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Source: *Ecology*, Vol. 71, No. 2 (Apr., 1990), pp. 657-667
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/1940320
Accessed: 31-03-2015 13:01 UTC

Ecology, 71(2), 1990, pp. 657–667

POST-DEFAUNATION RECOVERY OF FISH ASSEMBLAGES IN SOUTHEASTERN BLACKWATER STREAMS[1]

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Abstract. We analyzed fish assemblage structure at 37 sites in South Carolina streams before and nearly one year after experimental defaunation to test assemblage resiliency. Decreases in stream depth and width in the second year reflected an intervening drought, but habitat structure remained highly correlated between years. Fish assemblages recovered well over four scales of analysis. Total fishes sampled, collective assemblage properties (species richness, density, biomass, and mean mass of fish), local assemblage structure, and single-species attributes generally did not significantly differ after defaunation, as determined by species- and individual-abundance correlations, detrended correspondence analysis, and a proportional similarity index. These assemblages were not randomly structured units, but were largely deterministic systems highly predictable from local habitat structure.

Key words: community ecology; defaunation; diversity; field experiment; fish assemblage structure; habitat; recovery; resilience; South Carolina; streams.

INTRODUCTION

A major goal of community ecology is to determine whether communities are predictable and persistent entities, structured by a combination of biotic interactions and abiotic features, or unpredictable local associations of independent populations largely influenced by stochastic events. Approaches to this problem include description of spatial (Whittaker 1975, Angermeier and Karr 1983) or temporal (Moyle and Vondracek 1985) variation in structure, modeling hypothetical communities (Strong et al. 1979, Simberloff 1983), exploring details of resource use (Schoener 1974, Mendelson 1975, Ross 1986), or perturbing a community and monitoring patterns and rates of recovery (Simberloff and Wilson 1969).

Resilience, the ability to return to a pre-perturbation state (Holling 1973), can provide strong evidence for deterministic community structure. The least ambiguous way to demonstrate resilience is through experimental manipulation of replicated sites (e.g., Malanson and Trabaud 1987). If communities are more than random associations of independent species, and are influenced by predictable environmental features (e.g., habitat structure, species interactions, resource availability), then defaunation of an area should be followed by recovery to a structure similar to the original state. This resilience may be governed by strong habitat selection dictating types and frequencies of species that return, or by biotic interactions that sort out species abundances. Alternatively, recovery may result from random movement of colonists in proportion to their abundance in nearby source areas. Thus, resilience is not unequivocal evidence of determinism of community structure, since a stochastic mechanism, simple diffusion, may give rise to the same endpoint.

In a previous paper (Meffe and Sheldon 1988) we demonstrated that fish assemblages in coastal, blackwater streams of South Carolina responded strongly to habitat structure. Local habitat structure (depth, width, current velocity, substrate, and type and extent of cover) was a good predictor of local assemblage structure. The habitat "template" was a primary factor affecting the fish assemblage at a particular point in a stream, indicating that these assemblages are predictable associations rather than random groupings of species.

In this study of assemblage resilience we analyze habitat variables and fish assemblage structure in the same systems before and nearly one year after defaunation. We ask whether assemblages recover to their previous states, or reform in a different or random manner. If habitat is indeed a strong determinant of biotic structure, then post-recovery assemblages should strongly resemble their pre-disturbance state, lending support to the claim of non-randomness in community structure.

MATERIALS AND METHODS

Field sampling

Studies were conducted on the United States Department of Energy's Savannah River Plant (SRP), in the central Savannah River drainage near Aiken, South Carolina. From 23 September through 21 October 1986 we sampled 37 localities in first- to third-order streams that had been sampled in an identical manner from 15

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[1] Manuscript received 30 January 1989; revised 6 July 1989; accepted 7 July 1989.

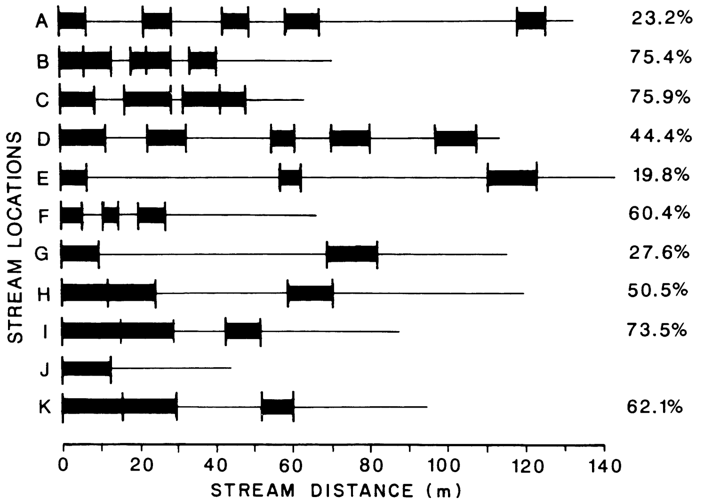

FIG. 1. Schematic representation of the relative sizes and positions of the 37 defaunation sites (solid areas divided off by vertical lines) at the 11 stream locations (A–K). Numbers at right indicate the percentage stream area defaunated at each site. There were originally four other defaunation sites at location J, but they were destroyed by a beaver dam.

October to 19 November 1985 (Meffe and Sheldon 1988), and from which fishes had been removed as completely as possible by procedures outlined below. Consequently we studied assemblages that presumably had developed from local source areas during the intervening year, and can compare the structure of undisturbed and recovered assemblages at individual sites, relative to habitat parameters.

The original study included 44 sites. Seven of these were not included in this analysis because one contained no fish in the initial study and six were disturbed by beaver dams or logging. Thirty-seven sites remained usable over the 1-yr period.

Sites (4–15 m long; longer units on wider streams) were selected to represent various single habitats (e.g., pool, clear sandy run) and to cover the range of habitats at 11 locations (Fig. 1: A–K) on five streams in three independent drainages to the Savannah River. Defaunation sites were a small enough percentage of local stream length that potential recolonization source areas remained available (Fig. 1). However, because defaunation sites were clustered, recolonization was unlikely to be a trivial matter of simple random movement from adjacent reaches. The mean area defaunated within a location was 52% of total area available (range: 20–76%), and 12 of 37 sites (32%) were adjacent. Therefore, recolonization must have been largely an active process from more distant areas.

At each site in these low-gradient, sandy streams we blocked either end with 6-mm mesh, weighted seines to prevent fish from escaping, and recorded the following habitat data: site length, width at 1-m intervals, cross-stream depth measurements at each interval, and substrate type (sand, silt, mud, gravel, leaves, or roots) at each depth point. Cover (wood, brush, coarse roots [>5 mm diameter], fine roots, vascular plants, undercut banks, and floating leaf packs) was recorded on diagrammatic maps of the site. Fishes were then collected to near depletion by multiple passes with a backpack electroshocker, and preserved in 10% formalin. The last one to two passes typically produced few to no fish, indicating that most fish within the site were collected by this method. Upon removal of block seines, current velocities were measured with a Marsh McBirney Model 201 current meter at 0.6 times local depth at a series of points. More complete site descriptions and details of sampling methodology are in Meffe and Sheldon (1988).

Fish from each collection were later identified to species, measured to the nearest millimetre standard length (SL), blotted dry, and collectively weighed by species to the nearest 0.01 g.

COMMENTS ON SCALE

Interpretation of ecological experiments is scale- and duration-dependent (Wiens et al. 1986). Our design incorporated small units (~10-m stream segments) and a moderate time interval (1 yr). In selecting an appropriate-sized experimental unit, we considered the pool/riffle system (Frissell et al. 1986) to be the smallest appropriate scale for investigation, since individual fish can traverse a unit in minutes or less and smaller defaunation units would thus be trivial. We also were influenced by the views of Gerking (1959) who suggests that many stream fishes are sedentary and occupy single riffles or pools. Our own analysis (Meffe and Sheldon 1988) of assemblage composition and habitat use strengthened our opinion that a pool or run and its fishes was a fundamental, meaningful entity, and that, at this scale, recolonization by any locally occurring species was possible. Consequently, members of a post-defaunation assemblage could be drawn from the entire available local (e.g., several hundred metres) species pool, and could consist of many possible species combinations. By defaunating individual pools and runs, and testing for similarity of recovered assemblages to the original assemblages, we tested against a null model of randomness, since the complete local species pool had access to sites that would contain only a subset of those species after recovery.

We avoided larger stream segments since these would average over the habitat variability that was our primary interest, substantially increase the amount of destructive sampling necessary, and reduce the number of replicates. If major sections of stream (i.e., hundreds of metres) were defaunated, then the new assemblage, at least during a relatively short time such as a year, might be restricted only to the most mobile species. In that case, post-defaunation assemblage composition would be a function of size of experimental unit and species mobilities, rather than relevant habitat or biotic attributes.

We allowed system recovery for nearly one year to ensure comparability of numbers and of age and size structure after the pulse of reproduction in spring and summer. Discharge and other habitat features, such as leaf accumulations, also should be more comparable on an annual basis. The interval between collections is long relative to potential dispersal by some species but shorter than the minimum generation time of most of the fishes. Thus, recolonization was by immigration, not by reproduction of individuals within the units. This is appropriate, given that we are largely dealing with adults rather than juveniles. Recovery of juveniles could be due to immigration or recruitment, and may have very different dynamics.

The relatively short dispersal distances and long time involved ensured that if recovery occurred it would be observed. However, convergence of local assemblages on pre-disturbance structure was certainly not guaranteed, because all local species have physical access to defaunated units and are then presumably "sorted" by habitat features or biotic interactions. If such assortative recovery is observed in our experiment it provides a reference for experiments at other temporal and spatial scales (cf. Wiens et al. 1986).

ANALYTICAL TECHNIQUES

Analyses were conducted with the Systat statistical package for microcomputers (Wilkinson 1987). Means of stream depths, widths, and current velocities, and percentage representation of each substrate category, were calculated from raw data. Percentage area of each cover category was calculated by tracing maps with a Lasico Model I-40 Compensating Polar Planimeter. Because distributions of most habitat variables were skewed, these data were transformed to log X, or arcsine $\sqrt{X}$ for proportion data. Biological data (biomass and densities) were strongly skewed, with the variance being a function of the mean; this was corrected with a transformation using the Taylor power law (Taylor 1961), as follows. If the means ($\bar{X}$) and variances (s^2) are related as

$$\log s^2 = a + b \log \bar{X},$$

where a and b are estimated by linear regression, then the appropriate variance-stabilizing transformation is $Z = X^p$, where $p = 1 - b/2$ (Elliott 1971, Taylor et al. 1980, Hanski 1982).

Habitat data were compared between years with univariate, paired t tests on each of 15 habitat parameters (with alpha level adjusted for multiple tests by the Bonferroni method), and a principal components analysis (PCA) of all habitats in both years, using the correlation matrix, which makes the parameters scale-free and directly comparable. We compared the scores of sites on the first four principal component axes between the two years by correlations of individual component scores between years.

Biotic data were compared between years on four levels, from large to small scale (below). In all cases data were transformed to meet statistical assumptions. Where assumptions could not be met, non-parametric tests were used. At most levels, comparisons were made between pre- and post-disturbance samples (i.e., between years) using paired t tests and correlation coefficients. Paired t tests quantify the magnitude of change for individual sites or species. Even though significant changes may occur after disturbance, there still may be strong correlations between yearly samples, indicative of similar direction and magnitude of change among all sites or species. Thus, a species or site may change significantly after disturbance (as shown by a significant paired t test), but in direct proportion to changes in other sites or species (as shown by a significant correlation coefficient).

The following levels of biotic organization were examined:

1. *Recovery of total sample.*—Fishes from all 37 sites combined were compared for pre- and post-disturbance samples. Constancy of species' rank abundances between years was analyzed with Spearman's coefficient of rank correlation (r_s) for all species, and for the most common 15 and 10 species ("core" groups), to detect possible spurious correlations due to constancy of rare species. Total number and total biomass for each species (with rare species eliminated; see Results) were tested for significant changes with paired t tests. Between-year Pearson's product-moment correlation coefficients were calculated for total numbers collected and biomasses.

2. *Collective properties.*—We compared species richness, mean density, biomass, and mean fish mass between pre- and post-disturbance samples across all 37 sites. This analysis ignores taxonomic composition of assemblages. Species richness was normally distributed and not transformed; the other parameters required a log transformation before analysis. Each property was tested for significant changes between years

TABLE 1. Univariate habitat data. Data are mean and SD for each year, the Student's paired t value, and the probability of a type I error.

Parameter	Year 1		Year 2			
	$\bar{X}$	SD	$\bar{X}$	SD	t	P*
Mean depth (cm)	20.3	11.8	17.0	9.1	3.59	<.001
Mean width (m)	3.5	1.7	3.2	1.6	3.30	<.002
Mean velocity (cm/s)	12.8	7.3	11.7	6.9	1.25	.221
% substrate						
Sand	49.3	21.3	48.0	21.7	0.58	.566
Silt	24.4	14.7	31.6	18.7	2.93	.006
Mud	6.2	11.3	1.5	2.7	2.82	.008
Leaves	10.4	8.5	7.6	7.5	1.95	.060
Gravel	7.7	13.4	6.6	11.3	1.04	.305
% cover						
Wood	6.0	7.5	6.7	5.5	0.81	.425
Brush	2.5	6.5	1.0	2.0	1.32	.196
Coarse roots	1.3	2.4	1.2	1.8	0.03	.975
Fine roots	0.7	1.2	2.2	3.2	3.50	<.001
Undercut banks	1.2	2.0	0.9	1.4	0.83	.413
Leaf packs	0.2	0.7	0.1	0.4	0.58	.563
Plants	5.2	21.8	3.2	14.7	1.16	.253

* The Bonferroni adjusted significance level is 0.0034.

with a paired t test. Pearson's correlations between years were also calculated to determine if the degree of change was correlated among sites.

3. *Local assemblage structure.*—Species were separated into size classes following protocol established in Meffe and Sheldon (1988). After transformation by the Taylor power function (Meffe and Sheldon 1988), taxon (=species size class) densities in both years at all sites were analyzed with a detrended correspondence analysis (DCA; Hill 1979, Hill and Gauch 1980). This procedure ordinates sites along axes based upon similarities and differences in species composition and abundance, and accommodates the typical nonlinear relationships within biological data sets and species turnover along environmental gradients.

Assemblage recovery at each site was also assessed using Schoener's (1968) proportional similarity index (PSI):

$$PS_{ij} = 1 - 0.5\sum_{n=1}^{s} |p_{in} - p_{jn}|$$

where PS_{ij} is proportional similarity (from 0.00, completely different, to 1.00, identical) between two samples i and j, s is the number of species, and p_{in} and p_{jn} are species proportions of total numbers of individuals in the i^{th} and j^{th} samples. This index provides a more quantitative assessment of local assemblage similarity after recolonization, and also allows direct comparison with other published studies.

The small sampling scale used here should result in greater influence of small, random events that bias against recovery; this can be investigated by calculating PSIs at larger spatial scales. Consequently, indices were also calculated for the sum of all sites within each location (Fig. 1: A–K, excluding the single-site location J), and for all 37 sites combined. A similarity measure was thereby obtained at the level of local defaunation sites, at larger stream reaches (as though the several sites at each location were one defaunated unit), and over the entire range of samples.

4. *Individual species' recovery.*—Mean densities for each taxon were tested for between-year change using the Wilcoxon rank sum test (neither raw nor transformed data were normally distributed). Correlation of densities between years was provided by Spearman's coefficient of rank correlation.

RESULTS

Univariate analysis of paired habitats indicated that 3 of 15 variables changed significantly in the two years (Table 1). Stream depth and width decreased, and percentage of fine roots increased. Summer 1986 was the worst drought period on record in the southeast, and even though rains returned in August and September before sampling, prolonged drought is reflected in lower depths and widths.

The first four principal components (PC) of the 15 habitat variables for both years combined explained 58.9% of the total variance in habitat characteristics (Table 2). Correlations between habitat variables and PC scores are similar to those obtained in 1985 (Meffe and Sheldon 1988), and are similarly interpreted: the first axis is a current-velocity component, the second a stream-size component, the third a gravel/leaf/wood component, and the last a root/undercut component.

Site scores on all four principal components were significantly correlated between years (Table 2). This, combined with univariate analyses, indicated that sites changed somewhat in depth and width, but site characteristics remained similar relative to one another (e.g., the deepest sites in year 1 remained deepest in year 2, although absolute depth significantly decreased). Thus, relative suitabilities of sites for fishes remained similar

TABLE 2. Correlations between PCA scores and habitat parameters for the first four principal components for both years combined. For clarity, we list only those correlations greater than 0.300.

Parameter	I	II	III	IV
% sand	−.858			
Mean velocity	−.848			
% silt	.716		−.352	
% leaves	.636		.414	
Mean width	−.510	.609		
Mean depth		.880		
% mud		.647		−.319
% leaf packs			.608	
% wood			.585	
% gravel		−.317	.560	
% undercut banks		.393		.692
% coarse roots	.351			.684
% fine roots			−.331	.415
% brush		.340		.451
% plants	−.398			
% variance explained	21.2	15.0	11.9	10.8
r*	.847	.846	.687	.402

* Pearson's correlation of factor scores in the two years ($P < .01$ in all cases).

over the two samples, even though sites overall had lower discharge in the second year.

We collected 2188 fish in 27 species in year one and 2081 fish in 27 species in year two at these 37 sites (Table 3). Two rare species in the first year (lake chubsuckers, *Erimyzon sucetta* [$n = 5$] and chain pickerel, *Esox niger* [$n = 1$]) were not recorded in the second. Conversely, lined topminnows (*Fundulus lineolatus*, $n = 5$) and spotted suckers (*Minytrema melanops*, $n = 2$) were taken in the second year but not the first. All other species were common to both samples.

Recovery of total sample

For all sites combined, species rankings in the two years (Table 3) were significantly correlated (Spearman's coefficient; $r_s = 0.93$; $P < .001$), indicating that degree of commonness did not generally change. Core groups of the 10 and 15 most common species also were significantly correlated ($r_s = 0.83$ and 0.90, respectively, both with $P < .001$), indicating that correlations were not simply a function of the rare species remaining rare.

Total numbers of individuals per species are also similar in the two years. The correlation coefficient for log-transformed total numbers of the 22 most abundant species in the two years (rarest species omitted) is 0.93 ($P < .001$). The most abundant species, the yellowfin shiner (*Notropis lutipinnis*), so greatly dominates the samples that it could bias results toward significance. However, dropping yellowfin shiners from

TABLE 3. Number of individuals and biomass for all fishes collected in the two years, with rank order in parentheses. Species are listed by rank order of numerical abundance in the first year.

Species	Family*	Number		Biomass	
		1985	1986	1985	1986
Notropis lutipinnis	Cyp	874 (1)	883 (1)	700.4 (7)	604.3 (7)
Aphredoderus sayanus	Aph	225 (2)	190 (3)	942.6 (6)	773.5 (4)
Notropis cummingsae	Cyp	223 (3)	224 (2)	52.6 (21)	64.1 (17)
Nocomis leptocephalus	Cyp	145 (4)	96 (4)	603.9 (8)	274.2 (10)
Lepomis auritus	Cen	91 (5)	71 (7)	1251.4 (3)	1142.3 (1)
Noturus leptacanthus	Ict	91 (6)	39 (12)	200.9 (12)	47.5 (20)
Etheostoma olmstedi	Per	74 (7)	80 (6)	95.9 (16)	81.1 (15)
Lepomis punctatus	Cen	67 (8)	46 (10)	1237.9 (4)	725.0 (6)
Gambusia affinis	Poe	54 (9)	49 (9)	23.6 (25)	12.7 (25)
Anguilla rostrata	Ang	53 (10)	42 (11)	1790.6 (1)	1067.2 (2)
Erimyzon oblongus	Cat	41 (11)	51 (8)	1106.1 (5)	755.8 (5)
Percina nigrofasciata	Per	40 (12)	36 (13)	67.1 (19)	54.5 (18)
Ictalurus natalis	Ict	32 (13)	27 (15)	1412.2 (2)	1009.2 (3)
Semotilus atromaculatus	Cyp	31 (14)	30 (14)	192.5 (13)	211.5 (12)
Noturus insignis	Ict	29 (15)	27 (17)	342.0 (10)	235.0 (11)
Notropis chalybaeus	Cyp	27 (16)	90 (5)	14.6 (26)	32.6 (23)
Noturus gyrinus	Ict	23 (17)	12 (19)	94.6 (17)	42.6 (21)
Etheostoma fricksium	Per	20 (18)	23 (16)	26.8 (23)	29.8 (24)
Esox americanus	Eso	12 (19)	20 (18)	399.2 (9)	380.3 (8)
Hypentelium nigricans	Cat	12 (20)	11 (20)	155.4 (14)	315.2 (9)
Lepomis marginatus	Cen	11 (21)	10 (22)	94.5 (18)	100.6 (14)
Erimyzon sucetta	Cat	5 (22)	0	138.8 (15)	0
Acantharchus pomotis	Cen	2 (24)	3 (24)	39.2 (22)	42.5 (22)
Ictalurus platycephalus	Ict	2 (24)	11 (21)	204.6 (11)	125.3 (13)
Micropterus salmoides	Cen	2 (24)	2 (26)	55.9 (20)	51.5 (19)
Umbra pygmaea	Umb	1 (26.5)	1 (27)	2.6 (27)	3.8 (27)
Esox niger	Eso	1 (26.5)	0	26.7 (24)	0
Fundulus lineolatus	Cyt	0	5 (23)	0	4.5 (26)
Minytrema melanops	Cat	0	2 (25)	0	74.5 (16)
Total		2188	2081	11 272.6	8261.1

* Ang = Anguillidae; Aph = Aphredoderidae; Cat = Catostomidae; Cyp = Cyprinidae; Cyt = Cyprinodontidae; Cen = Centrarchidae; Eso = Esocidae; Ict = Ictaluridae; Per = Percidae; Poe = Poeciliidae; Umb = Umbridae.

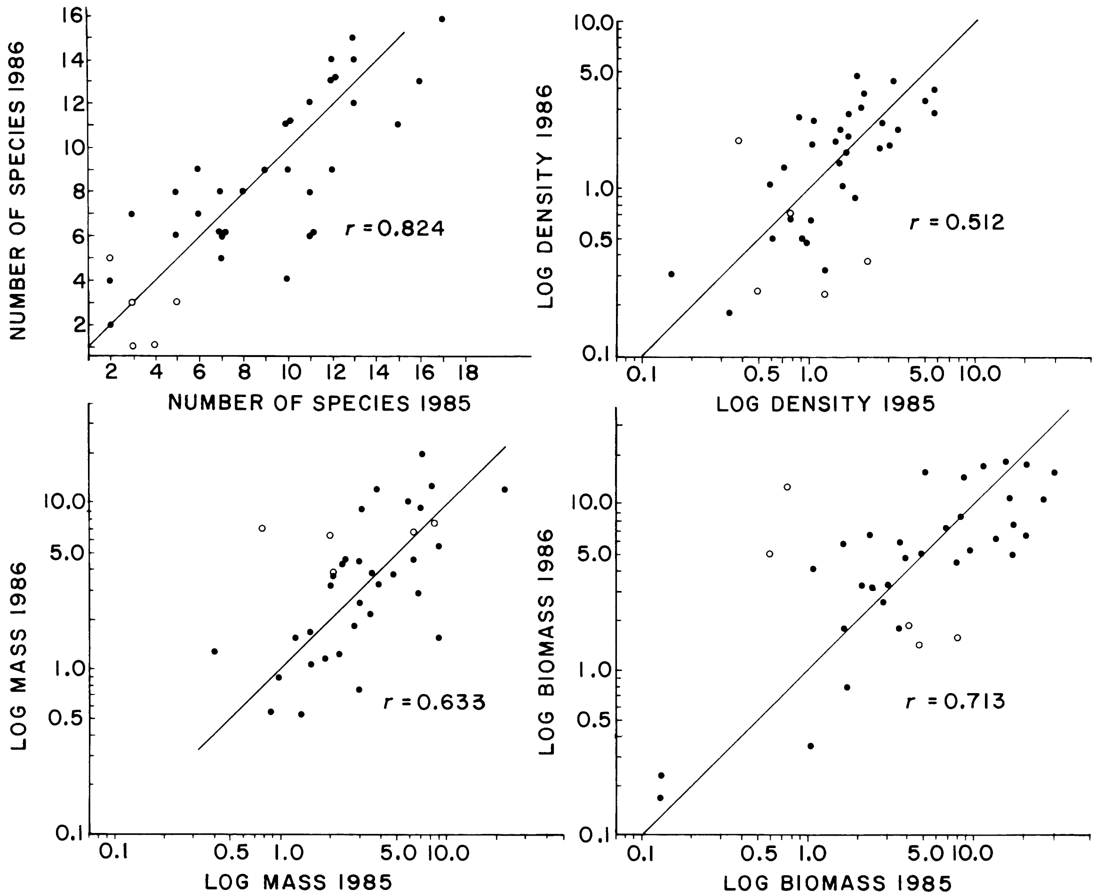

FIG. 2. Plots of collective properties for post-defaunation (year two) vs. pre-defaunation (year one). Correlation coefficients are noted for each. The 45° lines indicate zero-change isolines, and are not regression lines. Points above the line indicate a higher value after recovery, points below, a lower value. Open circles denote small, headwater sites. Mass was measured in grams, density in number of fish per square metre, and biomass in grams per square metre.

the analysis still results in a correlation of 0.886 ($P < .001$) for the remaining species, indicating that recovery for all sites combined was significant. Subsets of the 10 or 15 core species produced even higher correlations. A paired t test of log-transformed species totals between the two years shows no statistically significant change ($t = 0.871$, df $= 21$, $P = .395$).

The correlation coefficient for log-transformed biomass in the two years is 0.942 ($P < .001$). A paired t test of biomass indicates marginally significant biomass decreases in the second year ($t = 2.047$, df $= 21$, $P = .054$).

Collective properties

Paired t tests comparing species richness, and log-transformed densities, biomass, and average mass between years indicated no significant differences. Correlations between years in each property are high and significant (Fig. 2). The most extreme sites are usually from five collections in one small, shallow, first-order tributary (Fig. 1: location B). These tiny habitats supported only small fish assemblages in both years (typically 1–3 species, and only a few individuals). Consequently, any change between years, even of single individuals, will manifest itself as a large proportional shift, biasing the system toward significant change. Despite including these small, erratic sites, collective properties did not change significantly between years.

Local assemblage structure

Bivariate plots of the first two DCA scores in both years (Fig. 3) indicate little change in species composition, with significant product-moment correlations of site scores between years. The small tributary sites discussed above had the largest biotic shifts, several of which appear to be outliers. When these are removed, the correlation for axis II increases appreciably (Fig. 3).

Assemblage proportional similarities within sites covered a broad range (Fig. 4), with a mean value of 0.55. Most of the lower values (0.0–0.3) are from the five small headwater sites or from other shallow, narrow sites that contained few species or individuals. However, three larger sites without these characteris-

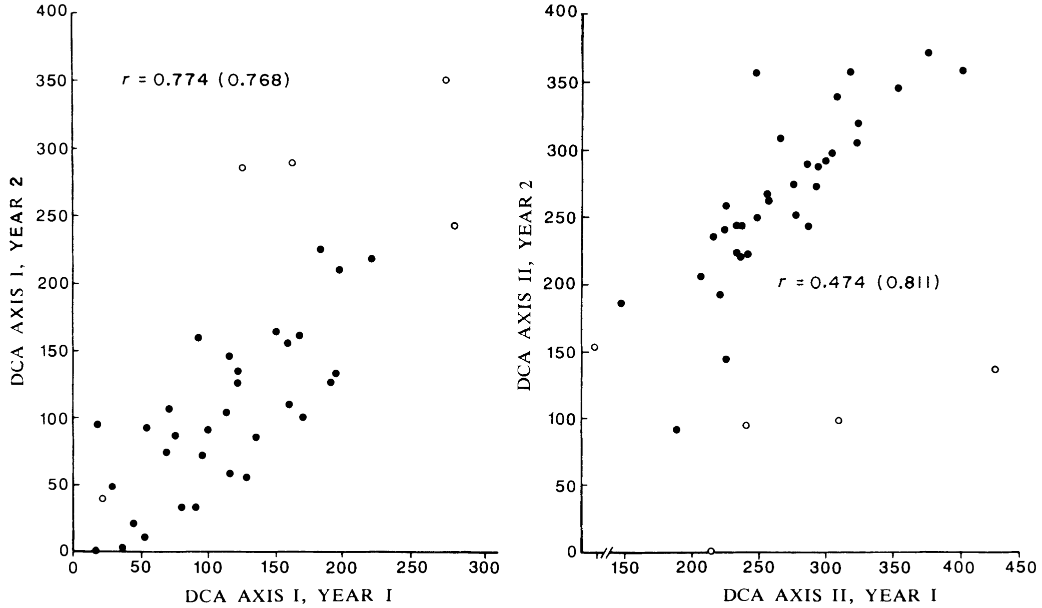

FIG. 3. Bivariate plots of site scores on the first two DCA axes, comparing assemblage compositions before and after defaunation. Open circles denote small, headwater sites (numbers in parentheses are correlations with these headwater sites removed).

tics also had unexpectedly low similarity indices (Fig. 4); these sites truly did not recover well. One of these was within a location (Fig. 1: site J) in which we eliminated four other sites due to beaver dam construction. We had thought that the fifth site was unaffected, but apparently this was not the case. We do not know why the two other sites, both at the "K" locality, had low PSIs; they had no unusual characteristics.

When combined by sampling locality, the lower PSIs disappear (Fig. 4), and the mean increases to 0.70. The lowest value, 0.43, is again from the headwater sites; all other values are >0.6. This scale of analysis is more comparable to other stream fish studies, which typically sample 50–200 m of stream. Our individual sites were an average of only 9.0 m long; combined into localities, they averaged 32.2 m long. At the largest scale of analysis, all 37 sites combined produced a PSI of 0.91.

Matthews et al. (1988) sampled several midwestern streams in 200–400 m sites over several years. Their values for samples taken from the same sites in adjacent years are plotted in Fig. 4 for comparison to this study. The range of values for our combined sites falls within their range, and our mean is somewhat higher, even though they sampled on a larger scale.

Individual species' recovery

The behavior of individual species, broken down by size classes, is less predictable than any other level of analysis. Like the small stream sites discussed above, lower predictability is a consequence of small numbers of individuals in each of the categories. Even so, densities of most taxa (paired by sites) did not differ significantly between years (Wilcoxon rank sum test), and most species had densities that were significantly correlated in the two years over 37 sites as estimated by

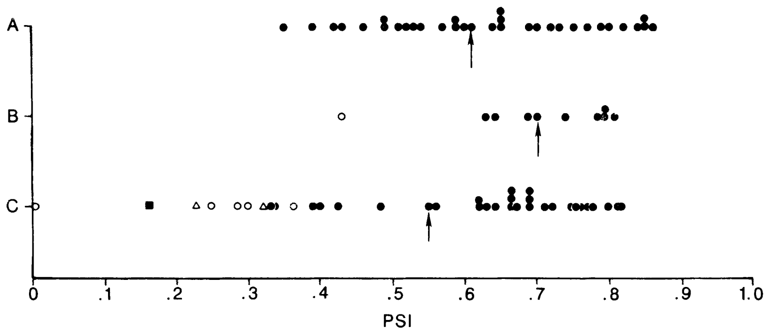

FIG. 4. The proportional similarity index (PSI) for (A) midwestern streams sampled by Matthews et al. (1988), (B) the 11 defaunation localities A–K (i.e., combined sites), and (C) the 37 defaunation sites. ↑ = mean PSI values; ○ = five small headwater sites, ■ = a site probably affected by beaver dam construction between years 1 and 2, and △ = two sites at location K that appeared normal.

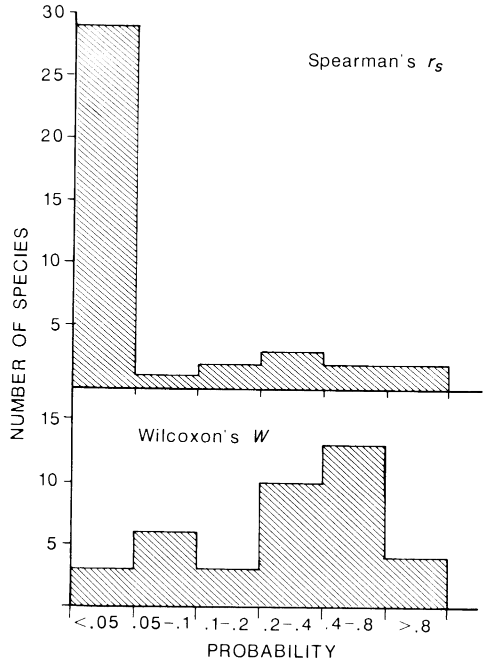

FIG. 5. Frequency distributions for significance levels of Spearman's correlation coefficients (above) and Wilcoxon paired ranks test for species density changes between years.

Spearman's coefficient. Probability distributions of these test statistics over all species (Fig. 5) indicate that not only are few of the changes in mean density (Wilcoxon W) significant, but the majority have large probabilities, far from significance. Similarly, the stability of spatial pattern as measured by Spearman's r_s is strongly skewed toward lower probability values, indicating that most species were affected by defaunation in a similar manner, and their densities were highly correlated in the two years.

DISCUSSION

Stability of stream fish assemblages has been intensively debated in recent years, stimulated by Grossman et al.'s (1982) study of a non-equilibrium fish assemblage in Indiana, followed by critiques (Herbold 1984, Rahel et al. 1984, Yant et al. 1984), a rebuttal (Grossman et al. 1985), and a series of other studies (Matthews 1985, 1986, Ross et al. 1985, Meffe and Minckley 1987, Matthews et al. 1988, Meffe and Berra 1988).

Resilience of stream fish assemblages has been investigated following severe drought (Larimore et al. 1959), pesticide kills (Olmsted and Cloutman 1974), pollution (Krumholz and Minckley 1964), and destructive flooding (Seegrist and Gard 1972, Harrell 1978, Matthews 1986, Minkley and Meffe 1987). Controlled experimental studies of resilience are few, and include only Gunning and Berra's (1968, 1969) and Berra and Gunning's (1970) repopulation studies of selected species in Louisiana. They found that defaunated pools were repopulated within a year, and in some cases biomass exceeded pre-defaunation levels.

In our study, replicated sites from which most fishes were removed recovered within 11 mo to assemblage structures similar to the pre-disruption state. This recovery was predictable from habitat structure, with gradients in current velocity and stream depth the primary determinants of species composition and abundance (Meffe and Sheldon 1988). Strong habitat selection is further demonstrated by significant correlations (Mantel analysis) in year 1 between species positions in habitat (PCA) space and biotic (DCA) space (Meffe and Sheldon 1988).

The degree of recovery is impressive considering the scale of study. Connell and Sousa (1983:792) state that "The spatial scale of a study will also affect judgements of the stability or persistence of a population or community. If the population or community is defined for the purposes of the study as the assemblage on a small area, it is unlikely to be either stable or persistent, since even small perturbations could cause local extinction." Many stream fish studies use large sample sections, typically one to several hundred meters long (e.g., Echelle and Schnell 1976, Grossman et al. 1982, Matthews 1985, Meffe and Minckley 1987, Matthews et al. 1988). Our study used small sample sites, at the level of individual pools or runs, which are more subject to random events than are larger sampling units. Despite this inherent bias toward instability, we observed significant recovery in these assemblages. This further suggests that our chosen scale may be an important functional unit of fish assemblage structure.

We can reject a random model of assemblage structure in this system. It is clear that assemblage structure was similar before and after defaunation and that recovery was non-random and largely predictable from habitat structure.

It is plausible that recolonization was simply a matter of random movement (diffusion) of fishes into de-

Table 4. Collective properties in both years over all 37 sites, with results of paired t tests comparing years and probability (P) of a type I error.

	Richness $\bar{X}$ ± SD	Density (no./m^2) $\bar{X}$ ± SD	Biomass (g/m^2) $\bar{X}$ ± SD	Mean mass (g) $\bar{X}$ ± SD
Year 1	8.6 ± 4.1	1.80 ± 1.39	7.9 ± 8.0	4.5 ± 4.4
Year 2	8.2 ± 4.1	1.75 ± 1.27	6.5 ± 5.3	4.9 ± 4.4
t (P)	1.01 (.317)	0.95 (.347)	0.09 (.930)	0.58 (.568)

faunated reaches from adjacent areas, rather than deterministic reassembly directed by habitat structure. However, we reject this diffusion model because study sections were carefully chosen on the basis of homogeneity of habitat type and distinctness from adjacent areas. A defaunated pool, for example, was typically bounded on either end by a shallow reach with higher velocities and a very different species composition. Recolonization by diffusion would have resulted in sites resembling adjacent assemblages, rather than their predefaunation conditions. Also, multiple sites were defaunated within a short reach of stream at most localities (Fig. 1), and colonists typically had to arrive from more distant sites, travelling through several habitat types. Finally, diffusion from adjacent reaches should have resulted in significantly reduced densities and biomass in our sites because small populations from adjacent reaches would now be spread over larger areas; however, density and biomass were not significantly different in the two years (Table 4). Diffusion from nearby areas is therefore not a realistic basis of recolonization.

We do not know the specific dynamics of resiliency in this system. Recolonization could result from several processes, including seasonal and directed long-range movements of fishes, cumulative short-range exploratory movements, agonistic interactions in source areas resulting in displacement to new habitats, and larval drift or in situ reproduction. The latter two mechanisms could only account for the smallest post-defaunation individuals. It is likely that many processes lead to high resiliency over this relatively short period of time. These processes need to be explored in controlled experiments.

Uncertainty about details of the recolonization process should not obscure the fact that our defaunated sections were resilient at the temporal and spatial scales investigated. A parsimonious explanation of the similarity of pre- and post-defaunation collections invokes both high mobility (yielding density-independent equilibrium with source populations) (Sheldon 1984), and strong habitat selection (Meffe and Sheldon 1988). The possible importance of intra- and interspecific interactions cannot be evaluated with our data. Unfortunately, if immigration rates are as high as we suspect, manipulations of component species in open systems to test biotic interactions will be extremely difficult.

Funk (1955) proposed that stream fish populations consist of sedentary individuals, such as those observed by Gerking (1950, 1953, 1959), and mobile individuals that may move long distances. Stott (1967) estimated that >30% of the individuals of two minnow species were mobile, and the remainder sedentary. Power (1984) documented extensive movements of loricariid catfishes among pools in a Panamanian stream as a result of natural or experimental habitat perturbations. Linfield (1985) suggests that cyprinid populations are mobile and respond in age-specific fashion to flow and temperature patterns. Under this model, populations are defined not by small neighborhoods (Addicott et al. 1987) or restricted home ranges (Gerking 1953) but by continuous fluxes of individuals through entire stream systems. Sheldon (1987) also suggested that stream fish faunas were best viewed as open systems and, like Linfield (1985), predicted collapse of immigration-maintained populations in streams isolated by dams.

The sizes of our stream fish neighborhoods are unknown but may vary from small home ranges for centrarchids (Gerking 1959, Whitehurst 1981) to large open populations (possibly the yellowfin shiner). Neighborhood sizes could be estimated by marking, or by defaunating larger sections (Addicott et al. 1987). The former alternative is ethically and practically superior. Defaunation of larger stream segments would only place recovery on a longer time scale, and recolonization mechanisms would largely be the same (movement from source pools), regardless of defaunation scale.

Although there are no comparable, controlled defaunation studies in streams, several studies in marine intertidal systems offer insights on similar scales. Thomson and Lehner (1976) repeatedly defaunated two tide pools in the northern Gulf of California over 7 yr; both were highly resilient and stable despite this perturbation and a severe winterkill. Grossman (1982) removed fishes from tidepools in central California 14 times over a 29-mo period and documented stability of the assemblages. Beckley (1985) repeatedly defaunated three tide pools in South Africa over 2 yr and reported high resilience. Recolonization was by both juvenile recruitment and immigration of adults from adjacent areas. Like our South Carolina streams, these localized marine habitats appear to be strongly resilient and stable.

In contrast, Sale's work (summarized in Sale 1988) on reef fishes indicates very different assemblage dynamics. In defaunation experiments on Australian reefs (Sale and Dybdahl 1975, 1978) recolonization produced local assemblages that typically differed from the pre-disturbance state, and microhabitat use did not determine subsequent species composition. In later, non-manipulative studies (Sale and Douglas 1984), successive sampling of a series of patch reefs indicated that assemblage structure continually changed through time, and that habitat structure (other than patch size) was of little value in predicting fish assemblage structure. Fish assemblage dynamics on those coral-patch reefs thus appear to differ in a fundamental way from those of our stream "patches."

Resiliency, driven by species-specific habitat preferences, is likely to be a pervasive aspect of assemblage structure in stream fishes, and is indicative of nonrandom, structured systems. It is not surprising that patterns of habitat use developed over evolutionary time should be a major force in affecting assemblage structure and recovery.

ACKNOWLEDGMENTS

We thank David Kling, Stephen Kyles, and Amy Powell for assistance with field work and laboratory analyses, Philip Dixon for statistical advice, and Tony Echelle, Peter Morin, Mary Power, Peter Sale, and two anonymous reviewers for comments that greatly improved earlier versions of the manuscript. Research was conducted under contract DE-AC09-76SR00-819 between the U.S. Department of Energy and the University of Georgia. A. L. Sheldon was supported by the SREL Faculty Research Participation Program and a University of Montana sabbatical assignment.

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