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Author(s): Andrew J. Boulton, Christopher G. Peterson, Nancy B. Grimm, Stuart G. Fisher

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STABILITY OF AN AQUATIC MACROINVERTEBRATE COMMUNITY IN A MULTIYEAR HYDROLOGIC DISTURBANCE REGIME¹

ANDREW J. BOULTON,² CHRISTOPHER G. PETERSON,³ NANCY B. GRIMM,⁴ AND
STUART G. FISHER

Department of Zoology, Arizona State University, Tempe, Arizona 85287-1501 USA

Abstract. We compared rates and directions of benthic aquatic macroinvertebrate succession following eight spates of varying magnitude that occurred in different seasons over 3 yr in Sycamore Creek, a Sonoran Desert stream. A consistent cycle of seasonal change in assemblage composition occurred each year, little altered by spates. Changes reflected variations in presence or absence rather than relative abundance of taxa. Seasonal patterns were confirmed by plotting temporal changes in densities of common taxa. Invertebrate abundance (mostly oligochaetes and mayflies) peaked in spring. “Summer” dominants included the gastropod *Physella virgata* and the caddisfly larva *Cheumatopsyche arizonensis*. Assemblage composition remained relatively consistent during spring over 3 yr when high discharge was prolonged, whereas there was a major change in autumn community structure between 1984 and 1986, probably reflecting low discharge during a drought in 1986. Drying apparently influenced assemblage composition more than spates, possibly by altering habitat availability and the intensity of biotic interactions as surface stream volume shrank.

Assemblage resistance to disturbance by spates was variable. Similarly, resistance of individual common taxa varied within and among taxa, and like assemblage resistance, was not simply a function of spate magnitude or timing (season). Resilience was generally high. Succession rate (degree of change in assemblage composition) declined during succession in all but spring sequences, which displayed no consistent trend. The two summer sequences had highest initial succession rates (in first 30 d postspate), possibly reflecting higher water temperatures, and also exhibited late-successional increases in succession rate. Spatial variation in assemblage composition was uncorrelated with any physical variable measured.

Factors known to influence ecosystem-level processes such as primary productivity (e.g., inorganic nitrogen flux, days since spate) also affected community-level aspects such as aquatic invertebrate assemblage composition in Sycamore Creek. Discharge and water temperature had lesser but detectable effects, and probably contributed to the marked seasonality in assemblage composition. Further comparisons of collective properties of ecosystems and communities within other biomes may identify “common denominators” that characterize responses to disturbance and environmental change. This will remove the different perceptions about stability we gain by using response variables that are assessed only at a community or ecosystem level.

Key words: aquatic invertebrates; community structure; disturbance; ecosystems; multivariate analyses; seasonality; spates; stability; stream; succession.

INTRODUCTION

Ecologists have recently recognized the importance of disturbance in structuring communities and ecosystems (Pickett and White 1985) including those of streams (Resh et al. 1988, Grimm and Fisher 1989), and have begun to incorporate the concept of succes-

sion into stability theory (sensu Webster et al. 1975) as a major component of resilience (Pickett et al. 1987, Fisher 1990). Most studies of succession have been largely anecdotal, based on change following single severe events such as fires or hurricanes, and have dealt with long-lived species (e.g., forest trees). Temporal sequences have been inferred by comparing sites at different successional stages (Pickett 1988). In desert streams, succession of benthic organisms occurs after intense disturbance by flash floods (Fisher et al. 1982, Grimm and Fisher 1989). As several floods may occur each year and the aquatic denizens are short lived, this obviates the need for space–time substitution (cf. Pickett 1988) and renders these systems attractive for research on succession (Fisher 1983).

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² Present address: Department of Zoology, University of Adelaide, Adelaide 5001, South Australia.

³ Present address: Natural Science Department, Loyola University of Chicago, 6525 North Sheridan Road, Chicago, Illinois 60626 USA.

⁴ Address correspondence to this author.

Grimm and Fisher (1989) described the biota's resistance (measured as change in chlorophyll *a*, ash-free dry mass, and invertebrate density and biomass) to 27 and recovery after 20 of 35 spates that occurred in a Sonoran Desert stream (Sycamore Creek, Arizona) over 3 yr. Resilience (rate of change in the same variables after flood recession) was high relative to other streams because of high biotic production in this system. They found no seasonal difference in macroinvertebrate resilience (as rate of increase or time to maximum numbers or biomass), but algal biomass increased most rapidly in summer and fall. Recovery of macroinvertebrates and algal standing crops was linear or asymptotic for most sequences, although macroinvertebrate density declined sharply during the later stages of six sequences when reductions in food quality may have accelerated mortality (Grimm and Fisher 1989).

Desert streams might be expected to fall near the "harsh" end of the continuum of habitat characteristics described by Peckarsky (1983), and hence theory would predict that they support "non-equilibrium" (*sensu* Wiens 1977) communities. Such communities are composed of species that are relatively independent of one another, have low persistence, contain populations limited primarily by abiotic factors in a density-independent manner, and possess both low resistance to disturbance and low resilience (Lake and Barmuta 1986). This view is simplistic. Given interflood periods that are long relative to the life-span of organisms in desert streams (Gray 1981), biotic interactions may intensify with time (Fisher and Grimm 1991), so that communities eventually approach the opposite extreme of Peckarsky's (1983) continuum. By analyzing temporal change in community structure of eight post-flood recovery sequences examined by Grimm and Fisher (1989), we investigated the extent to which these features of non-equilibrium communities were evident in macroinvertebrate assemblages in Sycamore Creek. We predicted these assemblages would show low resistance but high resilience to spates, and that succession rate would be initially rapid and decelerate as the assemblage recovered and stabilized. We expected variation in assemblage structure to be great at first, reflecting stochastic recolonization, decline as the assemblage developed, and then rise in response to increasing habitat complexity as diverse algal mats became established (*cf.* Fisher et al. 1982).

To understand the response of complex, natural ecosystems to disturbance, we must identify characteristic features of the ecosystem that could act as indicators of response to a known disturbance (review in Kelly and Harwell 1990). Ecologists describing the complexity of ecosystems quantify broad-scale features such as trophic biomass or energy flow and nutrient fluxes and transformations, whereas community ecologists examine finer scale properties such as assemblage composition, species diversity and evenness, species interactions, or individual species responses. Bias in our

perception of the response of an ecosystem to a disturbance inevitably stems from the scale, perspective, or observation set we adopt (Harris 1980, Levin et al. 1984, O'Neill et al. 1986). Grimm and Fisher (1989) focused on responses of collective properties of a desert stream ecosystem to spates. In this paper, we examine the same data set in terms of selected community-level properties. We employ multi- and univariate techniques to detect change in macroinvertebrate assemblage structure, describe rate and direction of postflood succession in different seasons, investigate correlations between these community parameters and other environmental features, and finally, compare results obtained from this "community-level" perspective with those from the ecosystem study. Given current recognition of the importance of scale, hierarchical level, and observation set for generating meaningful conclusions from ecological studies (e.g., O'Neill et al. 1986, Wiens 1989), we specifically wished to address the following questions: Do variables that explained most of the variance observed in collective, whole-system attributes (Grimm and Fisher 1989) account for as much variance in community attributes? Do aspects of disturbance (e.g., magnitude, frequency, timing) that influenced ecosystem properties have equivalent effects upon some properties of aquatic macroinvertebrate communities in this stream?

METHODS

Study area

Eight postspate sequences were tracked over 3 yr (Table 1) in a 100-m gravel-bed run in Sycamore Creek, a desert stream in central Arizona with spatially intermittent flow. Substrata were uniformly sorted fine gravel and coarse sand; such runs comprised 45–60% of stream length during the study (the remainder was cobble-boulder riffles and deep pools). Modal stream flow is low (0.01–0.05 m³/s in summer; 0.1–0.5 m³/s in winter), but is punctuated by summer flash floods when discharge rises (up to several orders of magnitude greater than base flow) and falls within hours, and by less abrupt winter spates generated by prolonged rains. Water temperature averages 20°–30°C in summer and 10°–20°C in winter. Details of the climate, hydrology, and morphology of Sycamore Creek are published elsewhere (Thomsen and Schumann 1968, Grimm and Fisher 1989).

Field and laboratory methods

Five macroinvertebrate samples were collected along the reach as soon as possible after each spate (3–10 d) and approximately weekly thereafter (Table 1) by using a corer (80 cm²) inserted 10 cm into the substratum. Enclosed sediments were removed and elutriated through 250- μ m mesh. Animals were fixed in 10% formalin, then sorted, identified to order (Oligochaeta, Hydracarina), family (some Diptera), genus (Tipulidae,

TABLE 1. Characteristics of the eight postflood recovery sequences examined in Sycamore Creek, a Sonoran Desert stream. Ellipses denote missing data.

Sequence	Flood date	Previous interflood interval (d)	Peak discharge, Q_{\max}		Preflood sample (d before flood)	First postflood sample (d after flood)	Sequence length (d)	Season
			Previous flood (m^3/s)	Present flood (m^3/s)				
1	3 Oct 1984	7	0.5	0.5, 0.3*	14	8	41	F
2	21 Feb 1985	26	...	10.0	...	6	158	Sp, S
3	1 Aug 1985	158	10.0	6.3	2	4	47	S, F
4	25 Nov 1985	57	1.7	9.9	11	7	70	F, W
5	17 Mar 1986	6	11.4	26.0	13	10	145	Sp, S
6	23 Jul 1986	127	26.0	2.4	1	5	81	S, F
7	11 Oct 1986	80	2.4	1.0	3	3	38	F
8	28 Feb 1987	29	1.1	4.8	...	10	150	Sp, S

* Sequence initiated by two floods occurring over a 2-d period.

Cryptolabis sp.; Ceratopogonidae, *Probezzia* sp.) or species (Gastropoda, *Physella virgata* Gould; Trichoptera, *Helicopsyche mexicana* Banks and *Cheumatopsyche arizonensis* Ling; Ephemeroptera, *Fallceon quillieri* Dodds, *Leptohyphes packeri* Allen, and *Tricorythodes dimorphus* Allen), and enumerated. For brevity, species will be referred to hereafter by genus.

Stream discharge was computed as the product of cross-sectional area and mean current velocity. Peak discharge (Q_{\max}) was estimated by measuring distance between high-water marks, depths to substratum surface from a tape stretched between these marks, and using the Manning equation (Richards 1982) to estimate velocity as a function of slope and bed roughness (see Grimm and Fisher 1989). Measurement of variables analyzed by Grimm and Fisher (1989) and further examined here is described fully in that paper. Briefly, water temperature measurements were taken as spot measures using a mercury thermometer; chlorophyll *a* was sampled in a patch-weighted fashion, extracted in methanol, and assayed spectrophotometrically; and inorganic nitrogen (N) flux was calculated as the product of ammonium-N + nitrate-N concentrations and stream discharge.

Data reduction and analysis

Eight postspate sequences were selected from the larger data set of Grimm and Fisher (1989) because they were relatively long (>30 d), spanned all seasons and a range of flood magnitudes (Table 1), and contained nearly complete sets of invertebrate samples. Our sequences 1–8 correspond to sequences 4S, 5, 7, 11, 12, 15, 17, and 19, respectively, of Grimm and Fisher (1989). Only the 12 most common taxa consistently encountered in samples across these sequences were used in the analyses (i.e., those occurring in nearly all, seven or eight, sequences and in >30% of samples from at least two sequences); rare species were discarded to reduce “noise” (sensu Gauch 1982) capable of distorting results. Many studies have shown that most information on community structure can be derived from common taxa (review in Gauch 1982, Boul-

ton 1988, Marchant 1990). Although common, dragonfly nymphs were omitted from analyses because they were inadequately sampled using cores.

Multivariate analyses

To detect gross annual and seasonal patterns, we ordinated the data using detrended correspondence analysis (DCA, Hill and Gauch 1980) run with DECORANA (Hill 1979), and hybrid nonmetric multidimensional scaling (HMDS, Faith et al. 1987) performed with the KYST subroutine in ECOPAK (Minchin 1986). Before ordination, all data were $\log_{10}(x + 1)$ transformed. DECORANA employs a chi-squared dissimilarity measure (Chardy et al. 1976) and generates ordination scores for only four axes. When using HMDS, we opted for the recommended dissimilarity measure (Kulczynski) and threshold (0.8) (Faith et al. 1987, Minchin 1987), and used 10–20 random starting configurations. We selected the appropriate number of dimensions based on Procrustean analysis of root mean squares of residuals of the starting configurations (Schönemann and Carroll 1970) and the inflection of the curve of stress plotted against dimension number. Analysis of the total data set by HMDS was restricted by the high number of comparisons with large dissimilarities. Rather than lower the dissimilarity threshold below 0.8, we removed the single “winter” sequence (sequence 4) and ran HMDS on the smaller, 338-sample matrix. To determine whether patterns evident from the ordinations were due to changes in species representation or species abundance, we also ran the analysis on presence/absence data.

Seasonal variation in community structure

Variables that influenced collective ecosystem properties in Sycamore Creek (Fisher and Grimm 1988, Grimm and Fisher 1989) were superimposed on ordination plots to detect nonlinear trends in ordination space. These variables included season (i.e., spring, summer, autumn, winter), water temperature, ambient discharge, algal standing crop (as chlorophyll *a*), inorganic N flux, successional age (days postspate), max-

imum discharge of present spate, and maximum discharge of previous spate. To taxonomically characterize sample clusters, we superimposed species abundances on the HMDS plot; as DCA simultaneously ordines species and samples, species scores were plotted directly in sample dissimilarity space. Pearson product-moment correlations (Zar 1984) were computed between three dependent variables (succession rate and ordination scores on the first two DCA axes) and ambient discharge, nitrogen flux (both \ln transformed), chlorophyll *a*, days postspate, and water temperature. As many of these independent variables were intercorrelated, we calculated partial correlations (Zar 1984) to correct for this.

Mean abundances of each taxon were plotted with time (September 1984–August 1987) to ascertain whether gross seasonal patterns in abundance occurred despite the impact of spates. Additional data available between sequences 7 and 8 were included in these plots. We examined seasonal differences using one-way ANOVAs on log-transformed data, and used Scheffé's multiple-comparison test to determine differences among means (Day and Quinn 1989). Because of large annual differences in total numbers, changes in the *relative* abundance of common taxa among years and within seasons were similarly assessed (after arcsine transformation, Zar 1984).

Resistance and succession rate

To examine resistance to spates, we compared displacements of invertebrate assemblage structure before and after spates using distances (standardized for elapsed time) between the pre- and postdisturbance centroids on ordination plots. Resistance of individual taxa was estimated for each sequence by comparing mean abundances before and after each spate using *t* tests on log-transformed data. If these differences were not significant ($P > .10$), we considered the taxon resistant. We used $\alpha = .10$ because this allowed us to assess reductions of $>75\%$ in individual taxa that had low but highly variable pre-flood densities. These comparisons were conducted for 12 events for which we had pre- and postspate data; successional sequences after some spates lasted <3 wk and contained too few sampling dates for other analyses.

Successional trajectories were derived by computing the centroid (as the arithmetic mean of ordination scores on each axis) of each group of five replicate samples and linking consecutive centroids (e.g., Boulton and Lake 1992). Distances between consecutive centroids estimated temporal change in community composition (in two dimensions) and were standardized to give daily succession rates that could be compared among sequences and seasons on the same ordination plot. These standardized rates were plotted against days postspate to examine temporal change in succession rate among seasons and sequences. Seasonal effects were assessed by testing for differences (pooled by season) of rates

during the first 30 d postflood using a one-way ANOVA on log-transformed data, followed by Scheffé's tests. To examine the effect of temperature upon succession rate, we converted rates using degree-days, and reran the ANOVA on temperature-corrected data.

Spatial and sequence-specific variation

We estimated variation in assemblage structure on each sampling date by computing the standard error of sample scores of the five replicates about their centroid as the sum of standard errors about the means on Axes I and II. This variation was then plotted against successional time to detect temporal changes in spatial variation of assemblage structure. Sequence-specific patterns were examined in detail by plotting changes in succession rate, total numbers of individuals, and densities of two of three taxa identified by multivariate analyses as characteristic of particular clusters (*Fall-ceon*, *Physella*, and *Helicopsyche*) with time since flood. We compared these changes with simultaneous changes in log discharge, log inorganic N flux, and benthic chlorophyll *a*. These analyses enabled us to determine if variables shown to be important at the ecosystem level (Grimm and Fisher 1989) also influenced macroinvertebrate community structure.

RESULTS

Annual and seasonal patterns in community structure

Ordination analyses.—A broad seasonal cycle in community-structural change over 3 yr was evident on the first two axes of both DCA and HMDS plots (Fig. 1). Samples collected in spring 1985, 1986, and 1987 shared relatively low scores on Axes I and II whereas summer samples were more variable, and many possessed high scores on both axes. Spring samples contained high densities of mayflies, water mites, stratiomyid larvae, and *Cryptolabis*. *Helicopsyche* and *Cheumatopsyche* shared high scores on Axis II, typifying summer samples from sequences 3 (1985) and 5 (1986). Summer samples with low Axis I scores contained many *Physella*, and were primarily from recovery sequence 8 (1987) (see Fig. 2).

Winter (sequence 4) and spring samples formed a cluster, sharing many common taxa. Fall 1984 samples (sequence 1) also lay in the spring cluster whereas samples from fall 1985 (sequence 3) and 1986 (sequence 7) had higher Axis I scores, shared few species with spring samples, and contained more *Physella*. While consistent seasonal sequences in assemblage composition change were evident each year, there was considerable annual variation within seasons, especially fall (Fig. 1).

Superimposing abiotic variables upon ordination plots revealed no systematic relationships for maximum spate discharge, maximum discharge of the previous spate, or sequence length, although these were

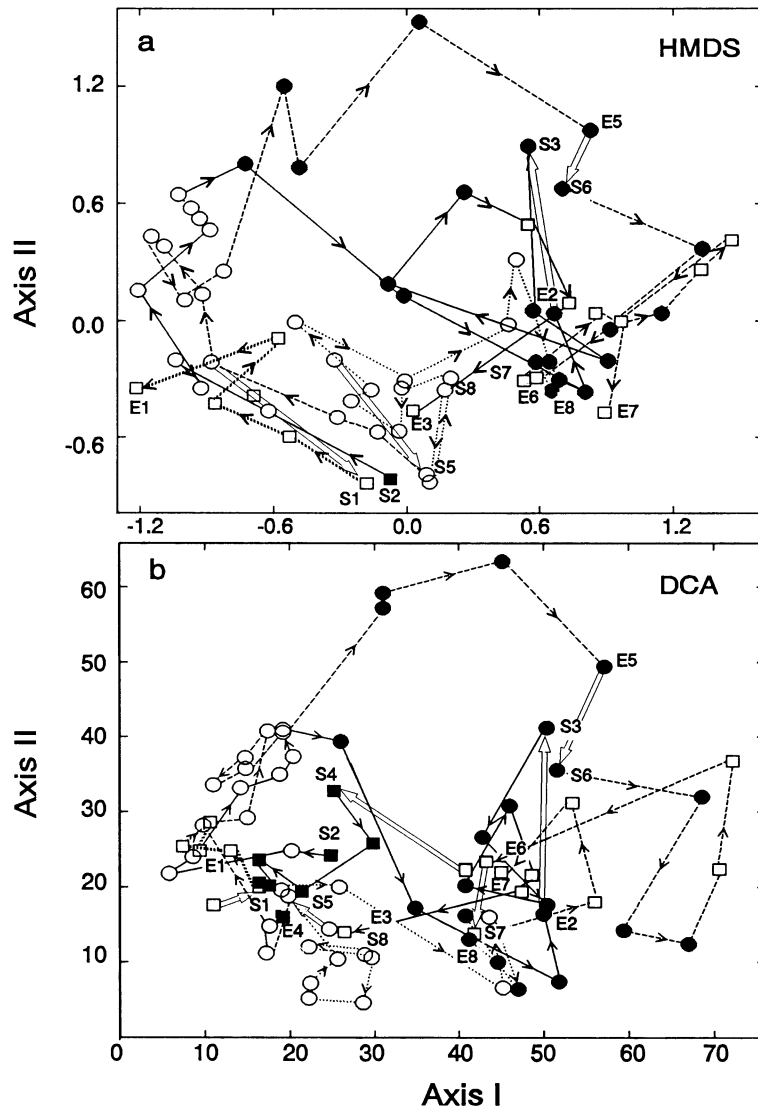


FIG. 1. Ordination plots of the first two dimensions of HMDS (a) and DCA (b) ordinations of faunal samples from seven and eight postflood recovery sequences, respectively, in an Arizona desert stream. Winter samples (recovery sequence 4) were omitted from the HMDS (see *Methods: Multivariate analyses*). Seasons are differentiated by symbols as follows: ○ spring, ● summer, □ fall, and ■ winter. Consecutive centroids are linked by (1984), — (1985), --- (1986), and ····· (1987). Preflood and earliest postflood samples are linked by open arrows; arrow length is a measure of resistance (see *Results: Resistance and resilience to floods*). S and E mark the start and end, respectively, of each recovery sequence.

predictably related to season. Ordination scores on DCA Axis II were not correlated with any physical variable (Table 2). Axis I scores correlated negatively with discharge and nitrogen flux and positively with temperature and chlorophyll *a*. Partial correlations of abiotic variables with Axis I scores were negative for nitrogen flux and days postspate and positive for benthic chlorophyll *a*. Succession rate was negatively correlated with nitrogen flux and days postspate (Table 2).

Ordination of presence/absence data yielded similar solutions in two dimensions; seasonal cycles persisted on these plots (not presented for brevity). We conclude

that major annual and seasonal changes in assemblage composition reflected changes in species representation more than changes in relative abundance.

Direct gradient analyses.—Seasonal patterns in community structure evident from multivariate plots were due to seasonal differences in abundance of many common invertebrate taxa (Fig. 2, Table 3). Total invertebrate numbers were highest in spring; spring dominants included *Falleon*, *Tricorythodes*, and oligochaetes (Table 3). Chironomid larvae were most common in spring and winter and least common in summer. Summer dominants included *Cheumatopsyche*, *Helicopsy-*

TABLE 2. Total and partial correlation coefficients relating the dependent variables (ordination score on DCA axis 1, ordination score on DCA axis 2, and succession rate) to five independent variables. *p* = probability that correlation coefficient equals zero. Coefficients significant at $\alpha = .05$ level are bold-faced.

Independent variables		Axis 1 scores		Axis 2 scores		Succession rate	
		Total	Partial	Total	Partial	Total	Partial
Discharge*	<i>r</i>	-0.422	-0.145	-0.189	-0.134	-0.237	-0.082
	<i>P</i>	.001	.422	.128	.284	.083	.552
Temperature	<i>r</i>	0.362	-0.212	0.202	0.139	0.271	0.163
	<i>P</i>	.002	.087	.091	.264	.036	.234
Chlorophyll <i>a</i>	<i>r</i>	0.553	0.437	0.131	-0.015	-0.013	-0.197
	<i>P</i>	<.001	<.001	.270	.903	.918	.150
N flux*	<i>r</i>	-0.664	-0.595	-0.068	0.161	-0.308	-0.320
	<i>P</i>	<.001	<.001	.576	.195	.017	.017
Days postspate	<i>r</i>	0.150	-0.372	0.178	0.171	-0.252	-0.347
	<i>P</i>	.196	.002	.126	.170	.045	.010

* In-transformed.

che, and *Physella*. Only *Leptohyphes* showed no consistent seasonal variation in abundance (Fig. 2, Table 3).

Most taxa exhibited significant interannual differences in abundance (Fig. 2, Table 4) reiterating results from the ordinations (Fig. 1). Summer dominants were particularly common in 1986 and numbers of many taxa declined sharply in 1987 (Fig. 2). Densities of the tipulid *Cryptolabis* were high only in 1985. Although

spates reduced total density, these events had little effect on seasonal patterns in invertebrate abundance and community composition across years (Fig. 2).

Relative densities differed among years within seasons (Table 4). For example, the three mayfly taxa common in spring 1985 and 1986 virtually disappeared in spring 1987. Conversely, relative abundance of *Physella* across all seasons, and chironomids in spring and summer, rose from 1985 to 1987. *Cryptolabis* was

TABLE 3. Seasonal differences in abundances (individuals/m²) of all taxa (total) and 12 common taxa in an Arizona desert stream.

Taxon		Spring (Sp)	Summer (Su)	Fall (F)	Winter (W)	<i>F</i> (prob.)*	Comparison of seasons†
Total	\bar{X}	45 128	20 710	25 338	35 304	18.30	Sp <u>W</u> Su F
	SE	3056	1864	4536	5801	<.001	
Hydracarina	\bar{X}	803	530	594	877	6.59	Sp <u>W</u> Su F
	SE	85	96	135	231	<.001	
<i>Fallceon</i>	\bar{X}	2235	1058	510	265	10.69	Sp <u>W</u> Su F
	SE	457	277	143	94	<.001	
<i>Cheumatopsyche</i>	\bar{X}	840	935	61	92	9.50	Su <u>W</u> Sp F
	SE	279	301	21	44	<.001	
Chironomidae	\bar{X}	15 162	1883	8429	20 833	48.96	Sp <u>W</u> F Su
	SE	1545	348	1429	3447	<.001	
<i>Cryptolabis</i>	\bar{X}	1443	1536	150	73	6.81	Sp <u>Su</u> F W
	SE	443	463	66	23	<.001	
<i>Helicopsyche</i>	\bar{X}	211	1390	303	83	5.67	Su <u>W</u> Sp F
	SE	47	297	119	16	.002	
<i>Leptohyphes</i>	\bar{X}	885	120	179	227	1.66	Sp Su F W
	SE	25	25	74	183	.176	
Oligochaeta	\bar{X}	21 119	7742	12 492	9862	17.57	Sp F Su W
	SE	1824	1259	3341	2802	<.001	
<i>Physella</i>	\bar{X}	191	1789	1156	260	48.39	Su F W Sp
	SE	49	292	462	53	<.001	
<i>Problezzia</i>	\bar{X}	1031	1013	571	1348	14.73	Sp <u>W</u> Su F
	SE	105	144	134	344	<.001	
Stratiomyidae	\bar{X}	334	369	24	108	13.79	Sp <u>Su</u> W F
	SE	53	125	8	40	<.001	
<i>Tricorythodes</i>	\bar{X}	798	227	82	123	32.98	Sp <u>Su</u> W F
	SE	106	87	27	45	<.001	

* Probabilities (*P*) that abundances do not differ among seasons are presented below *F* values (ANOVA) on In-transformed data.

† Seasons that do not differ ($\alpha = .05$ level) in mean abundance are underlined (seasons listed from highest to lowest In-transformed means).

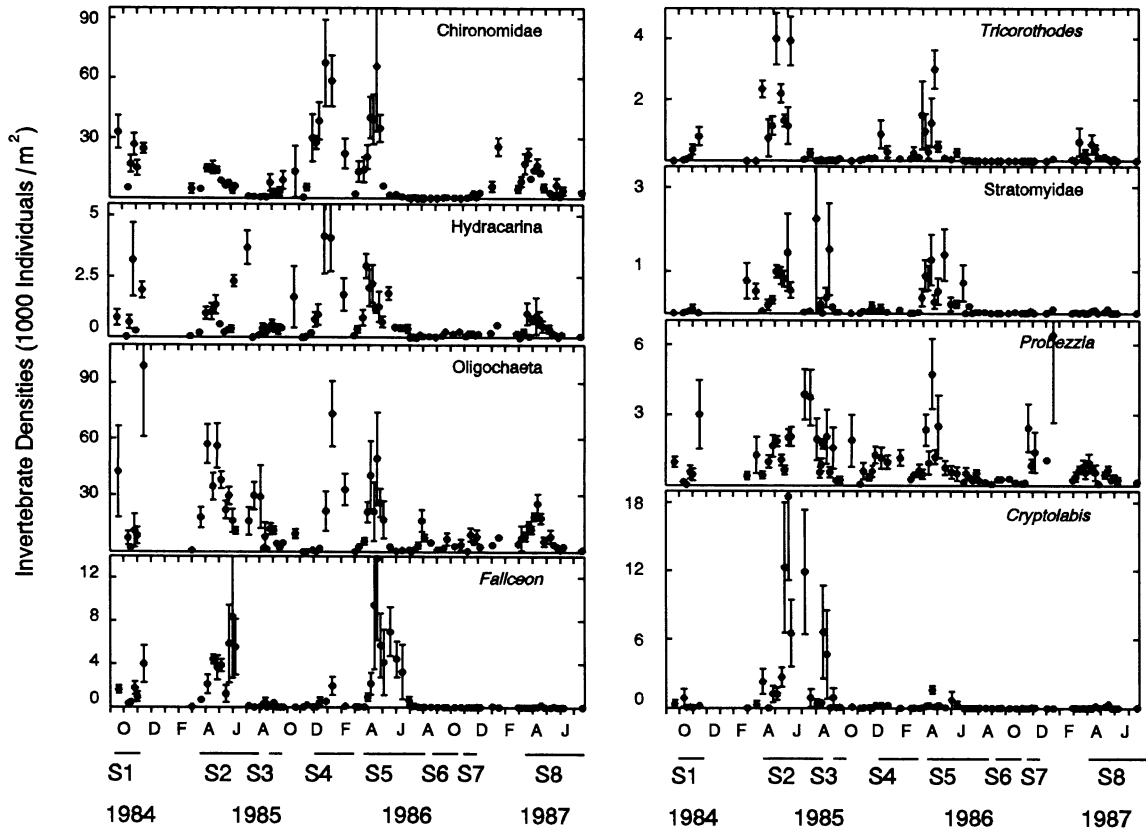


FIG. 2. Seasonal changes in abundance (mean \pm 1 SE) of Chironomidae, Hydracarina, Oligochaeta, *Fallceon*, *Tricorythodes*, Stratiomyidae, *Probezzia*, *Cryptolabis*, *Cheumatopsyche*, *Helicopsyche*, *Physella*, and *Leptohyphes* during eight postflood recovery sequences (S1–S8).

common in spring, summer, and fall of 1985 but contributed <1% to the total invertebrate standing stock in other years (Table 4).

Resistance and resilience to floods

Resistance.—Displacement of invertebrate assemblage structure (as distance between centroids of pre- and immediate postspate samples) varied substantially

and was unrelated to season (Fig. 1). Nonetheless, except for sequence 4, these displacements were too small to traverse seasonal boundaries (Fig. 1). Total invertebrate density declined significantly after spates of 0.3–26.0 m³/s but not after others of a similarly wide range of peak discharges, indicating that spate magnitude had little bearing on whether total densities fell (Table 5).

Resistance of individual taxa was not a simple func-

TABLE 4. Mean relative abundances (%) of common taxa among years within seasons, in Sycamore Creek, Arizona, fall 1984–summer 1987. Annual means within a given season that do not differ significantly ($\alpha = .05$, Scheffé multiple comparison) are identified with similar superscript letters.

Taxon	Spring			Summer			Fall
	1985 (n = 40)	1986 (n = 49)	1987 (n = 55)	1985 (n = 45)	1986 (n = 42)	1987 (n = 20)	1984 (n = 30)
Hydracarina	1.04 ^a	3.48 ^b	2.03 ^a	3.42 ^a	1.67 ^a	1.38 ^a	2.29 ^a
<i>Fallceon</i>	5.91 ^a	5.35 ^a	0.30 ^b	2.16 ^a	6.71 ^b	0.00 ^a	3.43 ^a
<i>Cheumatopsyche</i>	1.44 ^{ab}	1.66 ^a	0.17 ^b	1.63 ^a	8.41 ^b	0.00 ^a	0.04 ^a
Chironomidae	16.39 ^a	50.34 ^b	40.90 ^b	8.48 ^a	3.49 ^a	33.16 ^b	55.05 ^a
<i>Cryptolabis</i>	8.17 ^a	0.39 ^b	0.52 ^b	10.81 ^a	0.33 ^b	0.22 ^b	0.71 ^a
<i>Helicopsyche</i>	1.10 ^a	0.22 ^b	0.07 ^b	2.36 ^a	15.79 ^b	0.28 ^a	0.16 ^a
<i>Leptohyphes</i>	0.32 ^a	0.14 ^{ab}	0.08 ^b	0.57 ^a	0.73 ^a	0.00 ^b	0.55 ^a
Oligochaeta	56.53 ^a	30.75 ^b	42.08 ^c	37.81 ^a	27.12 ^a	29.80 ^a	32.67 ^a
<i>Physella</i>	0.05 ^a	0.02 ^a	3.60 ^b	8.34 ^a	18.09 ^a	16.65 ^a	0.06 ^a
<i>Probezzia</i>	3.02 ^a	3.42 ^a	2.90 ^a	9.80 ^a	2.61 ^b	6.16 ^b	1.17 ^a
Stratiomyidae	1.55 ^a	0.54 ^b	0.16 ^c	1.44 ^a	1.92 ^a	0.00 ^b	0.10 ^a
<i>Tricorythodes</i>	2.88 ^a	1.69 ^a	0.85 ^b	1.08 ^a	0.28 ^a	0.94 ^a	0.45 ^a

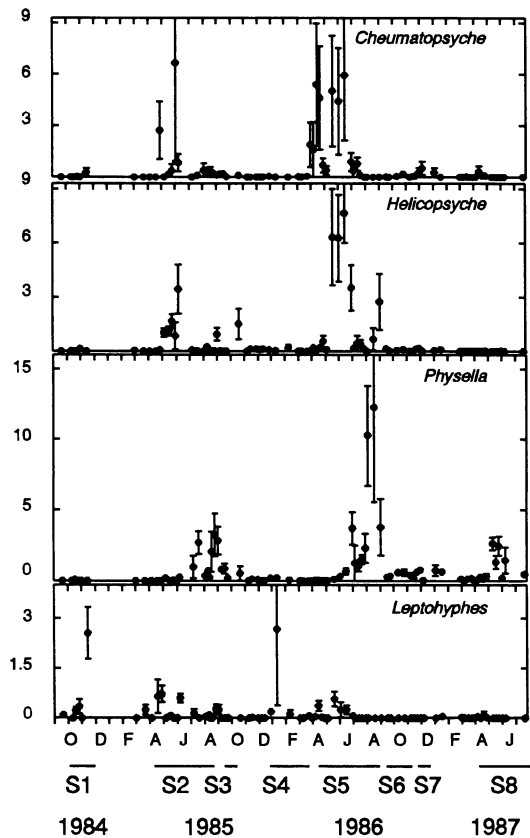


FIG. 2. Continued.

tion of flood magnitude. For example, the spate that initiated sequence 6 (2.4 m³/s) reduced densities of water mites, chironomids, and stratiomyids, whereas two other events of similar magnitude (3.3 and 2.4 m³/s) did not reduce densities of these taxa (Table 5). Resistance, as detected by these measures, reflected initial density; variance at low density probably masked many declines in abundance. Resistance to floods of different magnitude and timing also varied within and

TABLE 4. Continued.

Fall		Winter		
1985 (n = 15)	1986 (n = 45)	1985 (n = 25)	1986 (n = 30)	1987 (n = 10)
3.65 ^a	3.18 ^a	0.85 ^a	2.24 ^b	1.38 ^a
0.25 ^b	0.02 ^b	1.31 ^a	0.66 ^a	0.16 ^a
2.60 ^b	0.28 ^a	0.00 ^a	1.43 ^a	0.57 ^a
29.06 ^b	7.89 ^c	66.59 ^a	40.81 ^b	49.71 ^b
3.02 ^b	0.34 ^a	0.12 ^a	0.43 ^b	0.00 ^a
0.08 ^a	5.15 ^b	0.67 ^a	0.66 ^a	0.22 ^a
0.00 ^b	0.00 ^b	0.05 ^a	0.29 ^a	0.04 ^a
37.12 ^a	50.65 ^b	9.74 ^a	35.59 ^b	27.11 ^b
11.31 ^b	16.58 ^b	0.48 ^a	2.39 ^b	3.10 ^b
6.01 ^a	4.09 ^a	5.96 ^a	7.32 ^a	12.31 ^a
1.24 ^b	0.10 ^a	2.67 ^a	0.07 ^b	0.09 ^{ab}
0.23 ^a	0.00 ^b	0.68 ^a	0.27 ^a	0.09 ^a

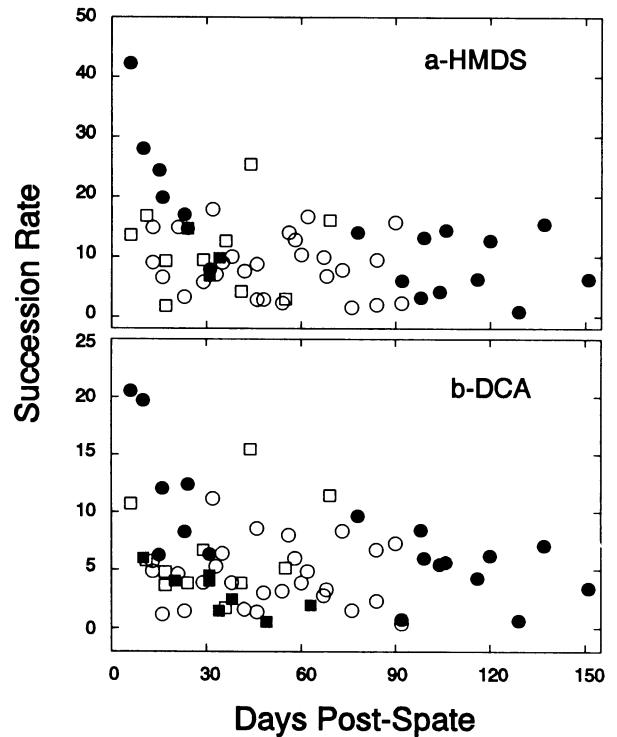


FIG. 3. Succession rates, estimated as distances between consecutive centroids, derived from HMDS (a) and DCA (b) ordination plots of invertebrate taxon abundances plotted against days since flood of an Arizona desert stream. Symbols as in Fig. 1.

among taxa. Oligochaetes, the most common taxon, had low resistance to several spates; however, oligochaete density actually increased after two spates. Of taxa examined, oligochaetes and water mites appeared most sensitive to spates (Table 5).

Resilience.—Highly resilient assemblages recover rapidly to predisturbance composition. The trajectory of a resilient assemblage displaced by a spate should turn back on itself, converging with the centroid of pre-flood samples. This occurred for five of six sequences for which we had pre-flood data (Fig. 1b), although the degree of resilience varied from sharp recovery trajectories (e.g., sequence 3) to recovery into only the broad general area of pre-flood samples (e.g., sequences 4 and 5). Sequence 6, for which the earliest post-flood samples were taken 13 d after the event, showed little recovery to pre-flood assemblage composition (Fig. 1). We emphasize these recovery trajectories were examined only in the first two dimensions that together explained most of the variance (>70% of DCA axes I–IV), and that they depend heavily on time elapsed between the flood and the first post-flood collections.

Succession rates, measured as distance between temporally consecutive centroids, were similar in relative magnitude between ordination plots (Fig. 3). Time since spate and succession rate were unrelated, except after

TABLE 5. Taxa exhibiting significant changes in density across 12 flood events of an Arizona desert stream. Significance of density change across spates was tested using *t* tests. *P* = probability that pre- and postdisturbance densities do not differ.

Flood date	Se- quence no.	Peak dis- charge, Q_{max} (m^3/s)	Pre- vious inter- flood inter- val (d)	Pre- flood Sam- pling (d before flood)	Post- flood sam- pling (d after flood)	Taxon	% change	<i>P</i>
8 Aug 1984	...	23.4	19	9	2	Hydracarina	-100	.078
						Oligochaeta	+1476	.020
26 Sep 1984	1	0.5	26	14	7	Total numbers	-81.6	.007
3 Oct 1984		0.3				Hydracarina	-97.0	.009
						<i>Fallceon</i>	-78.5	.072
						Chironomidae	-84.1	.001
						Oligochaeta	-82.6	.057
						<i>Probezzia</i>	-84.6	.057
1 Aug 1985	3	6.3	158	2	4	Total numbers	-82.6	.072
						Hydracarina	+275	.085
						<i>Helicopsyche</i>	+	.001
						Oligochaeta	-92.5	.084
						<i>Physella</i>	+100	.084
17 Sep 1985	...	1.7	19	1	2	Chironomidae	-98.1	.012
						<i>Helicopsyche</i>	+	.071
25 Nov 1985	4	9.9	57	11	7	Total numbers	-97.5	.001
						Hydracarina	-100	.047
						<i>Helicopsyche</i>	-100	.006
						Oligochaeta	-97.9	.011
						<i>Probezzia</i>	-97.4	.001
15 Feb 1986	...	8.5	81	11	3	Total numbers	-96.5	.001
						Hydracarina	-100	.017
						Chironomidae	-95.6	.001
						<i>Leptohyphes</i>	-97.2	.017
						Oligochaeta	-98.2	.001
						<i>Probezzia</i>	-74.4	.092
						<i>Tricorythodes</i>	-100	.076
17 Mar 1986	5	26.0	6	4	10	Total numbers	-94.8	.001
						Hydracarina	-95.8	.002
						Chironomidae	-90.1	.022
						Oligochaeta	-98.9	.001
						<i>Probezzia</i>	-78.3	.043
23 Jul 1986	6	2.4	127	1	5	Hydracarina	-100	.018
						Chironomidae	-100	.074
						Stratiomyidae	-100	.075
10 Oct 1986	7	1.0	80	3	3	<i>Helicopsyche</i>	-83.3	.056
19 Nov 1986	...	3.3	39	1	6	Total numbers	+466	.054
						Hydracarina	+250	.078
						Oligochaeta	+704	.018
7 Dec 1986	...	2.4	18	5	2	<i>Cryptolabis</i>	+	.071
10 Dec 1986	...	4.9	3	1	6	<i>Helicopsyche</i>	-100	.073
						<i>Physella</i>	-96.7	.004

* Taxon present in postflood samples but not pre-flood samples.

summer spates when initial changes in assemblage structure were swift and declined as postspate succession progressed (Fig. 3). Seasonal differences in succession rates were significant ($F_{3,16} = 8.14$, $P = .002$; summer > all other seasons) during the first 30 d of recovery, the period for which we had data for all sequences and seasons. Beyond 30 d, all seasons were never fully represented because our longer sequences extended through spring and summer (Fig. 3, Table 1). After standardizing succession rates for temperature (expressed as degree-days), these differences became less significant ($F_{3,15} = 4.55$, $P = .019$). (The difference

in degrees of freedom reflects a missing temperature datum.)

Sequence-specific variation.—Sequence-specific variation precludes generalizations other than those concerning seasonality. Thus, we grouped sequences by season to examine sequence-specific community-level responses to variables influential at the ecosystem level. Discharge and N flux differed significantly only between the two fall sequences (Fig. 4); multivariate analyses suggested that N flux influenced changes in community structure (Table 2). Community-level change was particularly evident during the fall season

across years (Fig. 1), and discharge was significantly lower in fall 1985 and 1986 than in fall 1984 ($P < .001$). Total invertebrate density remained low during sequence 7 at a time when discharge averaged $<0.01 \text{ m}^3/\text{s}$, and N flux was low. In these respects, sequence 7 resembled summer sequences more than the other fall (1984) sequence (Fig. 4).

Chlorophyll *a* and total invertebrate numbers rose sharply during the first 60 d postflood except when discharge was low (two summer sequences and sequence 7; Fig. 4). Numbers of *Fallceon* and the grazers *Helicopsyche* and *Physella* were generally low in autumn and winter, despite relatively high chlorophyll *a* standing crop, whereas in summer (*Physella*) and spring (*Helicopsyche*), grazer densities increased (Fig. 4). *Fallceon* and *Helicopsyche* were rare during sequence 8 (1987), which followed a prolonged period of drying (summer–fall 1986).

Sequence-specific patterns in succession rate and spatial variability (as standard error around centroids) were not correlated with season (Fig. 5) or with changes in other environmental variables (Fig. 4). Our prediction that succession rates would be initially rapid and then decelerate was supported for autumn and winter sequences. Both summer sequences had rapid initial rates that slowed, then increased. Spring sequences were extremely variable and shared no consistent pattern (Fig. 5). These temporal changes in spatial variability did not match our prediction that variability would be initially high due to stochastic recolonization, decline as assemblages developed, and then rise in response to biotic interactions. Instead, the considerable variation observed (Fig. 5) was not significantly correlated with succession rate or any other variable we examined.

DISCUSSION

Community stability to flash flooding

The devastating impacts of flash floods upon biota in desert streams are well known (Fisher et al. 1982, Fisher and Grimm 1988, Grimm and Fisher 1989). Spates competent to move substrata can reduce total invertebrate densities by 98% (Fisher et al. 1982), “re-setting” successional trajectories that may then proceed uninterrupted for longer periods than in mesic streams (Fisher 1986, Grimm and Fisher 1989). At the community level, we found that assemblage composition is influenced more by seasonal and annual differences than by spates, although the variance in taxon-specific response is great. Based on successional trajectories derived from two ordinations, resilience of community structure following spates was generally high. Resistance varied considerably but was also often high. In Sycamore Creek, spates rarely displaced assemblage structure (cf. Westman 1978, Malanson and Trabaud 1987) into a region outside that typical of the season when the flood occurred, even when the disturbance occurred after interflood periods of up to 5 mo.

Taxon-specific differences in resistance were unrelated to flood magnitude. A large ($23.4 \text{ m}^3/\text{s}$) spate in August 1984 had a detectable negative impact on only one common invertebrate taxon. Less than 2 mo later, two consecutive smaller spates (0.5 and $0.3 \text{ m}^3/\text{s}$) below the threshold for substratum mobilization (Grimm and Fisher 1989) decimated the invertebrate community. These contrasting responses may reflect temporal variation in the stability of benthic algal mats that provide haven and food resource for many invertebrates, especially in Sycamore Creek where primary production is high (Fisher et al. 1982, Fisher 1986).

Recent flood history affects algal community resistance to subsequent spates (Stevenson 1990, Peterson and Stevenson 1992). After spates in Sycamore Creek, a succession of algal patch types, varying in morphology and hence in resistance (Power and Stewart 1987, Grimm and Fisher 1989, Peterson and Stevenson 1992), results in temporal variation in invertebrate community resistance. In summer 1990, dense late-successional mats harbored many invertebrates and were highly resistant to summer spates (C. G. Peterson, unpublished data). By mid-fall, these mats had degenerated to a flocculent benthic layer readily suspended by turbulence. Minor increases in discharge would disrupt these invertebrate refugia, likely reducing invertebrate densities as observed after small spates in Sycamore Creek in September 1984. Thus, algal community composition may directly affect the stability of invertebrate habitat, and hence invertebrate community resistance.

The marked seasonality and high (although variable) resistance of invertebrate community structure contrasts with the findings of Grimm and Fisher (1989) who reported that collective ecosystem-level attributes, such as benthic organic matter, benthic chlorophyll *a*, and total invertebrate density, exhibited little resistance to spates above a threshold magnitude, and little seasonality. High resistance at the community level (as assemblage composition) observed in the present study may be due to (1) equal susceptibility of all taxa to disturbance, (2) equal recolonization abilities, and/or (3) a limited suite of available colonists in each season, thus maintaining the observed marked seasonality in assemblage structure. These hypotheses require experimental testing and further information on life histories of the common taxa in Sycamore Creek.

Alternatively, apparently high resistance at the community level may reflect an inverse relationship between resistance and resilience among individual taxa, and our inability to detect which mechanism explains the presence of each. There are practical difficulties in obtaining data immediately before or after a spate. The longer the period between the spate and first postflood sampling date, the greater the difficulty in separating components of resistance and resilience. This is especially important when the biota of interest develop rapidly as in Sycamore Creek (Gray 1981). Although this problem is less severe in analysis of postfire plant

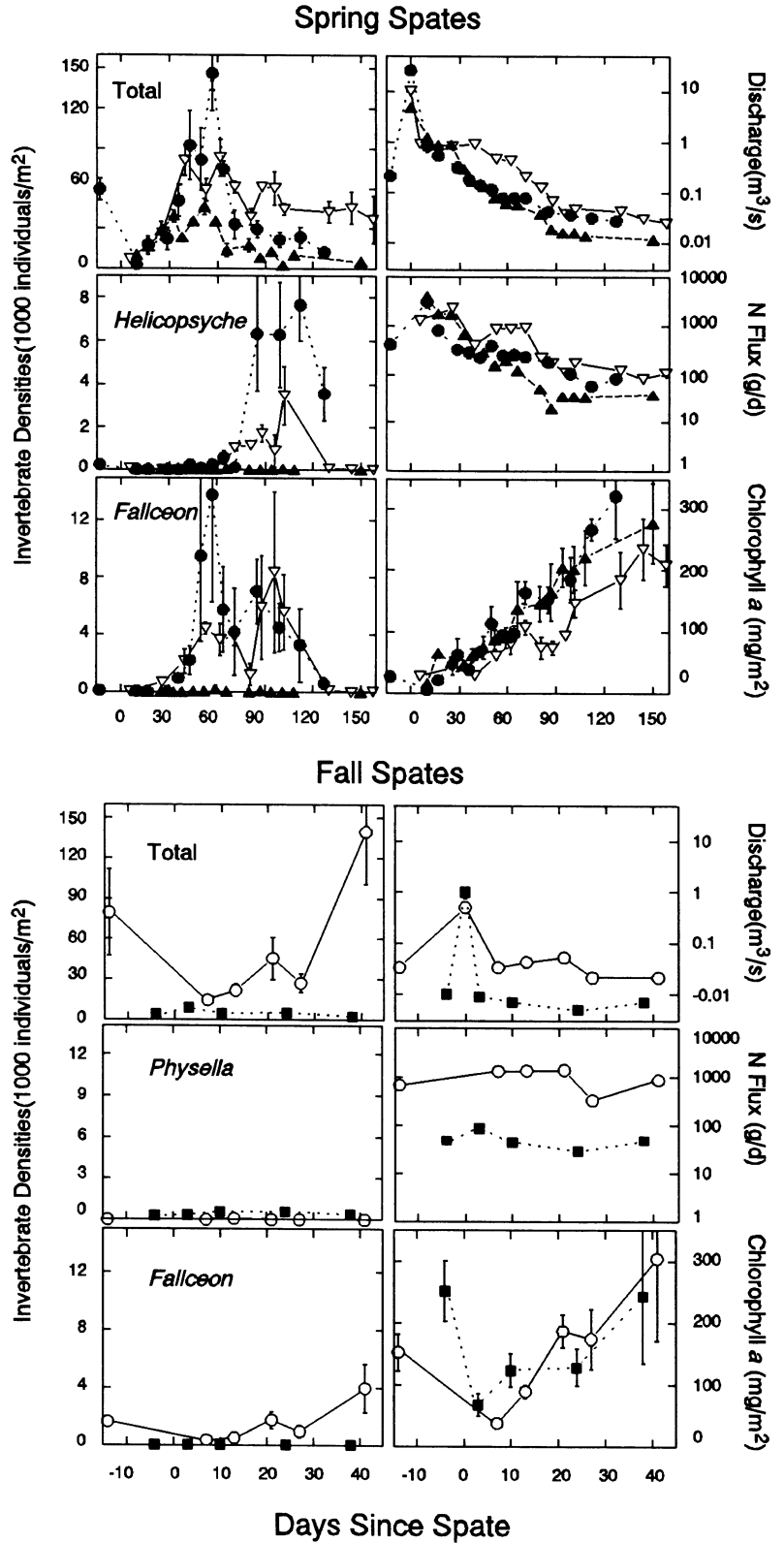
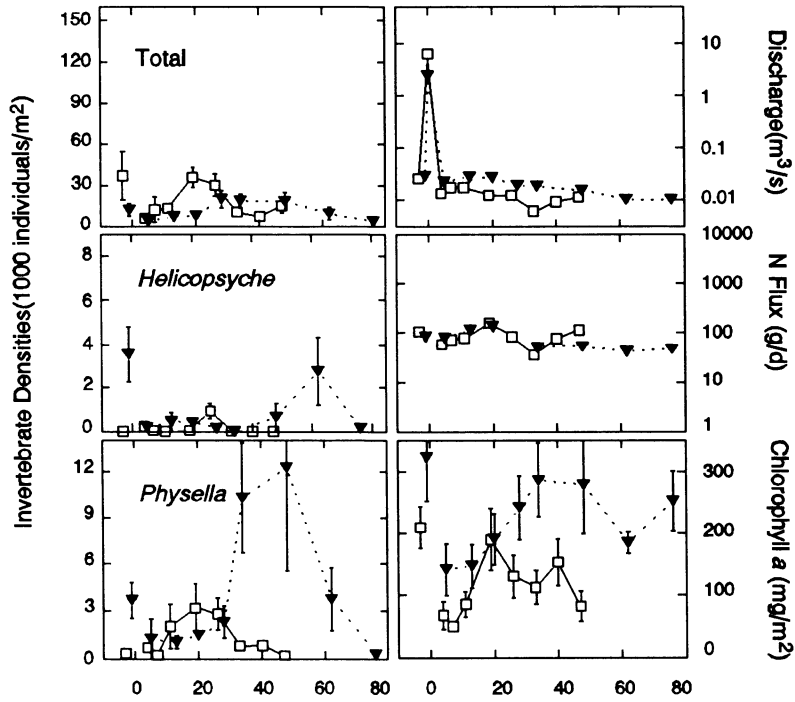
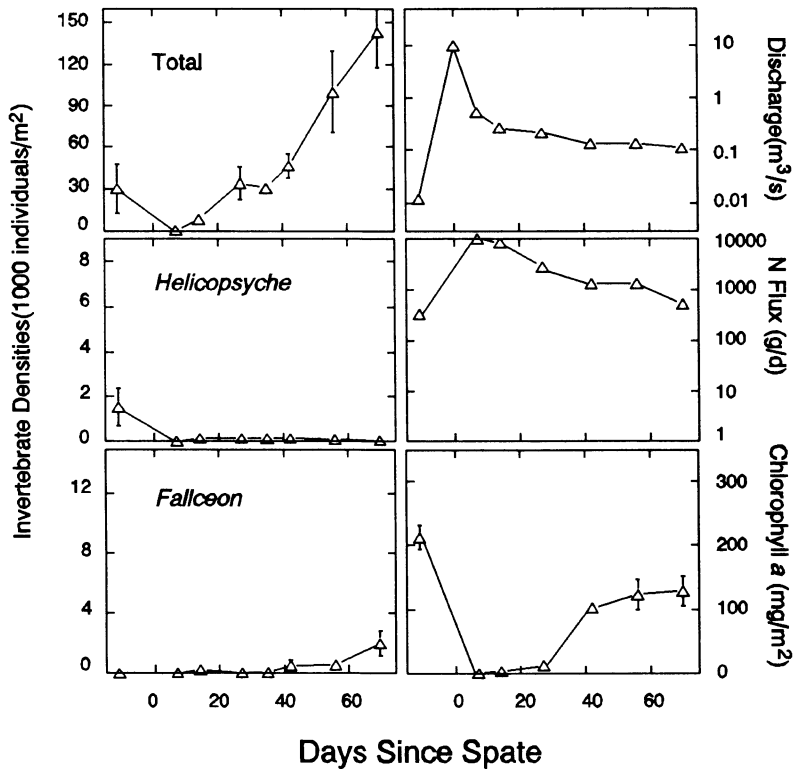


FIG. 4. Sequence-specific temporal changes in total invertebrate numbers, densities of selected taxa, discharge, N flux, and benthic chlorophyll *a* for sequences beginning after spates in spring, summer, fall, and winter in an Arizona desert stream. Data points correspond to recovery sequences 1–8 and represent means \pm 1 SE. Spring spates: 2 = ∇ ; 5 = \bullet ; 8 = \blacktriangle . Summer spates: 3 = \square ; 6 = \blacktriangledown . Fall spates: 1 = \circ ; 7 = \blacksquare . Winter spate: 4 = \triangle . Note differences in horizontal scales among seasons.

Summer Spates



Winter Spates



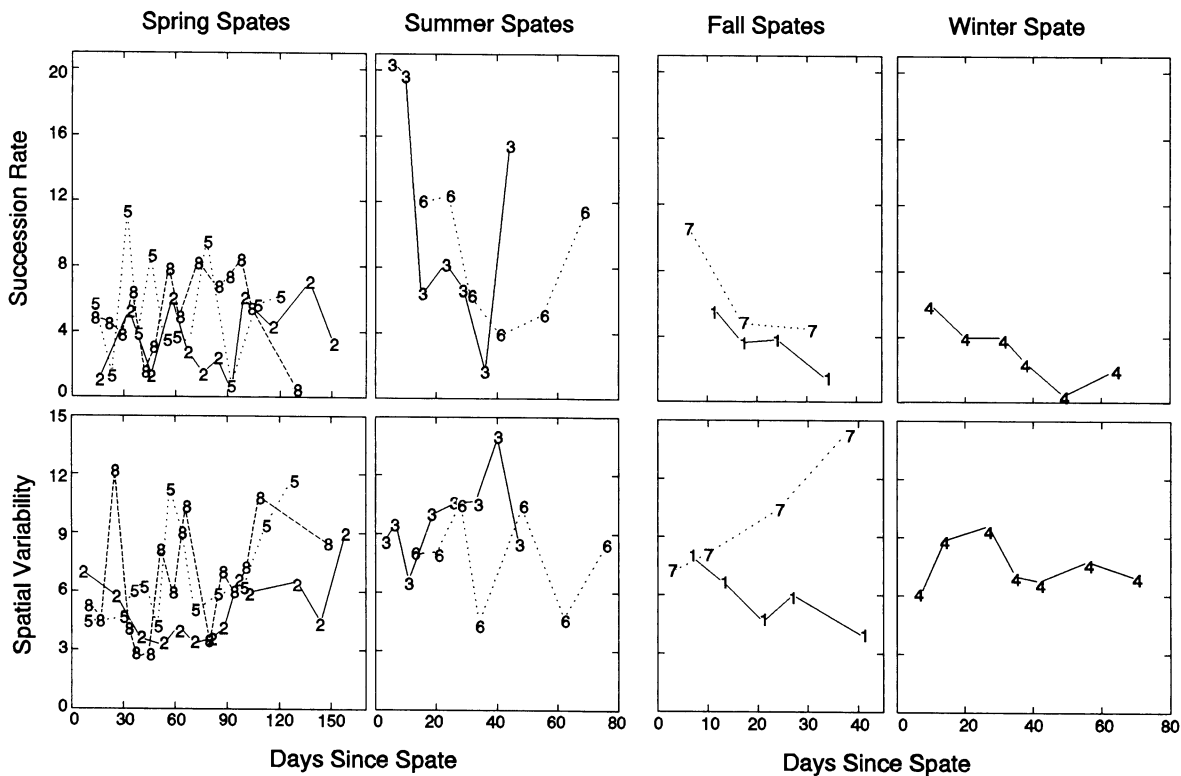


FIG. 5. Sequence-specific temporal changes in succession rate (estimated as in Fig. 4) and spatial variability (expressed as standard error around the centroid) for recovery sequences (numbered as in Table 1) occurring after floods in spring, summer, fall, and winter. Note differences in horizontal scales among seasons.

succession because of relatively slower response periods, it is still an issue (Malanson and Traubaud 1987).

Annual and seasonal patterns in community structure

Despite the occurrence of flash floods that varied in timing, magnitude, and frequency and were separated by varied periods of drying, invertebrate assemblage composition displayed a distinct seasonal cycle of temporal change in Sycamore Creek during 1984–1987. Assemblage composition was particularly consistent in spring, even when numbers of most taxa were low in 1987. Spring may be construed as a relatively “benign” (sensu Peckarsky 1983) period when flow is predictably high, flash floods are uncommon, and most sections of the stream are connected. All three spring sequences exceeded 100 d, and during their later stages, extended into May and June when the probability of spates is lowest (Gray and Fisher 1981).

In contrast, the structure of autumn macroinvertebrate assemblages differed considerably among years. In fall 1986, discharge and N flux remained low, and invertebrate assemblage structure resembled that typical of summer. Discharge may directly influence invertebrate assemblage structure in Sycamore Creek on at least two levels: (1) at any one time, ambient discharge constrains community structure, and (2) over

longer periods, variation in discharge extremes (as spates and drought) alters communities.

Nitrogen flux, benthic chlorophyll *a*, and successional time following disturbance all correlated significantly with assemblage composition (Table 2), as with the ecosystem-level variables of total algal and invertebrate standing crops examined by Grimm and Fisher (1989). In Sycamore Creek, these variables may be related to the quality or quantity of invertebrate food. Grimm and Fisher (1989) hypothesized that population crashes of collector/gatherer insects reflected diminution in the quality of detrital-based food consumed by these organisms due to reduced nitrogen availability. We observed shifts in invertebrate assemblage structure from collector/gatherers (e.g., mayflies, chironomids) to grazers (e.g., caddisflies, snails) from spring to summer that might similarly reflect a shift in the food base from “high-quality” detritus and microalgae (mostly diatoms) to one dominated by macroalgae (filamentous green algae, cyanobacteria) (cf. Fisher et al. 1982, Peterson and Grimm 1992).

Drought can have devastating effects upon macroinvertebrates in perennial and intermittent streams (Larimore et al. 1959, Iversen et al. 1978, Boulton 1988; but see Morrison 1990). Drying disturbance, although more subtle than flash flooding, has prolonged effects and usually isolates sections of stream, concentrating

predators (Boulton and Suter 1986) and increasing the likelihood of stochastic community change through strong biotic interactions within each isolated segment (Fisher and Grimm 1991). In a shallow, under-fit stream like Sycamore Creek, a slight decline in discharge may expose a large area of stream bed to desiccation. The limited taxonomic overlap between the surface benthos and the hyporheos of Sycamore Creek (Boulton et al., *in press*) implies that this habitat does not constitute an important refuge for surface invertebrate assemblages during drying.

Effects of the prolonged dry spell in 1986 on invertebrate assemblage composition were more long lived than those of spates that initiated summer sequences we examined: fall 1986 and spring 1987 sequences exhibited severely reduced total macroinvertebrate densities. Furthermore, a pronounced shift in fall assemblage composition from year to year was revealed by multivariate analyses. Finally, annual changes in relative abundance of some common taxa in Sycamore Creek were likely generated by the 1986 drought. For example, in 1987, relative densities of mayflies (*Fallceon*, *Tricorythodes*, and *Leptohyphes*) and caddisflies (*Helicopsyche* and *Cheumatopsyche*) declined significantly whereas *Physella* numbers increased sharply. Adaptations to floods (e.g., rapid generation times and short-lived aerial adults, Gray 1981) are of little value in the face of a prolonged drying disturbance that affects a large area of stream. Drought probably affected survival and oviposition success of adult insects (many of which live <1 wk [Gray 1981, Jackson and Fisher 1986]), while the many fish trapped in shrinking stream pools preyed more heavily on insect nymphs than on *Physella* (e.g., Gray 1980). Such hypotheses require experimental validation (cf. McCormick 1990) but imply that complex interactions mediate annual and seasonal patterns in community structure. Delayed effects of droughts (e.g., Feminella and Resh 1990, Boulton and Lake 1992) highlight the importance of long-term data sets to uncover historical effects that include annual time lags, even when the organisms involved are short lived but seasonally abundant.

Sequence-specific spatiotemporal patterns in community structure

Our data did not support the prediction that spatial variation in invertebrate community structure would be initially high, reflecting stochastic recolonization, decline as assemblages stabilized and developed, then rise again as patchiness and heterogeneity in resource and habitat availability increased. Instead, spatial variation differed substantially within and among sequences and did not correlate with any variable that influenced ecosystem parameters (Grimm and Fisher 1989). Spatial heterogeneity within the run and small sample sizes may have confounded estimations of variation. Ecological patterns often appear to be more predictable

at broader scales (whole ecosystems) because effects of local heterogeneity average out (Wiens 1989).

Changes in succession rate, a broader scale community characteristic, were more predictable and consistent across sequences. In all seasons except spring when succession rates were variable and unpredictable, succession rate was initially high (particularly in summer) before declining with time (Fig. 5), implying that assemblage structure of early colonists changed rapidly. However, in the two summer sequences, succession rates rose sharply again later in the sere. Lake et al. (1989) noted a similar trend in macroinvertebrate succession in a temporary pool, and attributed these changes to the influence of increased predation pressure as the pool dried. It is likely that biotic interactions intensify when surface water recedes in Sycamore Creek; further work is needed to adequately test this hypothesis (Fisher and Grimm 1991).

Aquatic macroinvertebrate assemblages in Sycamore Creek do not possess all features considered typical of nonequilibrium communities predicted to occur in "harsh" environments (Peckarsky 1983, Lake and Barmuta 1986). Assemblage composition exhibited predictable seasonal patterns and high resistance and resilience. Taxon-specific resistance, although often high, was variable and unrelated to season (except via changes in algal cover discussed above). Abiotic factors may regulate populations much of the time, although biotic interactions such as competition and predation probably come into play as the stream surface volume shrinks during drying (Fisher and Grimm 1991).

CONCLUSIONS

Multivariate and univariate analyses of temporal changes in macroinvertebrate assemblage composition after eight spates from 1984 to 1987 indicated that this community was resilient and exhibited consistent seasonal patterns despite a variable flow regime. Assemblage composition was influenced by seasonal correlates, especially benthic chlorophyll *a* and inorganic nitrogen flux. Drying disturbance may alter the intensity of biotic interactions and/or availability of habitat and resources. Resistance of invertebrate assemblage structure to spates over this period was generally high, but variable, and not simply a function of spate magnitude or timing. Resistance of individual common taxa was similarly unpredictable and not consistent across or within taxa.

Spatial variability in community structure was high, and did not change predictably over successional time whereas trends in succession rate were consistent. In all but spring sequences, succession was initially rapid and slowed with time. Higher rates in summer appeared to reflect increased water temperature.

Some variables found to be influential at the ecosystem level were also significantly correlated with assemblage composition at the community level in Sycamore Creek in 1984–1987. These variables include N

flux, chlorophyll *a*, and time since spate. But as these factors were also correlated with season, we are faced with the difficulty of separating seasonal patterns from successional ones (cf. Fisher 1990). The only major difference between our conclusions drawn at the ecosystem and community levels was with respect to resistance. This disparity may be more semantic than scientific. While terms such as resistance, resilience, succession, and stability may be defined similarly by community and ecosystem ecologists, the dependent variables used to assess these processes are often so different that comparisons across these levels are almost surely doomed. Resistance is a case in point. The biota may experience high mortality and concomitant reduction in rates of production, respiration, and nutrient cycling after disturbance. We would consider resistance (and stability), in terms of these ecosystem collective properties, to be low. However, if individual populations are decimated in proportion to their original abundance, there is little change in community composition and the assemblage would be considered relatively resistant and stable. We advocate further comparisons of resilience, resistance, succession, and stability at the ecosystem and community levels in other biomes to try and identify "common denominators" of response to disturbance (cf. Kelly and Harwell 1990). Choosing different response variables and different scales of measurement enriches our understanding of response by natural systems to disturbance but, if loosely defined, will only further confound our perceptions.

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