordered by riparian willows and allochthonous input seems significantly less than in Otter Creek.

The experimental section of the stream was chosen to approximate the depth and current conditions in Otter Creek. Cages were buried in areas where the river is divided into smaller channels. The substrate consists of generally more homogeneous rocks than in Otter Creek with some sections having gravel of finer consistency. The East River reaches depths of over a meter in main channels during periods of high flow and drops to 0.10 m during low flow or drought periods. The width ranges from <1 m near the source to 10–15 m. East River also does not freeze completely during winter months, but does have ice and snow cover. It provides an excellent sampling site due to its accessibility to the RMBL facilities, suitable substrate, and diverse fauna.

Methods

Apparatus—The stainless steel cages are designed for burial in the substrate of stony streams (Fig. 1). They have solid frames of 40×30×10 cm with screen of mesh size 0.813 mm on all sides—a compromise between that size large enough to allow free flow of interstitial current and dissolved materials and to prevent immediate clogging with silt or debris and that size small enough to retain reasonably small benthic invertebrates (instars with head capsule widths >1 mm). Removable lids, fastened in place with steel rods, allow the cages to be filled with natural substrate material which remains intact throughout the sampling period. The substrate rocks used approximated in size (4–12.5-cm diam), texture, and distribution those within the area of cage burial. Cages have center and end slots into which baffles of interchangeable mesh sizes (0.813, 2.095, 3.048 mm, and 1 cm) can be inserted depending on the sizes of organisms to be retained or allowed to invade the cages from a given direction.

Cages were buried in the substrate of each stream to a desired depth and covered with natural substrate material. Colonization time was chosen to allow enough time for retrieval of adequate numbers of insects for statistical analysis, for recovery by the area from disturbance of burial, the necessity to complete desired numbers of replicate trials per season, and to prevent equilibrium populations from occurring in the cages. At the end of the colonization period, a solid stainless steel baffle was placed over the screen baffle end of the cages to prevent loss; cages were retrieved and invertebrates hand-sorted and preserved in bottles of 70% ETOH for analysis in the laboratory. Animals were identified to species when possible, or to genus, with the taxonomic keys of Hilsenhoff (1975), Edmondson (1959), and Allan (unpubl.).

Experiments—During spring 1976, 12 cages were buried 10 cm under the surface of the substrate of Otter Creek for 3 days stocked with 0, *X*, 2*X*, and 3*X* initial densities. The *X* value and species assemblages were derived from Surber sampling volumes of substrate equivalent to cage volume on each of four dates (4, 13, 22, and 31 May). The values of *X* for each date were 40, 20, 15, and 15. These *X* values were not intended to be an accurate determination of an equilibrium cage density but merely an estimate which allowed the experimental initial densities to be chosen over a suitable range of crowding conditions. Only those sizes and species of insects which regularly colonize the cages were used; major species are listed below. Treatments were randomized on each date and replicates oriented for both upstream and downstream colonization; cages oriented with the baffle end allowing colonization by upstream movement are referred to as upstream and those allowing colonization by downstream movement as downstream cages. On the last three dates, species stocked in the cages were recorded so that net immigration and emigration could be calculated by comparison of initial to final numbers. Baffles of 1-cm mesh size were used.

During spring 1977, three replicate trials were conducted in Otter Creek on 25 April, 9 May, and 9 June of an experiment of slightly different design. Cages were buried with initial densities of 0, *X*/2, *X*, and 2*X* organisms all oriented for upstream colonization only. The values of *X* for each date were 28, 24, and 20. These modifications were made because the 1976 data indicated that the critical initial densities were those of less than the chosen *X* density and that cages oriented for downstream colonization were being contaminated by organic debris from interstitial currents. Some involuntary or passive colonization was undoubtedly included in the analysis. Since only active colonization is of interest here, all cages were then oriented for upstream colonization. During summer 1977, experiments similar to those of spring 1977 were conducted on 7, 17, and 29 July on the East River. The value of *X* for each date was 30. Cages were buried in pairs about 10 m apart beneath riffles in both streams. The same burial sites were retained throughout the sampling season.

Current velocity was measured at both streams by a Marsh-McBirney current meter (model 201) at the water surface and as close to the surface of the substrate as possible. Measurements were made at each pair of cages. The average surface current velocity in Otter Creek ranged from 30 $\mathrm{cm \cdot s^{-1}}$ during low flow to 87 during a spate in spring 1976. The range of current velocity during 1977 was 19–84 $\mathrm{cm \cdot s^{-1}}$. The East River flow in summer 1977 was 17 to 57 $\mathrm{cm \cdot s^{-1}}$. Water temperatures were recorded by a max-min thermometer after 10 June 1976; before this, readings were taken on arrival at the stream site on each sample date. Maximum and minimum temperatures were 24°–8°C, 19°–7°C, and 19°–6°C in Otter Creek spring 1976, spring 1977, and East River, 1977. The diel fluctuation ranged from 4°–10°C in Otter Creek and 8°–12°C in the East River.

Results and discussion

Net change in numbers per cage—When cages were retrieved, initial den-

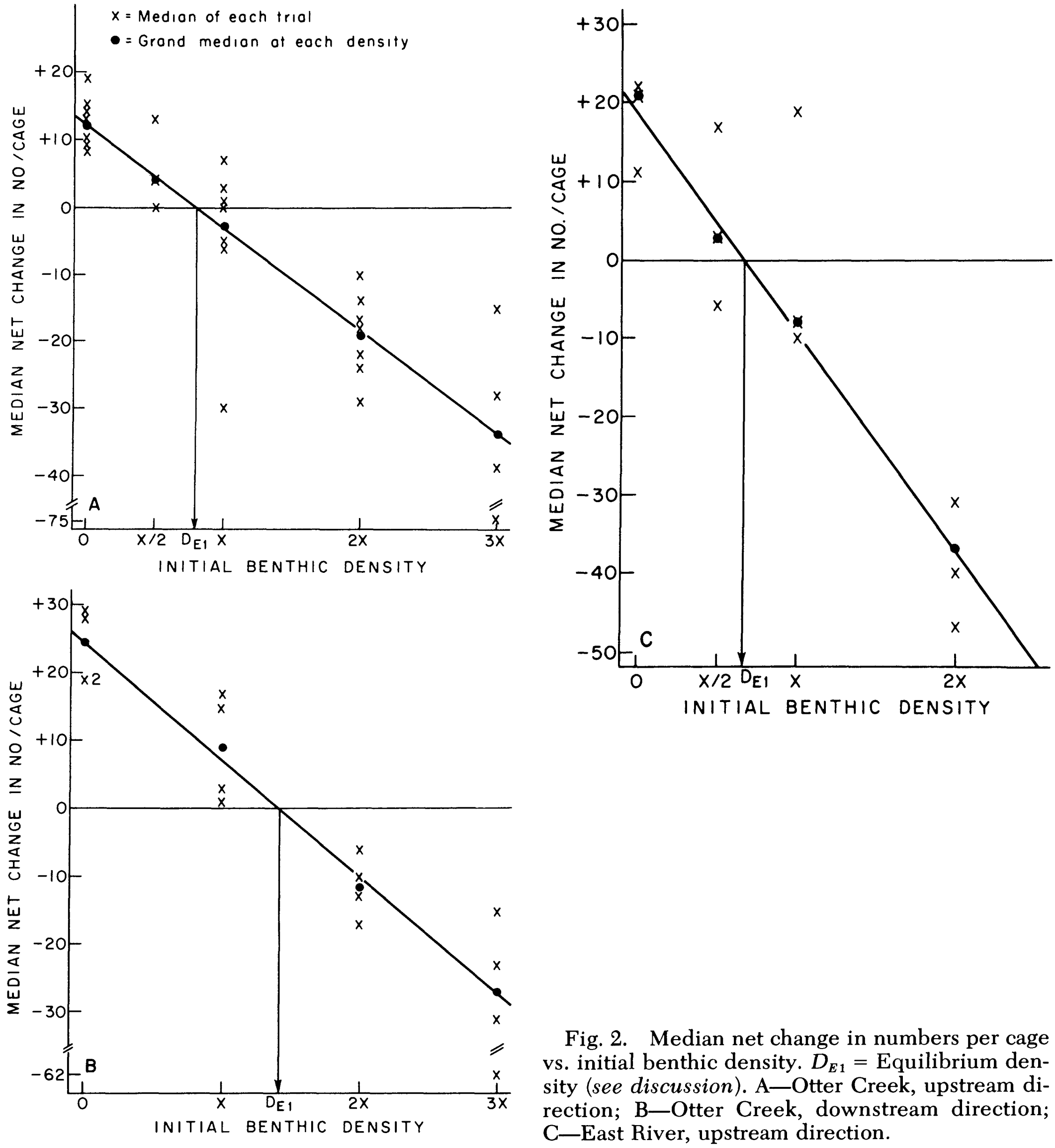

Fig. 2. Median net change in numbers per cage vs. initial benthic density. D_{E1} = Equilibrium density (*see discussion*). A—Otter Creek, upstream direction; B—Otter Creek, downstream direction; C—East River, upstream direction.

sities were subtracted from final densities to compute a net change over the experimental period. There was an inverse linear relationship between the net change in numbers in experimental cages and initial benthic density for trials in Otter Creek in both upstream and downstream directions (Fig. 2A, B) and also in the East River (Fig. 2C). Spearman rank correlation coefficients were calculated for net change vs. initial benthic density on all sampling dates. $r_s = -1.000$ (highly significant) on all dates except 22 May 1976 and 17 July 1977 where $r_s = -0.800$ (n.s.), $N = 4$. The rate lines, fitted by inspection through the medians of all the cages at each density, crossed the point of zero change about halfway between $X/2$ and X initial densities for upstream cages and between X and $2X$ initial densities for downstream cages. These points of intersection were interpreted as an equilibrium cage density (D_{E1}) where the number of organisms in the cages theoretically would not change.

The numerical value for D_{E1} ranged from 12 to 22 for upstream cages in Otter Creek, from 30 to 49 for downstream cages in Otter Creek, and from 17 to 22 for upstream cages in the East River. The reason for the difference in equilibrium densities of upstream and downstream cages is that the cages oriented for downstream directional colonization received organisms passively as well as actively. The accumulation of organic debris even at a depth of 10–20 cm in the substrate indicated that the colonization of these cages was being contaminated by drift. Therefore, the D_{E1} of the downstream cages was not an equilibrium determination and would probably increase with longer sampling. The upstream cages, however, showed remarkably consistent D_{E1} values on each date. During spring 1977, these values were 21, 21, and 22 for the three sampling periods. During summer 1977, values for D_{E1} were 22, 21, and 17 for the three East River sampling periods.

The magnitude of net change per cage was greater for downstream than for upstream cages in Otter Creek and comparable for all upstream experiments in the East River and Otter Creek. The difference between upstream and downstream cages in Otter Creek was, again, due to contamination by downstream drift. The East River cages showed a faster rate of change than either the upstream or downstream cages in Otter Creek. The slope of the net change line for the East River cages (Fig. 2C) was 1.7 times that of the Otter Creek net change lines (Fig. 2A, B). The reason for this difference is that the East River species displayed higher rates of activity. In preliminary colonization experiments on the East River during summer 1974, benthic populations recolonized clear areas of substrate in 3 to 4 days (Peckarsky unpubl.)

On successive sampling dates in both Otter Creek and the East River, the rate of change declined slightly indicating a reduction in activity from April through June in Otter Creek and through July in the East River. This phenomenon was more pronounced in the downstream cages because the decrease in current velocity throughout spring caused a decline in downstream drift.

Immigration and emigration—On each sampling date the number of animals of each species recovered after the sampling period was compared to that initially present. Increases in numbers were recorded as net immigration; decreases were considered net emigration. A composite of these values for all species was computed at each date for each initial benthic density. The inability to detect replacement of individual animals caused these net values to be underestimates of the true immigration and emigration rates. Net emigration increased linearly and net immigration decreased linearly with increasing initial density in Otter Creek upstream and downstream trials (Fig. 3A, B) and in the East River trials (Fig. 3C). The immigration and emigration lines, fitted by inspection through the medians at each density, intersected at points about halfway between $X/2$ and X initial densities for the upstream cages in Otter Creek and the East River, and at a point between X and $2X$ initial densities for downstream cages in Otter Creek. These points of intersection, where net immigration is equal to net emigration, can also be interpreted as theoretical equilibrium cage densities (D_{E2}). The values of D_{E1} and D_{E2} were highly comparable on all sampling dates. For example, during spring 1977 on 25 April, $D_{E1} = 21$, $D_{E2} = 20$; on 9 May, $D_{E1} = 21$, $D_{E2} = 19$; and on 9 June, $D_{E1} = 22 = D_{E2}$. During summer 1977 on 5 July, $D_{E1} = 22$, $D_{E2} = 25$; on 17 July, $D_{E1} = 22$, $D_{E2} = 21$; and on 29 July, $D_{E1} = 17 = D_{E2}$. This consistency confirms the accuracy of the methods in determining hypothetical equilibrium cage densities.

The D_{E2} for downstream cages was again higher due to drift effects. Trends were similar in the rates of immigration and emigration among the three plots. Immigration was significantly higher in downstream cages (Wilcoxon sign-rank

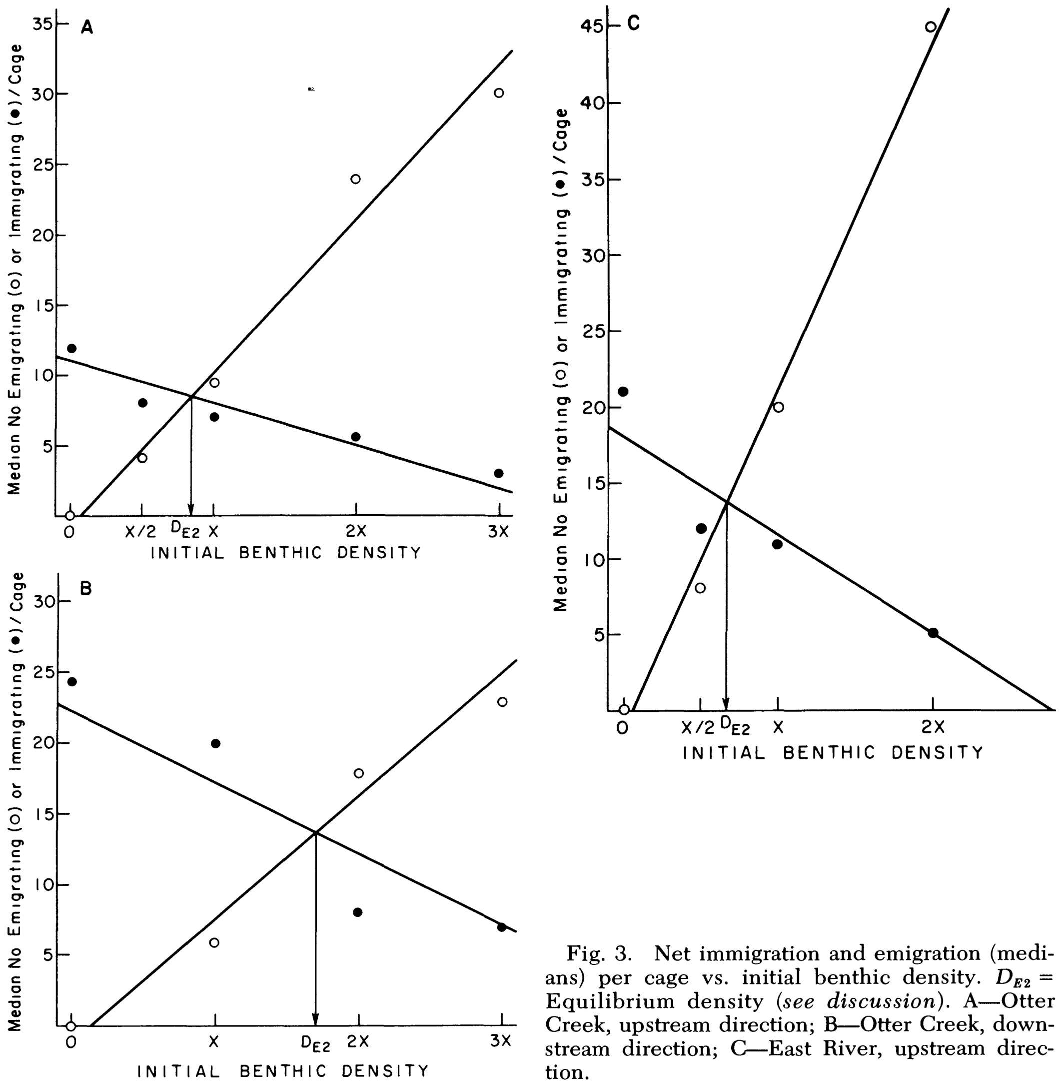

Fig. 3. Net immigration and emigration (medians) per cage vs. initial benthic density. D_{E2} = Equilibrium density (*see discussion*). A—Otter Creek, upstream direction; B—Otter Creek, downstream direction; C—East River, upstream direction.

test, $P < 0.005$), and immigration from upstream cages was slightly higher for spring 1976. Again, interstitial current caused higher final densities in the downstream cages in Otter Creek. The East River data showed a higher rate of immigration and emigration than upstream cages in Otter Creek, probably because of the high rate of activity of the East River benthos.

Net emigration rates decreased throughout spring and early summer in Otter Creek in both upstream and downstream directions; this was more pronounced for downstream cages due to the simultaneous decrease in current velocity. There was very little change of this sort in the East River. Net immigration rates showed less consistent fluctuations in Otter Creek for reasons discussed below. However, in spring 1976 there was a slight decrease in immigration rates from May to June. The East River showed a similar slight decrease during July 1977. These trends indicated that insect activity levels dropped through spring and into summer in Otter Creek and through summer in the East River,

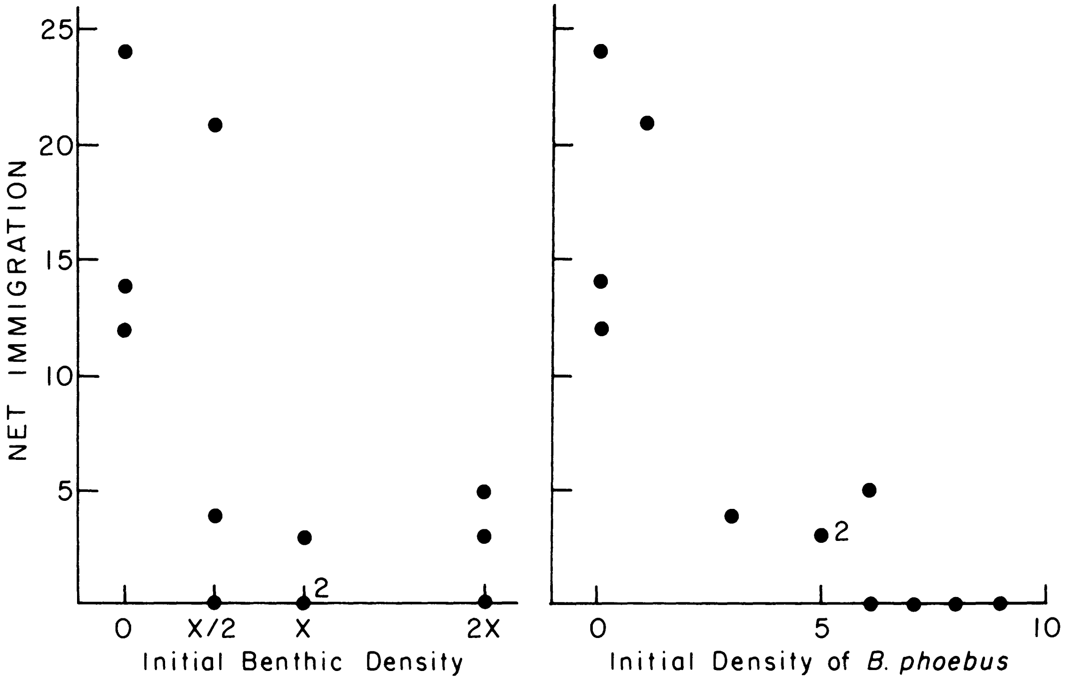

Fig. 4. Colonization of *Baetis pheobus*, Otter Creek, 13 May 1977.

probably reflecting temperature changes that caused emergence of many species, which removes the larger instars from the stream (Nebeker 1971). It is highly unlikely that a decrease in current velocity is the cause of decreased activity; one would expect the opposite effect (Bishop and Hynes 1969; Elliott 1971).

Individual species analysis—The emigration points (Fig. 3) fitted a linear relationship fairly well, but the immigration points showed a notable degree of deviation. Spearman rank correlation coefficients for all dates except 22 May 1976 showed highly significant $r_s = 1.000$ for emigration vs. initial benthic density; no dates showed significant r_s for immigration rates vs. initial benthic density. The reason for this is that all species of benthic invertebrates do not behave in the same fashion relative to density. The composite analysis assumed that all species showed density-dependent colonization patterns. However, individual species analysis suggested that certain species behaved in density-dependent and others in density-independent fashion.

Several experiments on the effects of initial population density upon dispersal rates are summarized by Bovbjerg (1964). Aggressive stream species such as the crayfish *Cambarus alleni* disperse at greater rates in response to higher population densities. Other species, for example the amphipod *Hyalella azteca*, have a tendency to aggregate. A third group of species, such as the amphipod *Gammarus pseudolimnaeus*, disperse at constant rates independent of initial density. The categories outlined below were assigned to 22 taxa in Otter Creek and 18 taxa in the East River.

Density-dependent dispersers decreased their immigration rates with increasing initial total benthic density and with increasing initial density of their own species. An example, *Baetis phoebus* (Ephemeroptera), Otter Creek, is shown graphically in Fig. 4. Spearman rank correlation coefficients for immigration vs. initial total benthic density and

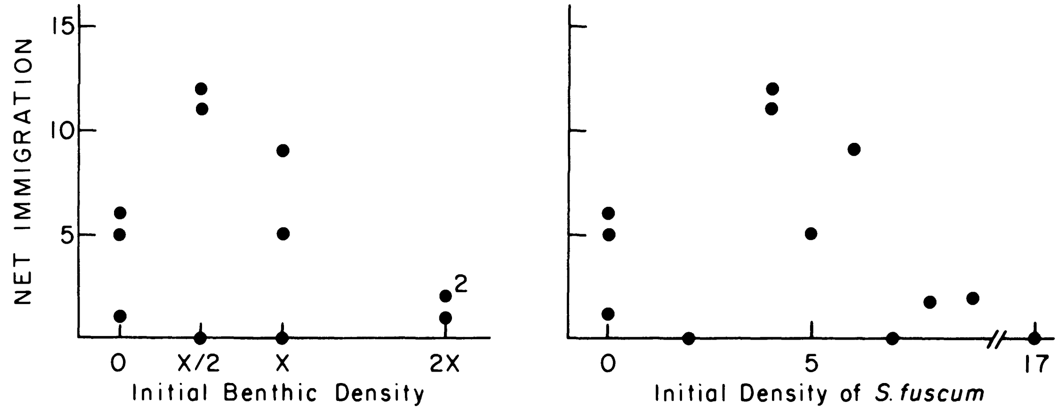

Fig. 5. Colonization of *Stenonema fuscum*, Otter Creek, 12 June 1977.

immigration vs. initial density of *B. phoebus* were −0.61 and −0.89 (significant, $N = 12$). The disperser species comprised the majority of those retrieved in cages from both East River and Otter Creek and probably accounted for the general trend observed. Some other density-dependent dispersers were *Ephemerella subvaria, Paraleptophlebia* (Ephemeroptera), *Amphinemoura delosa* (Plecoptera), *Micrasema rusticum* (Trichoptera), and *Optioservus fastiditus* (Coleoptera) in Otter Creek and *Baetis bicaudatus, Ephemerella doddsi, Ephemerella inermis, Rhithrogena hageni, Epeorus longimanus* (Ephemeroptera), *Zapada haysi, Pteronarcella badia* (Plecoptera), and *Rhyacophila* spp. (Trichoptera) in the East River. Density-dependent aggregators increased their immigration rates with increasing initial density of their own species. Examples of these were Chironomidae and *Simulium tuberosum* (Diptera) in Otter Creek and Chironomidae and Simuliidae in the East River.

The density-independent taxa fell into two groups. Those species in the first category did not show any recognizable pattern of colonization rates with changes in initial benthic density or initial species density. Figure 5 illustrates an example of this type of species (*Stenonema fuscum*, Ephemeroptera, Otter Creek). This species began to show some density dependence at the highest densities (2*X*). The r_s values for *S. fuscum* were −0.20 and −0.05 (not significant, $N = 12$). Other groups showing this behavior were *Hydropsyche, Lepidostoma* and *Pycnopsyche* (Trichoptera) in Otter Creek and *Cinygmula* and *Ameletus velox* (Ephemeroptera) in the East River. A second category of density-independent species also showed no recognizable trend in colonization rates with changes in initial density. However, final densities of these species covered a highly consistent range of values regardless of the initial benthic density. This pattern is illustrated for *Alloperla* (Plecoptera, East River) in Fig. 6. The r_s values for this species were also not significant (−0.17 and −0.24, respectively; $N = 12$). Other species with this type of behavior were *Isoperla cotta, Acroneuria lycorius, Paragnetina media* (Plecoptera), *Atherix variegata* (Diptera), *Nigronia serricornis* (Megaloptera), and the fan-tailed darter (*Etheostoma flabellare*) and the black-nose dace (*Rhinichthyes atratulus*) in Otter Creek and *Megarcys signata* and *Kogotus modestus* (Plecoptera) in the East River. These results may indicate a space dependency in active prey search by these predators. The only dates on which this pattern was broken were just before emergence, when the predators probably ceased feeding and sought emergence sites (Davis and Warren 1965). Preliminary predation experiments in Otter Creek showed that *A. lycorius* (Plecop-

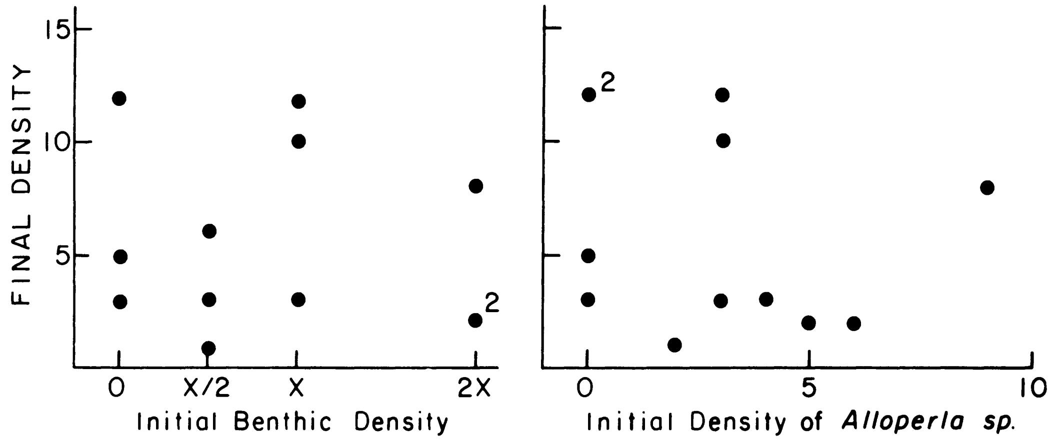

Fig. 6. Colonization of *Alloperla* sp., East River, 20 July 1977.

tera) did cease feeding before emergence.

This evidence was consistent with findings of another cage experiment in which known numbers of prey items were stocked in experimental cages and predators were allowed to colonize. Results showed no systematically higher colonization rates for invertebrate predators in cages initially inhabited by prey items than in those without prey. Thus, the invertebrate predators analyzed in these two streams appeared to search randomly for prey in a space-dependent fashion rather than via a density-dependent mechanism. Detection of prey, then, is probably a close-range tactile phenomenon.

Conclusion

My data appear to be in conflict with the evidence for patchy distributions characteristic of benthos in streams. However patchiness is essentially a function of the heterogeneity of the substrate in streams, since different substrates will attract different numbers and assemblages of species. These data do not refute those showing mosaic distributions in the substrate. They demonstrate that in similar patches of identical size, predictable equilibrium populations will occur.

This experimentally demonstrated equilibrium allows one to determine whether a particular habitat is undercolonized, and thus, whether immigration is likely to occur. The equilibria are not true equilibria because they do not include all species of invertebrates nor do they consider small instars. However, given the quality of habitat offered by the cages in a 3-day period, the equilibria do indicate a balanced condition for the sizes and species assemblages which prefer that habitat. Given longer colonization times and habitat changes such as siltation, the suitability of the cages for these species of invertebrates would change, and different numbers, sizes, and assemblages of species would characterize different equilibria.

The nature of the substrate habitat is initially responsible for attracting particular sizes and assemblages of species. These organisms then respond to each other's presence, in a density-dependent fashion for the most part, achieving a consistent optimum density within the particular habitat. These densities reflect an ability of benthic invertebrates to detect each others' presence and to colonize available habitats.

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