LETTERS AND COMMENTS/LETTRES ET COMMENTAIRES

Succession, Scale, and Hypothesis Testing in Streams

Succession is the sequence of changes that occur on a site after a disturbance. In desert streams, flash floods evince high mortality among biota, largely by scouring fine gravel substrates, and interflood periods are marked by pronounced, rapid change in a host of attributes, that is, succession occurs (Fisher et al. 1982). I proposed (Fisher 1983) that this pattern may not occur in New England streams where floods were more common (several during the life span of common invertebrates), the biota was adapted (or preadapted) to this regime, substrates were more stable, and consequent mortality associated with floods was lower.

Dr. Barbara Peckarsky's (1986) interesting recent paper in part purports to test the hypothesis that site-specific succession does not occur in typical New England streams. By placing denuded natural substrates in a small woodland stream in New York and monitoring changes over time in the insect fauna, she discovered that elapsed time after denudation was a significant predictor of numbers and species of aquatic insects. Change in depth alone was marginally significant. Change in temperature and velocity were not significant, nor was season during the 48-d autumn study period. This partial correlation analysis led Peckarsky to reject the null hypothesis in favor of the alternative that site-specific succession does indeed occur in this type of stream. As I am responsible for generating this hypothesis in the first place (Fisher 1983), I should like to comment on the adequacy of this test and implications of the result for stream ecology and the concept of succession.

Peckarsky's denuded substrate patches represent a smaller scale than that at which the disturbance operates and ecosystem succession occurs. For example, the manipulation effected no appreciable mortality among insects in the stream as a whole and therefore had no effect on the number of potential colonists, colonization distances, or species composition of the community of potential colonists. The manipulation and subsequent recovery seem enticingly analogous to gap replacement in forests; however, forest gaps are generated largely autogenically. Floods may roll rocks and thereby open gaps, but significant effects extend far beyond this scale of resolution. I would therefore argue that the scale of Peckarsky's study and the nature of the disturbance are discordant and leave the central question unanswered. I should hasten to add that the substrate patch is an appropriate scale at which to examine the role of species interactions in structuring communities. Peckarsky has exploited this opportunity cleverly in this and other papers.

Perhaps more importantly, the design of the experiment renders the initial hypothesis somewhat trivial in that it becomes virtually unfalsifiable. By that I mean that it is inconceivable that depopulated substrates in a sea of mobile organisms would remain so. Would any other outcome support the original null hypothesis? I will take the blame for the initial imprecision and try to make amends below.

Let me restate the question nontrivially, reword the hypothesis, and suggest a test. What independent variables have the most power in predicting biologic state variables (e.g. chlorophyll, numbers and kinds of animals) in New England streams? Of the multiple null hypotheses, the following addresses the succession question best: time since disturbance by flooding is an insignificant variable. If time since flooding is irrelevant to biologic state variables, then succession is by definition unimportant. This hypothesis can be tested by measuring biologic attributes and a suite of independent variables *at a scale large enough to reflect the spatial range of the disturbance*. A partial correlation analysis similar to that performed by Peckarsky would identify the significant variables and the variability explained by each. Incidentally, season may turn out to be a significant variable in this analysis if the study is carried out for at least an annual period. Peckarsky may have made a type II error in rejecting seasonal effect based on her too-short 48-d autumn study period.

I realize this correlation analysis is not as powerful a test as a well-designed, manipulative field experiment; however, at the scale at which the hypothesis is meaningful (the whole ecosystem), an appropriate planned experiment is at least impractical and expensive and may well be impossible — Stuart G. Fisher, *Department of Zoology, Arizona State University, Tempe, AZ 85287, USA.* (J8943a)

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Succession, Scale, and Hypothesis Testing in Streams: A Reply to Fisher

The purpose of the study in question (Peckarsky 1986, p. 701) was "to examine the colonization and subsequent patterns of species dominance on natural stream substrates confined to enclosures in a temperate, woodland stream...." As Fisher (1983) pointed out in his fine review of succession in streams, although colonization following disturbance is well-documented, little evidence exists for events following initial colonization. Thus, the critical second component of succession, that is, subsequent changes in dominance of species, needs more investigation. He urged stream ecologists to report their work in a successional framework regardless of the specific focus of their studies.

Fisher has two major objections to this study. His first is one of spatial scale. He suggests that the scale of the denuded substrate patch is smaller "than that at which the disturbance operates and ecosystem succession occurs." Further, he acknowledges that "Floods may roll rocks and thereby open gaps, but significant effects extend far beyond this scale of resolution." On this basis he feels that this "study and the nature of the disturbance are discordant...."

I do not agree that the substrate patch is an inappropriate scale at which to examine effects of disturbance in streams. This small spatial scale termed "micro-level" by Sheldon (1984), identified as the intended scale of this study, is certainly subject to disturbance by rock rolling (as demonstrated by McAuliffe 1983, 1984). Stones frequently overturn in streams from causes other than catastrophic flooding, opening up new habitat for subsequent colonization by macroinvertebrates. This phenomenon is analogous to gap formation in forest floors, as well as to "patch birth" in the marine rocky intertidal (Paine and Levin 1981). Numerous studies have been carried out in terrestrial and aquatic systems demonstrating the relevance of small-scale disturbances to the mortality of populations (Sousa 1984). My study was not designed to look at ecosystem-level succession following catastrophic scouring events, but to examine "redistribution of the benthos in response to availability of newly opened habitats" (Peckarsky 1986, p. 708). Perhaps my conclusions should have been more clearly stated as limited to this small spatial scale. However, I would argue that the scale of the experiments was one of a number of spatial scales relevant to the domain of disturbance in streams.

I agree completely with Fisher that disturbance also occurs at much larger scales, and that the study of colonization and subsequent species replacements is meaningful at the "meso-level" and "macro-levels" as well (Sheldon 1984); but that is not to say that the study of "micro-level" processes is unimportant, irrelevant, or inappropriate. The best studies are those that examine these processes at multiple spatial and temporal scales. In fact, Fisher (1983) pointed out that "variation in disturbance intensity and spatial coverage affect rates of colonization" (p. 12) and that "timing and severity of the disturbance and availability of nearby colonizers" (p. 13) are factors affecting recovery of stream populations. Paine's and Levin's (1981) study elegantly showed that the size of a disturbed patch governs the particulars of subsequent colonization and succession events. Implicit in their model is the underlying assumption that small patches are as biologically relevant as are large patches.

In summary, I have no argument with the importance of large-scale disturbances in desert streams, and the relevance of this phenonemon as a precursor to succession of biota. In applying Fisher's ideas to New England streams, as suggested in his 1983 paper, perhaps I misinterpreted his intent to narrow such applications to a large spatial scale. But I would argue that disturbance and succession have relevance at many spatial scales.

Fisher's second objection is that the experimental design "renders the initial hypothesis somewhat trivial" and thus unfalsifiable. I agree that one would not expect a depopulated substrate to remain so "in a sea of mobile organisms" at any spatial scale! Scale imposes limitations to rates of recovery, as discussed above, but large scale does not render the question any less trivial. Fisher suggests an alternative view of the question of succession by asking "What independent variables have the most power in predicting biological state variables ... in New England streams?" He rewords the best null hypothesis as follows: "If time since flooding is irrelevant to biological state variables, then succession is by definition unimportant." I feel that the study in question did exactly what Fisher suggests, but at a different scale and type of disturbance than he had in mind; that is, it tested this hypothesis by examining separate and interactive effects of season, time since disturbance, and abiotic regime on biological state variables.

I will briefly reiterate the relevant results of this study, since I think there has been some misunderstanding in their interpretation. The two-way ANOVA showed that time since disturbance had a highly significant effect and season (date of cage retrieval) a nonsignificant effect on the total number of individuals and species of benthic invertebrates colonizing cages. Interactions between season and time since disturbance were not significant (see Peckarsky 1986, table 2). I should point out here that Fisher correctly recognized that this study was conducted at a limited temporal scale. It should have been carried out over at least an annual period to draw conclusions regarding seasonal effects. Nonetheless, having demonstrated a significant effect of time since disturbance on biological state variables, I concluded that succession was important, rejecting the original null hypothesis.

Simple and partial correlations were also performed to examine the effects of other independent variables potentially affecting colonization (abiotic regime: water depth, flow, and temperature). Simple correlations showed that the number of colonists was not affected by the abiotic conditions on the cage placement or removal date, but was associated significantly with changes in depth, current velocity, and temperature over the period that each cage was in the stream (see Peckarsky 1986, table 3). Partial correlations showed that when abiotic factors (significant in simple correlations) were held constant, the association between colonization and time since disturbance became nonsignificant (see Peckarsky 1986, table 3). This analysis indicates that although time since disturbance explains a significant portion of the variance in colonization, this effect is largely a reflection of the relationship between time since disturbance and the change in abiotic regime.

In summary, this study tested the best null hypothesis, and a number of alternative hypotheses, as suggested by Fisher, identifying significant variables and the variability in colonization explained by each. Results of statistical tests supported rejection of the null hypothesis. Thus, I concluded that time since disturbance was a significant variable. Fisher's comment is valuable for pointing out that this study suffers (as do most studies) from having been conducted at a limited temporal and spatial scale. However, the small scale, which is the typical vision of a community ecologist, is no less meaningful than the large scale, the vision of an ecosystems ecologist. Pointing that out, I hope, is the value of this reply — Barbara L. Peckarsky, *Department of Entomology, Cornell University, Ithaca, NY 14853, USA.* (J8943b)

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Filtering Recruitment Time Series: Comment

Welch (1986) has recently described a method for filtering time series of fish recruitments to remove some of the variability induced by environmental effects. He observes that, for a long-lived species in which many age classes contribute to the spawning stock, stock size will change little from year to year compared with the changes in recruitment, and that large year-to-year changes in recruitment are therefore probably due to environmental effects. This has two consequences. First, it may be possible to construct filters, based solely on the reproductive age structure of the fish, that remove from the recruitment time series only high-frequency variability that does not depend on changes in stock size. This enables one to produce smoothed stock–recruitment plots (fig. 11). Second, the component of the recruitment time series that is due to stock effects will be serially correlated.

As well as producing smoothed pictures, Welch maintains that his method "results in a striking improvement in the potential to accurately define the relationship between stock and recruitment" (p. 117). I shall argue here against this claim of increased accuracy because (1) the serial correlation induced by age structure does not matter, and so estimates using unfiltered data are more accurate than Welch believes, (2) the reasoning used to justify filtering is invalid, and (3) Welch's Monte Carlo results do not support the claim of increased accuracy.

(1) The first point concerns serial correlation in recruitment and its effects on degrees of freedom. Welch notes that for a long-lived species, stock size in successive years will be correlated, and therefore recruitment will be serially correlated. He then argues that "the number of *independent* observations of the stock–recruitment dynamics occurring in the filtered data is considerably smaller than the number of filtered data points. The discrepancy occurs because the density-dependent processes of interest are serially correlated, and, as a result, several years must elapse between independent observations of the stock–recuitment dynamics" (p. 118, italics in original). This is true, but true only of the filtered data. Some sources of serial correlation in the dependent variable (recruitment) can cause trouble for regression methods. However, the source considered here, namely serial correlation in the independent variable (stock size), is innocuous. (If it were not, then the order in which measurements were made would influence all regression calculations, and all introductory books on the subject would describe how to allow for the order of measurement.) Although observations in successive years are made at stock sizes that are correlated, the unfiltered observations are independent in the only sense that matters for regression analysis.

The act of filtering, on the other hand, does cost degrees of freedom. After filtering, traces of an anomalous recruitment will appear at several nearby stock sizes, and so there will be serial correlation in the residuals, which does matter. (The fact that the filter is constructed from the age structure of the adult population, and not from the time series, is not relevant to this point.) Therefore, in table 2, filtered and unfiltered estimates are based on different numbers of degrees of freedom, and standard error is the wrong basis of comparison. Confidence regions would form a useful basis of comparison. They depend on standard errors and degrees of freedom; and they denote precise statements, open to tests independent of the detailed reasoning that created them.

(Of course, both the unfiltered and filtered time series may have other features that complicate their analysis. I am simply denying one point of similarity between them that Welch asserts.)

(2) The argument for filtering the recruitment time series goes as follows. If a stock is composed of many age classes, then variability in the recruitment time series will be attenuated in the process of forming the stock from recruitments in many years. Welch claims that this variability can therefore be removed "*from* the recruitment time series" itself (p. 112, italics added) "before assessing the form of the density-dependent relation between stock and recruitment" (p. 113). This simply does not follow. Variability that is attenuated in the process that produces future stock from recruitment cannot therefore be removed from the completely different process that produces recruitment from past stock. Welch operates largely in the frequency domain, where the difference is harder to see because the concepts of future and past are diffused, but this does not make the difference cease to exist.

The clearest statement of Welch's claim occurs in the paragraph spanning p. 113–114: "[If] variation in the recruitment is greater than the variation in the population fecundity, ... [then] the difference ... represents the proportion of the recruitment variability that must come from environmental factors influencing recruitment, ... which needs to be removed [before assessing the form of the density-dependent relationship between stock and recruitment]." The problem here is the meaning of the word "needs": we are basically asked to accept that need implies possibility. Removing variability unrelated to stock size would be convenient if it could be done, that is, if a method for doing so could be described and justified. Welch argues for the convenience, and describes a method, but the closest he comes to a justification is the *non sequitur* described above.

(As it happens, his statement is not always true. For example, if the stock equilibrium is on a steeply descending limb of a stock–recruitment curve, it may be unstable and lead to periodic or aperiodic fluctuations related solely to stock size — even with an age-structured population (e.g. caption to fig. 12). The variation in recruitment is greater than the variation in fecundity, and yet all the variation in recruitment is caused by variation in fecundity.)

(3) Of course, a method might work as described even when its theoretical underpinnings are incomplete. However, if Welch is to claim that filtering the recruitment time series "allows tighter confidence levels to be placed on the parameter values" (p. 117), it is reasonable to expect him to present simulations that demonstrate the truth of the claim. His Monte Carlo simulations do not address this point; they are restricted to showing the absence of bias. Why does he not compute 95% confidence regions for some model using the new theory, and demonstrate that 95% of them do indeed contain the true parameters, *and* that no more than 95% of the larger confidence regions he ascribes to methods using unfiltered data contain the parameters?

It would be useful to demonstrate the method on an underlying model that is simple enough to analyse exactly by other methods: say

$$\text{Recruitment} = \text{constant} + \text{noise}$$

("all of the recruitment variability present might possibly be due to [environmental] effects" (p. 114)), or

$$\text{Recruitment} = \text{constant} \times (\text{stock})^{2/3} \times \exp(\text{noise})$$

where noise is a zero mean Gaussian random variable, chosen independently in different years. (Independence of the noise ensures a lot of high-frequency variability in recruitment, so that Welch's method should work well. It does not imply that successive recruitments are uncorrelated. I assume that the Monte Carlo simulations described on p. 117 make this assumption: there is certainly no description of any time correlation in the noise.) Estimating the stock–recruitment relation, then, means estimating the constant, and is an elementary statistical problem. If these examples, with whatever long-lived age structure he likes, are not suited to Welch's method, perhaps he could explain why, and demonstrate the simplest model that is suitable — Geoffrey T. Evans, *Department of Fisheries and Oceans, Science Branch, P.O. Box 5667, St. John's, Nfld. A1C 5X1.* (J8718a)

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Use and Precision of Age Structure Based Recruitment Filtering Theory: Reply to Evans

It is unfortunate that Dr. Evans focuses on the accuracy of filter-based parameter estimates, since most of my paper (Welch 1986) involved the question of whether stock–recruitment (SR) parameter estimates can be made more precise by filtering. Recent work confirms the increase in precision gained by filtering recruitment data, and shows that a significant increase in accuracy can also be obtained for certain SR models (Welch 1987a). I suggest that the major problem in stock–recruitment analysis (SRA) is not whether a parameter estimate from some statistical exercise reflects the true value when averaged over many experiments (accuracy), but whether, given the single data set available in practice, the resultant point estimate lies close to the true value with acceptably high probability (precision).

(1) Dr. Evans' first assertions are that (i) serial correlation in the stock time series is of no consequence to SR analysis and (ii) the number of independent observations of the SR dynamics is smaller than the number of data points *only* for the filtered data. I shall argue that both points are false. Dr. Evans' criticisms partly arise from focusing on assumed properties of the recruitment data, and partly from ignoring the *bivariate* nature of the stock–recruitment relationship (SRR).

(i) If individual data points are to convey independent information, the autocorrelation of a time series must be zero at nonzero lags (Draper and Smith 1966, p. 17). I have listed in Table 1 the autocorrelation present in 5 of the 16 recruitment time series I originally analyzed. Significant autocorrelation is present either before or after filtering, and the conclusion for the remaining recruitment time series is the same. Thus, there are fewer degrees of freedom (df) than enumeration of the number of data points available for analysis would suggest, regardless of whether one filters the recruitment data. (This was also evident from fig. 5 in Welch (1986), since the spectra for the two sets of recruitment data shown there are far from flat. Uncorrelated time series have a flat spectrum, very different from those observed (Box and Jenkins 1976, p. 40).)

Unfiltered data are probably autocorrelated not just because of correlation in the stock time series, but also because many physical oceanographic processes that may influence survival are autocorrelated (e.g. Steele 1985). In addition, errors in correctly ageing the catch sample used to reconstruct recruitment strengths will further increase the level of autocorrelation. The belief that one can simply use the number of unfiltered recruitment data points as the number of degrees of freedom in calculating confidence intervals about SR curves is therefore false, since noise levels in adjacent years are not necessarily independent, as Dr. Evans assumes.

The suggestion that serial correlation in the stock time series must be innocuous because texts on regression would otherwise discuss it is interesting. Most introductory texts deal with the statistics of experimental situations, where individual experiments are independent (or should be). In field ecology, the scientist is often a passive collector of data generated gratuitously by nature — SR data collected from fisheries being an excellent case in point. The risks of ignoring the autocorrelation structure of data can be high.

Walters (1985) has shown that SR parameter estimates will be biased because of the serial correlation induced by age structure, and my own work (Welch 1987a) provides several examples of the level of this bias before and after filtering. On a more general note, there are several advanced texts (e.g. Box and Jenkins 1976) which address some of the statistical consequences of autocorrelated time series. Noakes et al. (1987) provide a recent application of one class of time series methods to SR analysis that explicitly exploits the autocorrelation present in recruitment data. While I disagree with Dr. Evans' suggestion that the effects of stock autocorrelation are innocuous, a greater awareness of the effects of autocorrelation on statistical studies in fisheries is clearly called for.

(ii) Dr. Evans' second claim is that filtering reduces the available degrees of freedom, since the autocorrelation of the recruitment time series is higher after filtering. However, the number of independent observations of the SR dynamics must be determined by the time series with the lower information content, since SR analysis compares the dependence of one time series on the other. Simply viewing the available degrees of freedom as a function of the number of data points and the autocorrelation structure of the recruitment data *alone* is inappropriate. This point can be most clearly illustrated by reversing Dr. Evans' argument.

Even unfiltered recruitment time series show significant autocorrelation (cf. Table 1), so there are fewer degrees of freedom available for SR analysis than there are SR data points. However, I can drive the recruitment autocorrelation as close to zero as desired *by adding uncorrelated noise to the recruitment data*, since autocorrelated effects on recruitment then become an arbitrarily small fraction of the overall variability. Does the lack of correlation caused by higher noise levels imply that *information on SR processes* has been added, simply because the individual data points in the recruitment time series are now uncorrelated?

An analogy with the degrees of freedom in an analysis of

TABLE 1. Calculated autocorrelations for the five longest recruitment time series used in Welch (1986) before (top) and after (bottom) filtering. Autocorrelations are calculated out to the first nonsignificant (ns) result. The lengths of the time series available for analysis are shown in parentheses

		Lag			
		1	2	3	4
Haddock	(42)	0.63	0.56	0.60	ns
(Georges Bank)	(34)	0.91	0.56	ns	
Pacific halibut	(26)	0.62	0.51	ns	
(Area 3)	(18)	0.95	0.79	ns	
Striped Bass	(26)	0.76	0.45	ns	
(Chesapeake Bay)	(18)	0.96	0.85	0.68	ns
Pacific sardine	(25)	0.72	ns		
(California)	(21)	0.89	0.62	ns	
Icelandic herring	(23)	0.68	0.44	0.45	ns
(summer spawning)	(17)	0.86	0.52	ns	

variance may help to make this point clearer. Assume that in some population stock size shifts instantaneously once every decade while recruitment varies between years in the manner prescribed by Evans. In this model, new information on SR processes can be obtained only once every decade, even if successive recruitments are uncorrelated. Assuming a total of 100 observations, there are only 10 df available in this model for looking at the SR dynamics, even though there are 100 observations on recruitment. Despite the uncorrelated nature of the recruitment, it would be incorrect to assume that the entire 100 df provide information for studying the SRR.

Dr. Evans' suggestion that SR parameters calculated from the filtered and unfiltered data should be based on different degrees of freedom would have merit if the criteria for filtering depended on information inherent to the time series being analyzed. Adjustment to the degrees of freedom would certainly be necessary in this case. However, knowledge of how the information content of SR data varies with frequency is based on an understanding of population dynamics plus a knowledge of the population's age structure. None of this information is based on the SR data, so any benefits of filtering can be compared by examining the relative magnitude of the standard errors before and after filtering.

(2) Dr. Evans charges that it is a logical fallacy to state that one can remove variability present in a recruitment time series that is not present in the parental stock time series. The basic justification for filtering was originally set out by noting that stock is defined as a convolution of the age-structure coefficients with past recruitments, i.e. as a form of weighted sum.

So long as stock can be described as the sum of past recruitments, filtering can be justified by Fourier's theorem. In Fourier theory the frequency domain representation of a time series is described as a set of sinusoids which are defined entirely by their amplitude and phase. Fourier theory therefore allows removal of the fraction of the recruitment variability present at each frequency that cannot be ascribed to variation in parent stock simply by changing the amplitude of the relevant sinusoid. The logical justification for filtering theory, based on the existence of the convolution, therefore also defines the method of treating the SR data. (See fig. 1–3 and p. 109–112 of Welch (1986) for an extended outline of the details of the approach.)

As a historical footnote, Feller used transform theory to simplify the study of the convolution of recruitment with age structure in a population dynamics problem as early as 1941. In my paper I used transform theory for *identifying* population mechanisms rather than for analyzing the consequences of specific mechanisms. However, the occurrence of a convolution in age-structured populations seems fundamental — it can be seen in essentially all population models that incorporate age structure, such as Lotka's or Leslie's models, as well as the McKendrick – von Foerster formulation.

As Dr. Evans points out, in a deterministic population model the amplitude of the recruitment oscillation is greater than the amplitude of the stock oscillation when an unstable SR equilibrium occurs, yet all the recruitment variability is caused by changes in population fecundity. However, the relative magnitude of the stock and recruitment variability at a single frequency is irrelevant; what is of concern is *how this ratio changes with frequency*. Since a deterministic model oscillating about an equilibrium has recruitment variation at only one frequency, such a comparison is impossible. If one were to design a filter to analyze the data from such a model, the best that could be done would be to design a filter whose gain at the oscillatory frequency was 1.0 (so as to pass all the recruitment variability unmodified), because there is no variability with which to compare this ratio at other frequencies.

(3) Dr. Evans' proposal that filtering theory should be applied to a model where recruitment is treated as a constant independent of stock size is of considerable interest. I have therefore analyzed the consequences of Evans' proposed model along with two other life history models (Welch 1987b) in an attempt to clarify the influence of age structure on the SR identification problem.

I invite the reader to judge the value of filtering theory from these three life history models, since the conclusions from the theory are analytically available without the need for numerical calculations. In particular, the third model analyzed provides a graphic example of how filtering can narrow SR confidence limits. In this model all of the extraneous recruitment variability present in the recruitment data is removed by filtering according to the adult age structure, so that after fitting the SR model the residual variance on which confidence limits are calculated is zero — David W. Welch, *Department of Fisheries and Oceans, Fisheries Research Branch, Pacific Biological Station, Nanaimo, B.C. V9R 5K6*. (J8718b)

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