COMMENT

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Comment on "Biological interactions as determinants of distributions of benthic invertebrates within the substrate of stony streams" (Peckarsky)

Peckarsky (1979) presents in situ studies of the movements of benthic stream invertebrates into and out of experimental cages. The conclusions drawn from these studies fall into two categories: species or species aggregates were characterized as having density-dependent or density-independent movements; and equilibrium benthic densities in cages were calculated and compared to natural densities.

It is not clear that Peckarsky's tests for density dependence are valid. The linear trend of emigration vs. density in her fig. 3 indicates that a constant proportion of animals leaves the cages *regardless of density*: density-independent emigration by the criteria of Reisen and Prins (1972), Hildebrand (1974), Corkum (1978), and Walton et al. (1977). This observation contradicts Peckarsky's conclusion (p. 59) that "Benthic invertebrates preferred low density areas of substrate to high density areas of comparable physical-chemical quality."

In the individual species analysis it is not clear that decreasing trends of "net immigration" vs. initial density provide evidence for density-dependent immigration. Peckarsky's net immigration, undefined in the individual species analysis, appears to be positive net change in numbers. Trends of decreasing net change in numbers vs. initial density (e.g. Peckarsky's figs. 2 and 4) can be generated from density-independent immigration and emigration processes. Thus, the analysis presented for species net immigration trends does not elucidate the role of biological interactions in determining the distributions of benthic invertebrates.

The second category of conclusions drawn by Peckarsky are derived from two graphical methods of calculating equilibrium benthic density. The first uses plots of net change in number per cage vs. initial benthic density (Peckarsky's fig. 2). The second involves plots of net immigration and net emigration vs. initial benthic density (Peckarsky's fig. 3). However, for each method one of two assumptions is implicitly made: either that all species act identically in their tendencies to immigrate and emigrate, or that the initial relative abundances of the various species are the same at each initial benthic density. For example, the implicit assumption of her second method of calculating equilibria is that all species act identically. This is a result of the definitions used; net immigration is defined to be a composite value for the net change in number determined from the species that showed increases in numbers, and net emigration is defined to be a composite value for net change in numbers of the species that showed decreases in numbers. For a single cage, net immigration and net emigration rates apply to different sets of species. Therefore, net immigration and net emigration rates cannot be compared between experimental cages unless the assumption is made that all species act identically in their tendencies to migrate. Peckarsky's conclusion that some species act differently from others suggests that this assumption is not warranted. If both immigration and emigration rates are estimated for each species in a cage—a difficult proposition—then composite rates for cages could be standardized for a particular set of species and could be validly compared.

Although Peckarsky has contributed an

important in situ technique, a conclusive analysis of in situ data to determine the density dependence of emigration and immigration of benthic stream invertebrates remains to be made. Assumptions implicit in her estimation of benthic equilibrium densities temper the conclusion that consistent equilibrium densities were demonstrated.

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References

CORKUM, L. D. 1978. The influence of density and behavioural type on the active entry of two mayfly species (Ephemeroptera) into the water column. Can. J. Zool. **56:** 1201–1206.

HILDEBRAND, S. C. 1974. The relation of drift to benthos density and food level in an artificial stream. Limnol. Oceanogr. **19:** 951–957.

PECKARSKY, B. L. 1979. Biological interactions as determinants of distributions of benthic invertebrates within the substrate of stony streams. Limnol. Oceanogr. **24:** 59–68.

REISEN, W. K., AND R. PRINS. 1972. Some ecological relationships of the invertebrate drift in Praters Creek, Pickens County, South Carolina. Ecology **53:** 876–884.

WALTON, O. E., JR., S. R. REICE, AND R. W. ANDREWS. 1977. The effects of density, sediment particle size and velocity on drift of *Acroneuria abnormis* (Plecoptera). Oikos **28:** 291–298.

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Reply to comment by Sell

Do benthic stream invertebrates randomly wander the substrate or is migration dependent on benthic density? Sell (1981) believes that the analysis presented by Peckarsky (1979) was not adequate to show the existence of biological interactions as a determinant of benthic distributions. Sell's most important objection is derived from my interpretation of a linear relationship between initial density and movement of benthic invertebrates in and out of colonization cages. He is correct in stating that such a relationship can be generated from a density-independent model. However, I will show that a linear relationship between these two variables is not exclusive to a density-independent model, and that the data can be further analyzed to demonstrate conclusively that migration of benthic invertebrates in two stream substrates is density-dependent.

The problem with my 1979 paper is that I did not analyze the data adequately to determine the best mathematical relationship between initial densities and net immigration and emigration. The points shown in figs. 2 and 3 are medians, the x-axis is a relative rather than an absolute scale, lines were fitted by inspection, and no equations were determined. I here present a more thorough and more accurate representation of the data. Proper conclusions can then be drawn.

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For immigration and emigration to be density-independent, a constant proportion of animals must enter or leave cages, regardless of initial benthic density. In such a case, the relationship between initial benthic density and migration must be linear and the y-intercept must be zero. As an illustration, a general linear equation for emigration is

$$E = aD + b \tag{1}$$

where E is emigration, and D is density. The proportion emigrating is

$$\frac{E}{D} = \frac{aD + b}{D} = a + \frac{b}{D}, \tag{2}$$

which is not constant, but depends on