

Colonization curves: application to stream insects on semi-natural substrates

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Sheldon, A. L. 1977. Colonization curves: application to stream insects on semi-natural substrates. - *Oikos* 28: 256-261.

Aquatic insects were allowed to colonize gravel filled trays placed in a small stream. The rate of accumulation of individuals on the trays can be described by a power function

$$N_t = at^b$$

or an equilibrium model of form

$$N_t = \frac{k}{m} (1 - e^{-mt}).$$

Both models fit the data but the empirical power function is more convenient. Colonization rates vary between taxa and depend significantly on location in the study section. The parameters of fitted curves permit objective comparisons of colonization by different species and in different environments. The significant location effect suggests that the fauna of each portion of the stream bottom is influenced substantially by that of adjacent units.

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Водным насекомым была предоставлена возможность заселения лотков, заполненных гравием и помещенных в небольшую речку. Скорость поселения животных на лотках может быть выражена степенной зависимостью:

$$N_t = at^b$$

или уравнением:

$$N_t = \frac{k}{m} (1 - e^{-mt})$$

Обе модели соответствуют полученным данным, но эмпирическое выражение степенной зависимости более удобно. Скорость колонизации неодинакова у представителей разных таксономических групп и в значительной степени зависит от их локализации в исследуемом участке. Параметры соответствующих кривых позволяют провести объективные сравнения колонизации различных видов в разных условиях. Сильный локальный эффект свидетельствует о том, что фауна каждого участка речного дна находится под сильным влиянием соседних участков.

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1. Introduction

Artificial and semi-natural substrates have long been used for sampling aquatic invertebrates (Moon 1940, Wene and Wickliff 1940, Hynes 1970). Recently such devices have been used in programs for assessment of water quality (Anderson and Mason 1968, Arthur and Horning 1969). With such applications in mind some authors (Dickson et al. 1971, Fullner 1974) have investigated the repeatability and representativeness attainable with such samplers. Others (Waters 1964, Ulfstrand 1968, Nilsen and Larimore 1973) have been more concerned with the dynamics of the colonization process. Some workers (Ulfstrand 1968, Nilsen and Larimore 1973) have described colonization by individuals of particular taxa while others (Patrick 1967, Cairns et al. 1969, Dickson and Cairns 1972, Schoener 1974 a, b) have measured rates of accumulation of species. Ulfstrand et al. (1974) have considered both aspects. Since species arrive as individuals, and equilibrium reflects the dynamics of colonization, the various approaches should be complementary.

In stream monitoring programs and population studies, samplers are often allowed a month or more to attain equilibrium. However Ulfstrand (1968) and Waters (1964) have suggested that population densities on such samplers stabilize much more rapidly. Since the risk of loss of samplers to spates or vandals increases with exposure time, there is a practical advantage in reducing the time the samplers are in the stream. In addition, the nature of the equilibrium results from a complex interaction of the sampler, the stream environment and the colonizing fauna. Detritus and algae accumulate on samplers (Ulfstrand et al. 1974), stream discharge varies and animal numbers decrease or increase with natural mortality or recruitment. I investigated the possibility that both loss and successional change could be minimized if the rate of colonization, as opposed to equilibrium densities, could be estimated from observations made during the first few days of colonization. Estimation of rates has required the fitting of quantitative expressions to colonization data. This paper describes colonization over short periods and statistical techniques for fitting colonization curves.

2. Methods

2.1. Field methods

Colonization rates were measured in Elk Creek (46° 52' N, 113° 22' W) a tributary of the Blackfoot River in western Montana, USA. At 1230 m elevation, Elk Creek is 3–5 m wide. The 100 m study section began at the downstream end of a long riffle. Proceeding downstream, a 40 m shallow (depth 30 cm) pool was followed by approximately 20 m of riffle, a second pool (35 m) and the head of another riffle.

The samplers were trays (inside dimensions 37 × 25 × 5 cm) with wooden sides and bottoms of plastic win-

dow screen (10 meshes cm⁻¹). Substrate for filling the trays was obtained from spoilings piles deposited when the stream was dredged for gold about 40 years ago. In size and shape this material was typical of that in the stream but, of course, lacked insects and an algal film. The material was sieved and half of the trays were filled with fine (1–2 cm) gravel and the remainder with coarse (2–5 cm) substrate. Trays were placed in mid-stream at 1 m intervals and rested flat on the bottom. Trays were recovered by sliding a metal pan beneath them. The trays and substrate were picked and washed in the field and the wash water filtered through a monofilament mesh net (pore size 423 μm). Insects were preserved for laboratory sorting and counting.

One hundred trays were placed in the stream on 30 August, 1971. The location of coarse and fine substrates was randomized. The experimental design called for the removal of four randomly allocated trays of each substrate type on each sampling date. Samples were taken on days 1, 2, 3, 4, 7, 9 and 14 of the colonization period. Seven samples only were taken on days 4, 7 and 9 so the total sample was 53 trays.

2.2. Colonization curves

I considered two mathematical models or descriptors of the colonization process. The first of these, termed the equilibrium model, follows from assumptions that a constant number (*k*) of individuals arrive per unit time while a constant proportion (*m*) of those present leave the tray. In differential form

$$\frac{dN}{dt} = k - mN. \quad (1)$$

Integration yields

$$N_t = \frac{k}{m} (1 - e^{-mt}) \quad (2)$$

where N_t is the number present at time *t*, *k*/*m* the asymptotic number of individuals present after infinite time and *e* the base of the natural logarithms. Ulfstrand (1968) apparently used Eq. (1) to generate a family of curves for comparison with observed data but did not specify the model in any detail. Eq. (2) was derived also by MacArthur and Wilson (1967) as an expression of their equilibrium theory of species diversity on islands. Thus the mathematical descriptions of colonization by individuals and species are identical and assume an equilibrium density (or diversity) and a balance between immigration and emigration (extinction). Equations of this form are quite general and have been used to describe many natural processes. Eq. (2) is used to describe growth of fish and Allen (1966) has developed statistical techniques for parameter estimation and curve fitting.

An alternative method is entirely empirical and the required computations are much simpler. I fitted power functions (Bliss 1970)

$$N_t = at^b \quad (3)$$

where N_t and t retain their previous meanings and a and b are constants. The power function can be converted to linear form

$$\log N_t = \log a + b \log t \quad (4)$$

and fitted by the usual method of least squares.

The relative merits of the two models and special problems of parameter estimation are discussed later.

3. Results

Colonization curves were fitted to data for 8 taxa: mayflies *Baetis* spp. (mostly *B. bicaudatus* Dodds), *Ameletus* sp. (? *cooki* McDunnough), *Ephemerella grandis* Eaton and Heptageniidae (mostly *Cynogmula* sp.); stoneflies Nemouridae (mostly *Zapada cinctipes* (Banks)); and caddis larvae *Sortosa* sp., *Rhyacophila acropedes* Banks and *Parapsyche elsis* Milne. *Parapsyche* was further separated into first and second year larvae (I, II).

Preliminary graphing of numbers against time showed the error variances to be strongly dependent on the means so all counts were transformed to $\log(x)$ or $\log(x + 1)$ which stabilized the variances (Elliott 1971a) and permitted significance tests of the regression statistics. This transformation, required on statistical grounds, suggested the application of Eq. (4). The *Baetis* data (Fig. 1) were fitted by linear regression and the residuals (Draper and Smith 1966) were examined for curvilinearity or correlation with other variables. Colonization by *Baetis* was strongly dependent on

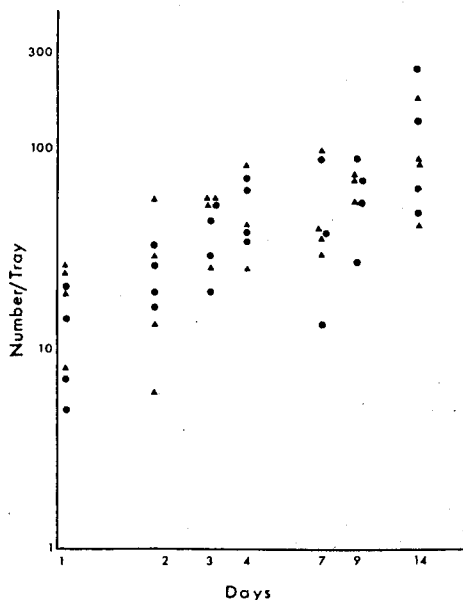


Fig. 1. Abundance of *Baetis* nymphs on samplers. Coarse (▲) and fine (●) substrates indicated.

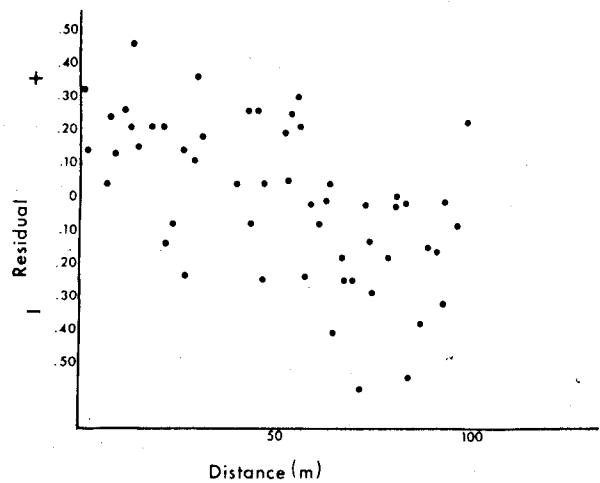


Fig. 2. Residual errors (logarithmic) about the regression relationship of Fig. 1. Distance given from the upstream end of the study section.

location (Fig. 2). Trays at the upstream end of the section were colonized most rapidly.

The multiple regression model which was finally selected included tests of the original experimental variables (time, substrate type) and variables intended to control the position effect described above. The applicability of the power function (4) was tested by regressing the transformed counts against $\log t$ and against $(\log t)^2$ as a test of curvilinearity. The importance of the substrate types was tested by the regression equivalent of analysis of variance (Draper and Smith 1966). Trays with fine substrate were coded 0 and coarse substrates as 1. The position effect was controlled by entering the variables d , d^2 , d^3 where d was the distance from the upper end of the section. The higher order terms were intended to describe the alternating pools and riffles of the section. The model with six independent variables was fitted by a backward stepwise procedure. Variables were deleted until all remaining terms were significantly ($P < 0.05$) related to insect numbers.

Results of the regression analysis are summarized in Tab. 1. Rare taxa (*Parapsyche* II, *Sortosa*, *Rhyacophi-*

Tab. 1. Summary of regression analysis of insect density on time (expressions in t), position (terms in d) and substrate type. Coefficients of time variables in (). Significance levels indicated in the usual manner. Multiple correlation coefficient (R) shown for each regression.

| | $\log t$ | $(\log t)^2$ | d | d^2 | d^3 | sub- strate | R |
|---------------------|-----------|--------------|-----|-------|-------|----------------|------|
| <i>Baetis</i> | ***(0.67) | | | ** | * | n.s. | 0.82 |
| Nemouridae | ***(0.48) | | | | ** | n.s. | 0.59 |
| <i>Parapsyche</i> I | | ** (0.36) | | | | n.s. | 0.43 |
| <i>Ameletus</i> | | | | ** | | n.s. | 0.38 |
| <i>Ephemerella</i> | *(0.22) | | | | | n.s. | 0.29 |
| Heptageniidae | ***(0.49) | | | | | n.s. | 0.46 |

la) are omitted since no component of the model was significant. Of the remainder, all but *Ameletus* showed a time effect. *Ameletus* density on the trays was weakly related to position and nothing else. *Baetis* and Nemouridae showed position effects although the major component of variation was the temporal pattern. Except for *Parapsyche* I where the rate of colonization increased with time, colonization was adequately described by power functions with slopes less than unity. The substrate variable had no detectable effect on *Baetis* (Fig. 1) nor any other species. Graphical comparison of the logarithmic form of the regressions (Fig. 3) indicates differences in abundance, colonization rate and position effects. The arithmetic form (Fig. 4) provides a different perspective on location effects and absolute abundance.

The power function is easily fitted and describes the data. However the equilibrium model (2) includes a biological mechanism which the empirical power function lacks. Allen's (1966) method for fitting Eq. (2) is not applicable since the insect abundances must be transformed to stabilize the variances. However this transformation implies that Eq. (2) should be written as

$$\log N_t = \log (k/m) + \log (1 - e^{-mt}). \quad (5)$$

This expression is not a linear function of time and can

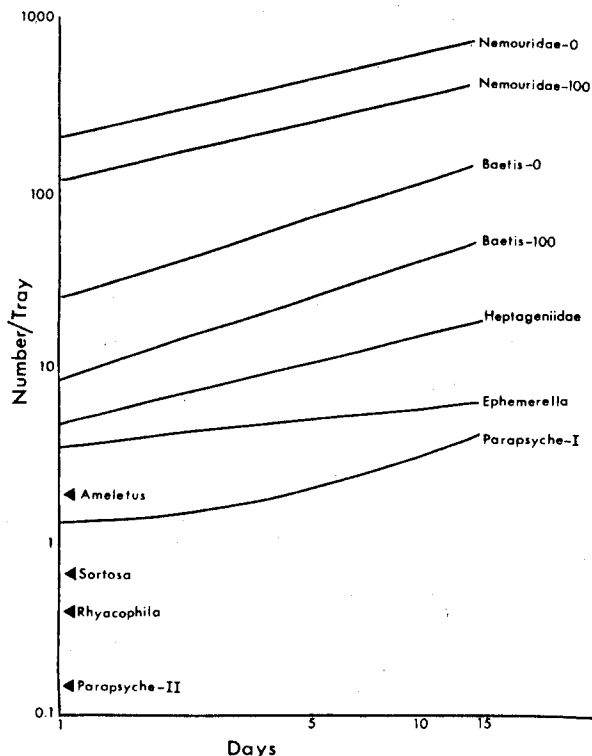


Fig. 3. Fitted colonization curves. Separate curves (Nemouridae, *Baetis*) shown for upstream (0) and downstream (100) ends of the study section.

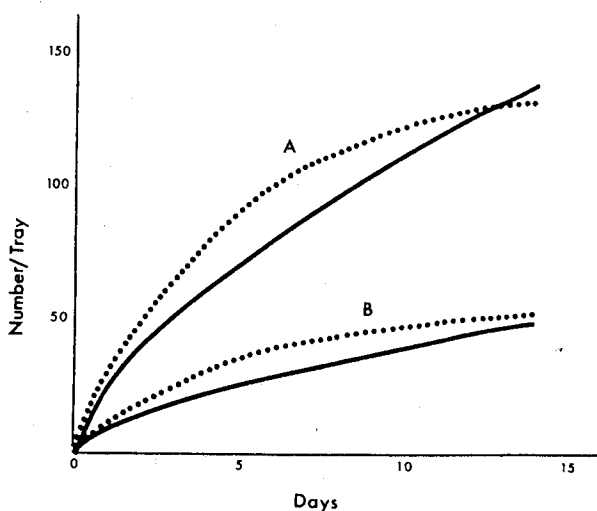


Fig. 4. Arithmetic form of fitted colonization curves for *Baetis*. Power function (—) and the equilibrium model (.....) are contrasted and differing rates of colonization for upstream (A) and downstream (B) ends of the study section are shown.

not be fitted directly. An iterative method was used. Trial values of m were guessed and a least squares regression of $\log N$ on $\log (1 - e^{-mt})$ computed. The best estimate of m should yield a slope of minus one on the independent variable. For the *Baetis* data, trial values of 0.12, 0.18 and 0.24 yielded slopes of -0.849 , -0.965 and -1.086 . Interpolating, an m of 0.20 gave a slope of -1.005 and coefficient of determination r^2 of 0.495. Allen's (1966) method applied to the geometric means for the seven sampling dates gave an m of 0.187. The slope criterion used here seems to provide a reasonable fit to the transformed data.

The equilibrium model was incorporated in a multiple regression with $(1 - e^{-0.2t})$ and d, d^2, d^3 as the independent variables. The coefficient of the bracketed term shifted to -0.96 in the multiple regression. Further iterations would be required to improve the estimate of m in the multiple regression. I considered this to be unprofitable, however, since the coefficient of determination for the equilibrium model (0.495) was virtually identical with that of the power function (0.501) with position effects ignored. Examination of the residual errors indicated no real difference between the models. The expected equilibrium curves are shown in Fig. 4 for comparison with the power function. Although the two models have rather different implications, especially if extrapolated, there is no statistical reason to choose one over the other. Equilibrium models were not fitted for the remaining taxa since none (Tab. 1) showed curvilinear departures from the power function except for *Parapsyche* I where the curvature was in the wrong direction.

4. Discussion

Colonization is indeed a rapid and reasonably predictable process. However the high variability which plagues all quantitative studies in stream ecology is present in my data as well. While standardized substrates may provide more precise estimates than samples from heterogeneous natural substrates, confidence limits may remain unacceptably wide. Since many samples will be required anyway, it seems reasonable to take them throughout the colonization period. This procedure yields information on the colonization process and mean density as well. Draper and Smith (1966), Cochran (1963) and most statistics texts describe the procedure for computing error limits about estimates of the dependent variable in regression. Such regression estimates will be as precise as those derived from a single sets of samples with the same number of observations.

The choice of model to describe the colonization process remains open. At this time I favor the empirical power function. It is easily fitted and the constants provide quantitative comparisons of different species or colonization in different environments. The intercept a is the geometric mean abundance of colonists on day 1 and slope b is an objective measure of curvature reflecting successional change or approach to equilibrium. Unlike the equilibrium model, the power function can accommodate cases in which the rate of colonization increases with time (Ulfstrand et al. 1974). Graphical comparisons (Fig. 3) are easily made. The power function is readily incorporated in multiple regression analyses.

The equilibrium model is biologically plausible and, in theory, the equilibrium density (k/m) and the rates of immigration and emigration can be estimated directly from colonization data. Disadvantages include the iterative method of fitting and the difficulty of multiple regression analysis. The very existence of a sustained equilibrium density is questionable and, unless the constants k and m can be estimated independently, the equilibrium model seems to offer few advantages.

The location effects on colonization have the practical consequence of increasing the variability of the data and raise a more fundamental question about the structure of stream communities. The spatial trend for *Baetis* (Fig. 2) reflects position as much as habitat since proximity to the large upstream riffle seems to have more effect than location in pools or the shorter downstream riffles. Perhaps every portion of the stream bottom is in transitory equilibrium with adjacent or upstream areas. If competitive interactions are important, a steady drift of fast-water species into small and infrequent pools could prevent the establishment of a stenotopic pool fauna or conversely. Waters (1964) and Minckley (1963) present evidence that such displacement can occur. Characterization of such dynamics will require integrated measurement of micro- and macropattern of habitat and benthos composition and

of drift and colonization rates. The colonization models used in this paper are compatible with the drift model of McClay (1970) and Elliott (1971b) and could be used in such an investigation.

Acknowledgments – R. A. Haick, L. Booth and P. Piper assisted in the field and laboratory. This work was supported in part by funds provided by the United States Department of Interior, Office of Water Resources Research as authorized under the Water Resources Act of 1964 and by the Montana Forest and Conservation Experiment Station, School of Forestry, University of Montana.

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