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Gary K. Meffe; W. L. Minckley

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Persistence and Stability of Fish and Invertebrate Assemblages in a Repeatedly Disturbed Sonoran Desert Stream

GARY K. MEFFE
Savannah River Ecology Laboratory, Drawer E, Aiken, South Carolina 29801

and

W. L. MINCKLEY
Department of Zoology, Arizona State University, Tempe 85287

ABSTRACT: Persistence, a measure of presence or absence of species, and stability, an estimate of assemblage equilibrium measured as constancy in species ranks or densities, should both be considered when assessing temporal change in natural assemblages. We measured persistence and stability in two distinct animal assemblages frequently disturbed by natural and severe flooding events, the fishes and benthic invertebrates in a Sonoran Desert stream. A persistence index (derived from colonization/extinction analyses) indicates high persistence of fishes for several decades, while benthic invertebrates were persistent except in periods of severe flooding. Stability of taxon rankings (measured by Kendall's W) was high for both assemblages, even though absolute population sizes fluctuated. Fish populations resisted even the most severe flood disturbances, whereas benthic invertebrates were decimated by particularly frequent and intensive flooding. The latter were resilient, however, and quickly recovered due to life history characters favoring rapid postflood recolonization. Although absolute numbers of organisms varied through orders of magnitude, more general aspects of assemblage structure (species' presence or absence, and relative rankings) remained relatively constant despite repeated and potentially devastating natural perturbations.

INTRODUCTION

In their synthesis of ecological stability and persistence, Connell and Sousa (1983) emphasized the utility of a multifaceted approach in temporal analyses of community structure. Drawing upon the works of Holling (1973), Boesch (1974), Orians (1974) and Whittaker (1974), among others, they presented qualitative and quantitative criteria to be considered when assessing changes in community structure over time. Qualitatively, *persistence* of species focuses upon their continued presence, particularly with respect to potentially devastating forces. Quantitatively, *stability* is the relative constancy of species abundances over time despite disturbances. Stability may result from resistance, when relative species abundances are unchanged despite potentially disruptive forces, or resilience, rapid return to the former state following disturbance. Both persistence and stability should be considered when attempting to understand community pattern and process (Holling, 1973).

The possibility of destructive disturbance is a necessary feature of communities that are used to investigate temporal change. ". . . for any situation to be included under the concept of stability . . .there must exist disturbing forces; without them, simple lack of change in numbers is of little interest" (Connell and Sousa, 1983). Consequently, responses of natural communities to disturbance are central to current ecological research (Dayton, 1971; Sousa, 1979, 1984; Matthews, 1986), and disturbance provides a framework upon which mechanistic understandings of community structure and function may be developed.

We examined persistence and stability of fish and benthic invertebrate assemblages in a Sonoran Desert stream that repeatedly experiences large, quantifiable natural dis-

turbances from flash-flooding. We investigated qualitative and quantitative aspects of assemblage structure in relation to known disturbances by addressing the following questions:

(1)Are assemblages persistent in the long term (= several generations) and/or short term (= consecutive sample periods within a generation)? That is, do major taxa persist after disturbance events or do disturbances result in repeated local extinctions and colonizations?

(2)Are assemblages stable? Do relative numbers of individuals remain constant or change as a function of disturbances?

(3)If assemblages are affected by disturbance, are they resilient? Do decimated populations respond by rapid population recovery to former levels?

Note that we use the term "assemblage" as a taxonomic subset of a "community." For example, a stream community may consist of assemblages of benthic invertebrates, bacteria, fishes, macrophytes, etc. Also, we imply no linkage between our fish and invertebrate data sets, nor common responses of these groups to identical flood events; temporal differences in sampling protocol and generation time preclude any direct comparison of fishes and invertebrates. We simply present data from two distinct animal assemblages that are part of the same stream community and independently assess assemblage persistence and stability over a span of time that incorporates numerous natural disturbances.

MATERIALS AND METHODS

Study area.—Aravaipa Creek is an unregulated middle- to low-elevation desert stream in Graham and Pinal counties, Arizona, that has been under biological investigation since the 1940s. Its biotic and abiotic features are well-known (Barber and Minckley, 1966; Deacon and Minckley, 1974; Minckley, 1981; Schreiber and Minckley, 1981). The stream consists of three distinct physiographic reaches. Perennial surface water rises from unconsolidated alluvium near 1,010 m elevation, flows for 10 km at an average gradient of ca. 2.5 m/km, then descends through a deep narrow canyon (10—100 m wide) for 17 km at gradients up to 25 m/km. The section downstream from the canyon flows for 14 km at gradients near 5 m/km in a steep-sided valley until disappearing into sands of the stream bed. Surface water reaches the intermittent San Pedro River (660 m elevation), several kilometers downflow, only during sustained flooding. Permanent tributaries are short, precipitous and generally located in the canyon reach.

Upper parts of the watershed are vegetated by Desert Grasslands; the lower creek flows through Sonoran Desertscrub (Brown, 1982). Channels are lined by mature gallery forests of cottonwood (*Populus fremontii*), willows (*Salix gooddingii*, *S exiqua*), and other large trees and shrubs, and are generally undisturbed by man, a rare feature in the American Southwest (Minckley and Brown, 1982). The native fish fauna, five minnows (Cyprinidae) and two suckers (Catostomidae), is intact, with only occasional records of transient nonnative species. As a result, Aravaipa Creek provides an unusual opportunity to study aquatic community structure under near pristine conditions in a well-defined system.

Like most unregulated arid-land waterways, Aravaipa Creek is subject to frequent and intense flash floods, highly erosive events that are rapid in onset and short in duration. Summer flooding is particularly spectacular, with discharges during storms increasing by orders of magnitude in minutes. Summer modal discharge in Aravaipa Creek ranges between 0.14 and 0.28 m^3/sec (Minckley, 1981), whereas records for maximum instantaneous discharges since 1920 are 566 and 1982 m ^{3}/sec (U.S. Geol. Surv., 1975, and 1983 unpublished records), thousands of times the modal flow.

Between 1966 and 1981 there was a minimum of 10 summer discharges in Aravaipa Creek with daily mean flows exceeding 30 m^3/sec, and seven winter floods >100 m^3/sec, including one with an instantaneous peak at 300 and another peaking at 463 (U.S.G.S. gage records). About 50% of the total amount of water flowing through the

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stream each year does so during only 6% of the time; 25% of the flow occurs during <1% of the time (Minckley and Meffe, 1987) indicating the importance of large floods to the hydrology and biology of the region. Floodwaters are known to elevate the stream surface >10 m in constrained canyon reaches, to uproot and transport large expanses of mature gallery forests, and to mobilize great quantities of bedload which vastly alters streambed and channel morphology. Studies in other Southwestern streams further document frequencies, intensities and impacts of flood disturbances in arid-land waterways (Fisher and Minckley, 1978; Collins *et al.*, 1981; Fisher *et al.*, 1982; Meffe, 1984; Minckley and Meffe, 1987).

Sampling protocol. — Relative abundance of fishes in Aravaipa Creek for up to 14 sampling years (between 1943 and 1979) were compiled by Minckley (1981). Original data differed; some were available as counts of individuals and others only as relative abundance for collections of unknown absolute size. As a result, the most reliable data are percentage occurrences and these are used in the analysis. Samples were taken by several individuals, but all collections since 1963 were under Minckley's field supervision. Sampling before 1974 was by 3.2- to 6.4-mm mesh seines and from 1974 to 1979 by 110V A.C. electrofishing of blocked stream segments. Collections since 1963 were bimonthly or quarterly at 6-8 stations over the entire 41 km of surface flow in years of intensive surveys (1965-1967, 1970-1972, 1975-1979), and at 2-4 stations one to three times in other years. Each annual datum is thus an average of several (usually 4-6) individual samples across seasons, and represents an estimate of mean yearly abundances within stream segments, incorporating all seasonal changes. Data are available for 12 years from upper Aravaipa Creek, 14 from the canyon, and 14 from the lower reach.

Invertebrates were collected by D. A. Bruns or Minckley using a Surber-type sampler (929 cm^2, 228-um-mesh) at three stations above, three within, and two stations below the canyon at 1-4 month intervals from January 1975 through April 1978 (Bruns, 1977; Bruns and Minckley, 1980), with additional observations by Minckley extending to December 1978. Two samples were taken at each station, one each from gravel and cobble, except for one station where a single collection was made from coarse sand. Twenty-six collections were preserved over the 40-month period and later analyzed by identification to family, genus, or species, and by counts of all organisms or appropriate subsamples. Data used here are averages from all stations taken from summary tables in Minckley (1981).

The time over which each assemblage was studied is sufficient for turnover of several generations. This is a critical feature of analyses that purport to examine assemblage persistence or stability (Connell and Sousa, 1983) since stability might otherwise be an artifact of long-lived individuals.

Data analysis. — Fish assemblages from the three physiographic sections of Aravaipa Creek were analyzed separately. Species richness/collection (S) provides a general indication of assemblage stability. A persistence measure was generated from an index of species turnover rates (Diamond and May, 1977; Jarvinen, 1979). The formula $T = (C + E)/(S_1 + S_2)$ [where C and E are the number of taxa that colonized or went extinct between sample periods, and S_1 and S_2 are numbers of taxa present in each sample period] measures the rate of species turnover (from 0 — 1) between two samples. A mean turnover rate for each assemblage ($\overline{T}$) was calculated as the average turnover of all k-1 adjacent sample periods (where k = number of samples). An index of persistence (PR), ranging from zero (no persistence) to one (complete persistence) was then calculated as $1 - \overline{T}$.

Stability of species relative abundance rankings was tested by their concordance over the entire study period (Grossman, 1982; Grossman *et al.*, 1982; Ross *et al.*, 1985). An assemblage at or near equilibrium would have more constant rankings of its constituent species than would a fluctuating assemblage. Relative abundances of fishes were ranked and evaluated for year-to-year concordance using Kendall's W (Conover, 1971), a nonparametric procedure that tests for overall concordance among multiple samples under

the null hypothesis of randomness. Lack of concordance supports the view of a non-equilibrium community; concordance suggests approximation of an equilibrium state.

Invertebrates from all 26 collections were analyzed as above. Four years of winter (January) and spring (April), and 3 years of summer (July/August) and autumn (October) samples were also analyzed separately for stability within season. Because Kendall's W is sensitive to rare events which bias results toward concordance (Grossman *et al.*, 1982), and to eliminate transient taxa, only the 12 most abundant taxa (of 52 in quantitative samples) were used in analyses. These 12 constituted an obvious "core group" of taxa and comprised 94.7% of 166,508 individuals collected. Data on the complete assemblage are in Minckley (1981) or are available from the authors. Most groups in the analysis were identified only to family or genus, obscuring species-level variation. However, several of these (*Baetis* spp., *Choroterpes* sp., *Ephemerella* sp., *Tricorythodes* spp., Hydropsychidae, Simuliidae, Ceratopogonidae, Cypridae) were represented by only one or two common species (Bruns, 1977; Bruns and Minckley, 1980), thus minimizing the problem.

RESULTS

Fishes.—Number of species per collection ranged from 6-7 in upper Aravaipa Creek. 5-7 in the canyon and 3-7 in the lower section (Tables 1—3, Fig. 1). The three most common species (longfin dace *Agosia chrysogaster*, desert mountain-suckers *Pantosteus clarki*, and Sonoran suckers *Catostomus insignis*) were present in all collections in all stream segments. Three additional species (speckled dace *Rhinichtys osculus*, spikedace *Meda fulgida*, and loach minnow *Tiaroga cobitis*) were represented in all collections in the upper segment; only the roundtail chub (*Gila robusta*) was occasionally missing there. The upper stream assemblage was thus most stable over a 14-year period (from the perspective of species numbers), whereas the lower stream segment was least stable. The index of persistence (Table 4) is consistent with these patterns. All measures were above 0.9 (suggesting high persistence of Aravaipa Creek fishes) and decreased from the upper to lower sections.

Fish species rankings in all sections were significantly concordant, as measured by Kendall's W, for up to 36 years (1943-1979) (Table 5). The null hypothesis is rejected in each case, indicating that relative rankings were stable over the periods tested.

Benthic invertebrates.—Number of major taxa (S) in samples ranged from 2-12 and de-

TABLE 1.—Fish assemblage structure in upper Aravaipa Creek. Data are percentage abundance of each fish species in a sample, with rank in parentheses. The first five species are cyprinids, the latter two are catostomids

	Year											
Species	1965	1966	1969	1970	1972	1973	1974	1975	1976	1977	1978	1979
Agosia	50.0	26.7	47.5	51.1	55.6	87.0	81.5	79.9	55.8	51.9	40.7	33.3
chrysogaster	(1)	(2)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)
Rhinichthys	1.0	4.1	3.1	2.9	0.3	5.5	3.5	4.7	16.5	21.3	20.7	19.4
osculus	(6)	(6)	(6)	(5)	(5.5)	(2)	(3)	(3)	(2)	(2)	(3)	(3)
Meda	5.0	1.9	0.7	1.3	0.3	0.8	11.5	1.2	2.2	1.0	1.7	0.9
fulgida	(4)	(7)	(7)	(7)	(5.5)	(5)	(2)	(6)	(5)	(7)	(5)	(7)
Gila	0.0	4.3	5.4	2.7	0.0	0.2	0.0	2.3	1.9	3.5	1.0	11.7
robusta	(7)	(5)	(5)	(6)	(7)	(7)	(7)	(4)	(6)	(5)	(6)	(4)
Tiaroga	4.0	5.2	6.0	7.4	15.8	0.5	0.3	0.4	0.9	1.1	0.8	2.1
cobitis	(5)	(4)	(4)	(3)	(3)	(6)	(6)	(7)	(7)	(6)	(7)	(6)
Pantosteus	32.5	31.9	23.4	30.7	16.3	4.5	3.0	9.1	12.4	13.2	10.9	11.5
clarki	(2)	(1)	(2)	(2)	(2)	(3)	(4)	(2)	(3)	(3)	(4)	(5)
Catostomus	7.5	26.0	13.9	3.9	11.7	1.5	0.5	2.2	10.3	8.0	24.2	21.1
insignis	(3)	(3)	(3)	(4)	(4)	(4)	(5)	(5)	(4)	(4)	(2)	(2)

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TABLE 2. — Fish assemblage structure in Aravaipa Creek canyon. Protocol as in Table 1

Species	Year 1950	1965	1966	1967	1969	1970	1972	1973	1974	1975	1976	1977	1978	1979
Agosia	31.7	35.1	22.9	27.3	31.4	40.6	29.9	27.5	36.6	32.3	31.8	11.4	9.5	7.0
chrysogaster	(2)	(1)	(2)	(2)	(1)	(1)	(1)	(2)	(1)	(2)	(1)	(3)	(5)	(6)
Rhinichthys	5.5	0.0	8.2	4.1	2.3	1.0	0.0	5.5	0.0	4.1	6.5	9.7	11.4	7.2
osculus	(5)	(6.5)	(5)	(6)	(7)	(6)	(7)	(6)	(7)	(5)	(5)	(4)	(3)	(5)
Meda	0.0	18.6	16.4	11.4	18.7	9.5	6.9	28.3	18.6	11.1	17.0	9.3	7.4	10.4
fulgida	(6.5)	(3)	(4)	(4)	(3)	(4)	(5)	(1)	(3)	(4)	(3)	(5)	(6)	(3)
Gila	0.0	2.8	5.1	9.2	3.4	6.7	11.1	7.6	6.0	3.3	4.0	9.0	11.1	9.8
robusta	(6.5)	(5)	(6)	(5)	(6)	(5)	(4)	(5)	(5)	(6)	(6)	(6)	(4)	(4)
Tiaroga	14.6	0.0	3.3	2.1	11.9	0.8	3.4	0.0	0.4	1.4	0.7	3.1	1.4	0.9
cobitis	(3)	(6.5)	(7)	(7)	(4)	(7)	(6)	(7)	(6)	(7)	(7)	(7)	(7)	(7)
Pantosteus	35.5	25.5	24.1	30.0	23.8	29.8	24.9	21.5	8.5	36.1	25.4	39.1	41.4	49.1
clarki	(1)	(2)	(1)	(1)	(2)	(2)	(2)	(3)	(4)	(1)	(2)	(1)	(1)	(1)
Catostomus	12.7	18.0	20.0	15.9	8.5	11.6	23.8	9.6	29.9	11.7	14.6	18.4	17.8	15.6
insignis	(4)	(4)	(3)	(3)	(5)	(3)	(3)	(4)	(2)	(3)	(4)	(2)	(2)	(2)

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TABLE 3. — Fish assemblage structure in lower Aravaipa Creek. Protocol as in Table 1

Species	Year 1943	1963	1965	1966	1967	1969	1970	1972	1974	1975	1976	1977	1978	1979
Agosia	74.5	97.2	97.5	81.9	83.5	88.7	83.2	82.0	70.0	73.5	78.1	60.2	50.4	55.3
chrysogaster	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)
Rhinichthys	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	1.0
osculus	(6.5)	(5.5)	(5.5)	(7)	(7)	(7)	(7)	(6.5)	(6.5)	(7)	(7)	(7)	(7)	(7)
Meda	0.0	0.0	0.0	3.1	1.1	0.3	0.9	1.3	1.0	1.4	3.8	5.1	3.3	6.1
fulgida	(6.5)	(5.5)	(5.5)	(3)	(5)	(5.5)	(4.5)	(5)	(5)	(5)	(4)	(4)	(4)	(4)
Gila	7.2	0.0	0.0	1.0	1.7	2.0	0.3	0.0	4.0	1.0	0.2	0.8	0.2	2.6
robusta	(3)	(5.5)	(5.5)	(5)	(4)	(3.5)	(6)	(6.5)	(4)	(6)	(6)	(5.5)	(5)	(5)
Tiaroga	0.7	0.0	0.0	2.3	0.8	0.3	0.9	1.9	0.0	5.7	0.7	0.8	0.1	1.1
cobitis	(5)	(5.5)	(5.5)	(4)	(6)	(5.5)	(4.5)	(4)	(6.5)	(3)	(5)	(5.5)	(6)	(6)
Pantosteus	12.4	2.6	1.3	10.9	9.7	6.7	11.3	12.6	18.0	13.9	12.4	27.1	32.1	23.7
clarki	(2)	(2)	(2.5)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)	(2)
Catostomus	5.2	0.2	1.3	0.8	3.2	2.0	3.4	2.2	7.0	4.5	4.8	5.7	13.9	10.3
insignis	(4)	(3)	(2.5)	(6)	(3)	(3.5)	(3)	(3)	(3)	(4)	(3)	(3)	(3)	(3)

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clined late in the study (Table 6; Fig. 2). Only one taxon (Chironomidae) was present in all 26 samples; all others underwent local extirpations and colonizations. The persistence index for the invertebrate assemblage is nevertheless quite high (Table 4). However, presence/absence data in context of discharge data (Fig. 3) indicate an obvious change in numbers of invertebrates per sample in July 1977. Prior to that time discharge was either moderate or floods were infrequent, and benthic invertebrates were abundant. July 1977 began a period of greater overall discharge and frequent and intensive flooding (Fig. 3); invertebrate populations were correspondingly low at this time. Consequently, we separately analyzed assemblages from pre- and post-July 1977 and found invertebrate persistence high for the initial 30 months, and sharply reduced during the subsequent flooding period (Table 4).

Rankings of invertebrate taxa were significantly concordant by Kendall's W for the entire sample period, and in seasonally designated collections (Table 7). The null hypothesis is rejected in each instance, indicating that relative rankings of benthic invertebrates, at the level of taxonomic detail employed, were stable over the sample period.

DISCUSSION

Flash floods are legendary in their suddenness and destructive power, making desert streams excellent systems in which to examine effects of natural disturbance on community structure. The fish community of Aravaipa Creek is little affected by flooding in the long term, as no native species became extinct or colonized since observations began early in this century. Likewise, minor fluctuations in species richness and high indices of persistence indicate short-term persistence of the assemblage. Stability of rankings is also high, with longfin dace, desert mountain-suckers and Sonoran suckers always present and generally most abundant, and the other four species relatively rare.

A natural test of persistence and stability through severe disturbance was provided in October 1983 with the most intense flooding in Aravaipa Creek on record. Instantaneous discharge peaked at 1,982.2 m^3/sec^{-1}, with water levels in the canyon >15 m above modal flow. Essentially all stream substrate other than large boulders was mobilized and >50% of the riparian gallery forest was destroyed. Fish samples throughout the stream 2 weeks before flooding and ca. 2 weeks later were qualitatively similar

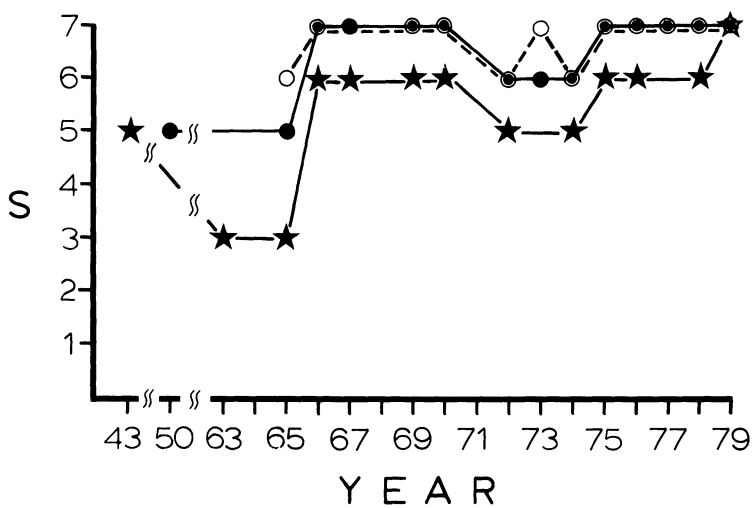

Fig. 1.—Number of species of fishes recorded in the three reaches of Aravaipa Creek from 1943 through 1979. Symbols: ●————● = canyon; o--------o = upper segment; *————* = lower segment

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(D.A. Hendrickson, pers. comm.). All seven fish species persisted after the flood and did so in roughly the same proportions as preflood samples.

Moyle and Vondracek (1985) reported similar concordance of species rankings for a fish assemblage in the Truckee River drainage of California, although absolute numbers and biomass varied from year to year. Ross *et al.* (1985) found fish assemblages in Oklahoma and Arkansas streams had high persistence, but the harsher Oklahoma stream had lower stability. Matthews (1986) studied the same Arkansas stream, including its worst catastrophic flood this century. Although there were moderate alterations of the fish fauna directly after flooding, the assemblage rapidly recovered and within 8 months closely resembled the preflood condition. All of these studies indicate persistence of stream fish assemblages, while stability may or may not obtain.

Grossman *et al.* (1982) investigated stability of an Indiana stream fish assemblage in an attempt to discern whether it was in equilibrium. Instability of trophic groups and rankings of common species by season for up to 12 years led to the conclusion of nonequilibrium assemblages, a finding which has drawn both methodological and conceptual objections (Herbold, 1984; Rahel *et al.*, 1984; Yant *et al.*, 1984), subsequently rebutted by Grossman *et al.*, (1985). Our index of persistence applied to their data yields persistence measures for spring, summer and autumn samples of .837, .947 and .937, respectively. Their "nonequilibrium" community is generally as persistent as Aravaipa Creek fish assemblages.

We advise caution in interpretation of the invertebrate data. Because the original investigators chose a coarse level of taxonomy, no doubt a consequence of difficulties associated with some aquatic insect identifications, our abilities to detect species-level changes within an assemblage are limited. Since several taxa in our study are defined only to family or genus, conclusions are provisional and should be interpreted only as a coarse view of invertebrate assemblage structure.

Assemblage persistence of Aravaipa Creek invertebrates was dependent upon flooding patterns. The persistence index was high, but then dropped coincident with a period of particularly frequent and intense flooding from July 1977 through all of 1978. Although stability of rankings was high, indicating that relative abundances fluctuated little during the 40-month period, stability of absolute population sizes was low (Table

TABLE 4.—Index of persistence (PR) for fish and benthic invertebrate assemblages

Fishes	PR
Upper	.965
Canyon	.919
Lower	.908
Invertebrates	**PR**
Jan. 1975 – April 1978	.852
Before July 1977	.926
After June 1977	.697

TABLE 5.—Analysis of fish assemblage stability using Kendall's Coefficient of Concordance (W). W indicates level of overall concordance from 0 (no correlation) to 1 (complete correlation). P = probability of a Type I error

Stream section	# Samples (years)	# Species	W	P
Upper	12	7	.634	<.001
Canyon	14	7	.705	<.001
Lower	14	7	.831	<.001

6, Fig. 3) with densities fluctuating through several orders of magnitude. Single spates reduced numbers of invertebrates by as much as 99% in habitats sampled (Minckley, 1981), but recolonization was rapid and noticeable populations often re-established only a few days after flooding. Recovery from massive losses occurred in a matter of several weeks to a few months depending on frequency of disturbance (Minckley, 1981), and taxon rankings generally returned to those of preflood states. Gray (1981) and Gray and Fisher (1981) reported similar patterns in Sycamore Creek, Arizona, another lowland Sonoran Desert stream. Invertebrate numbers were reduced in flood by an average of 86% and returned to preflood levels within 14 days if not further disturbed.

Although we did not directly investigate resilience of benthic invertebrates, persist-

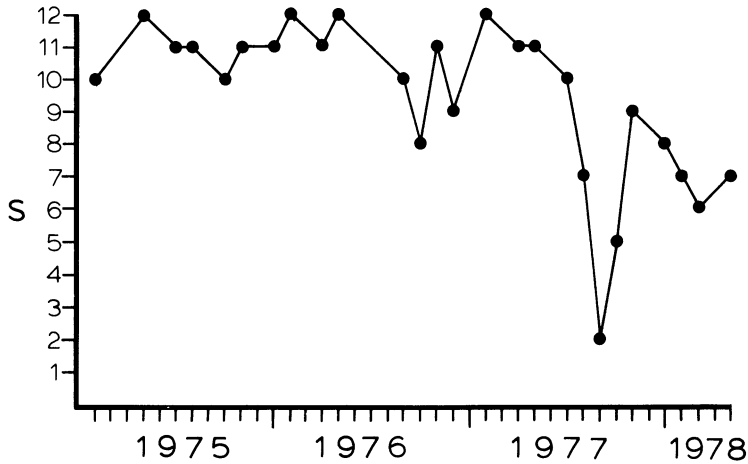

Fig. 2.—Number of taxa of 12 common benthic invertebrates recorded in Aravaipa Creek from January 1975 to April 1978. Each mark on the abscissa represents 1 month

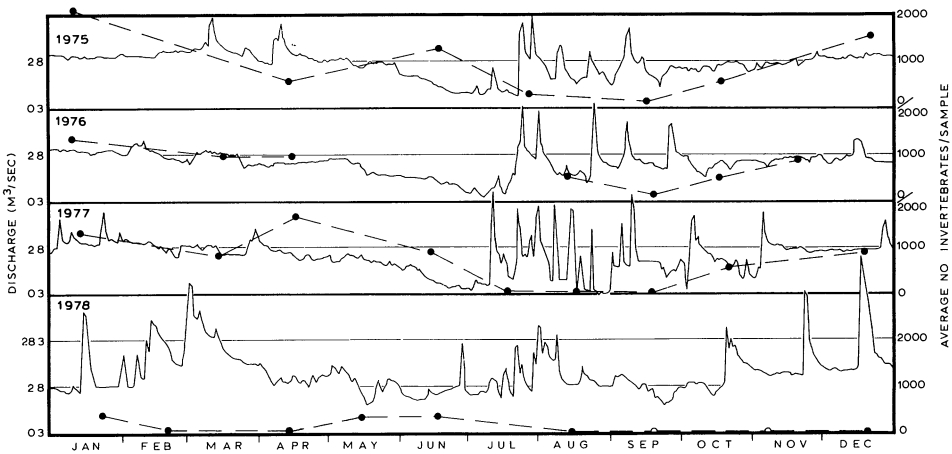

Fig. 3.—Mean daily discharges of Aravaipa Creek during the invertebrate study period (modified from Minckley, 1981). Note that instantaneous discharge peaks may exceed mean values shown by several orders of magnitude. Also plotted is mean number of benthic invertebrates collected per sample. Symbols: ● = quantitative samples (after April 1978 from Minckley, previously unpublished); o = qualitative estimates from on-site inspection

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TABLE 6.—Benthic invertebrate assemblage structure in Aravaipa Creek. Listed are average number of individuals per sample and rank (in parenthesis) for each sampling date

Taxon	1975 Jan.	April	June	July	Sept.	Oct.	Dec.	1976 Jan.	March	April	Aug.	Sept.
EPHEMEROPTERA												
Baetis spp.	565(2)	1306(2)	3639(3)	1056(1)	763(2)	3176(1)	4988(2)	5776(1)	3292(2)	5184(1)	474(2)	115(2)
Choroterpes sp.	172(5)	164(6)	2571(4)	870(2)	644(3)	861(3)	1382(6)	733(6)	1197(3)	987(5)	22(7)	25(4)
Ephemerella sp.	0(11.5)	495(4)	14(11)	0(11.5)	0(11.5)	0(12)	0(12)	570(9)	507(7)	1014(4)	0(11.5)	11(5.5)
Tricorythodes spp.	215(3)	379(5)	4928(2)	309(5)	224(5)	286(6)	615(7)	741(5)	625(6)	1359(3)	90(4)	0(10.5)
PLECOPTERA												
Capnia frisoni	32(8)	6(12)	0(12)	0(11.5)	0(11.5)	203(8)	1610(5)	86(12)	0(12)	9(12)	0(11.5)	0(10.5)
TRICHOPTERA												
Hydropsychidae	11(10)	18(11)	110(8)	116(7)	24(9)	234(7)	394(10)	313(10)	325(9)	448(7)	14(8)	161(1)
DIPTERA												
Chironomidae	2594(1)	1628(1)	6165(1)	690(3)	435(4)	1738(2)	6616(1)	5186(2)	4410(1)	2506(2)	99(3)	11(5.5)
Simuliidae	118(6)	100(9)	130(6)	472(4)	1171(1)	714(4)	2481(3)	1683(3)	268(10)	178(10)	2174(1)	47(3)
Ceratopogonidae	22(9)	55(10)	108(9)	49(9)	14(10)	143(9.5)	487(8)	714(8)	334(8)	73(11)	47(5)	4(7)
OLIGOCHAETA												
Undetermined sp.	205(4)	1241(3)	629(5)	24(10)	40(6)	621(5)	2000(4)	1482(4)	923(4)	255(9)	11(9)	2(8)
OSTRACODA												
Cypridae	0(11.5)	118(8)	38(10)	169(6)	28(8)	143(9.5)	137(11)	197(11)	205(11)	311(8)	4(10)	0(10.5)
ACARINA												
Undetermined spp.	43(7)	129(7)	121(7)	76(8)	32(7)	131(11)	437(9)	731(7)	755(5)	509(6)	24(6)	0(10.5)
Percentage of collection consisting of these 12 taxa	96.9	97.0	96.3	90.1	95.4	95.7	97.2	93.7	94.1	94.2	98.0	82.8
Average #/sample	2053	414	1371	304	252	616	1552	1388	975	973	504	151

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TABLE 6.—(continued)

Taxon	Oct.	Nov.	Jan.	1977 March	April	June	July	Aug.	Sept.	Oct.	Dec.	1978 Jan.	Feb.	April
EPHEMEROPTERA														
Baetis spp.	1101(2)	305(3)	3358(1)	1231(2)	1920(3)	1141(3)	30(5)	0(7.5)	3(5)	331(3)	2295(1)	38(5)	14(3)	39(1)
Choroterpes sp.	24(8)	22(8)	104(10)	372(5)	124(6)	216(4)	80(2)	0(7.5)	0(9)	0(11)	22(5)	27(6)	0(9.5)	11(4)
Ephemerella sp.	22(10)	0(11)	14(12)	0(12)	3(11)	14(8)	0(10)	0(7.5)	0(9)	0(11)	0(10.5)	0(10)	0(9.5)	0(10)
Tricorythodes spp.	0(12)	0(11)	594(4)	2143(1)	3021(1)	1644(1.5)	91(1)	0(7.5)	0(9)	75(4)	0(10.5)	229(2)	7(5)	1(7)
PLECOPTERA														
Capnia frisoni	7(11)	255(4)	325(7)	2(11)	0(12)	0(11.5)	0(10)	0(7.5)	0(9)	0(11)	393(4)	527(1)	129(2)	30(2)
TRICHOPTERA														
Hydropsychidae	108(6)	29(6)	36(11)	15(10)	832(4)	64(7)	3(6)	0(7.5)	0(9)	2(9)	0(10.5)	0(10)	0(9.5)	0(10)
DIPTERA														
Chironomidae	1609(1)	1563(1)	1848(2)	749(4)	2655(2)	1643(1.5)	37(3)	4(1.5)	11(3)	2056(1)	1835(2)	175(3)	158(1)	18(3)
Simuliidae	126(4)	492(2)	429(6)	1170(3)	38(8)	13(9)	2(7)	0(7.5)	4(4)	794(2)	1091(3)	46(4)	4(6)	0(10)
Ceratopogonidae	90(7)	104(5)	161(9)	29(9)	5(10)	109(5)	36(4)	0(7.5)	0(9)	30(6)	4(8)	0(10)	0(9.5)	0(10)
OLIGOCHAETA														
Undetermined sp.	171(3)	14(9)	244(8)	194(6)	14(9)	8(10)	0(10)	4(1.5)	15(2)	67(5)	8(6)	7(7)	11(4)	3(6)
OSTRACODA														
Cypridae	110(5)	0(11)	1270(3)	41(8)	74(7)	0(11.5)	0(10)	0(7.5)	0(9)	22(8)	0(10.5)	0(10)	0(9.5)	7(5)
ACARINA														
Undetermined spp.	23(9)	25(7)	495(5)	73(7)	176(5)	83(6)	0(10)	0(7.5)	30(1)	28(7)	5(7)	0(10)	0(9.5)	0(10)
Percentage of collection consisting of these 12 taxa	95.6	96.5	96.7	90.6	92.0	95.9	27.9	40.0	91.2	97.0	97.0	95.8	98.5	90.8
Average #/sample	393	972	1314	1606	1606	736	77	5	18	584	836	274	55	17

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ence and stability of ranks appears to be due to life history characteristics that enable rapid and effective recolonization after decimation (Gray and Fisher, 1981; Jackson, 1984). These include exceptionally short generation times (14 to 21 days for several genera), continuous reproduction throughout the year, rarity of diapause and presence of aerial adults at all times. However, despite these adaptations, much of the benthic invertebrate assemblage was still damaged by the more severe flooding.

> "Late in the study essentially all but baetid mayflies, plecopterans, and a few chironomid dipteran larvae were absent. Trichopteran larvae were essentially gone after July 1977, and coleopterans, hemipterans and odonates, were rare. These last groups [which were not included in the 12 abundant taxa analyzed herein] include those identified by Gray as lacking short life cycles in the Sycamore Creek drainage, and he also demonstrated their extirpation after a period of sustained flood . . . It is obvious that seasonal abundance of most individual taxa in Aravaipa Creek reflect the overriding force of summer flooding. This is especially evident in most substrate-surface dwellers as mayflies and ceratopogonid dipterans, and interstices- or burrow-dwellers such as chironomids, oligochaetes, and water mites. The former are free living, thus directly exposed to spates, and the latter are subject to decimation as substrates are mobilized and scour proceeds." (Minckley, 1981).

The high levels of persistence and stability of rankings in Aravaipa Creek assemblages are particularly impressive when one considers the extraneous sources of variance inherent in sampling ecological communities in general. In addition to the normal sampling variances and biases encountered in aquatic systems (Backiel and Welcomme, 1980) further sources of variance in the fish data include participation by a variety of collection personnel of various levels of experience, and a change in sampling gear in 1974. Such practices can only increase variance of collections. Despite these sources of extraneous variance, the invertebrate assemblage (for the 1st 30 months) and the fish assemblage showed high predictability and significant levels of stability. Furthermore, all measures of persistence are minimum estimates, since it is possible that taxa (particularly invertebrates) were present in Aravaipa Creek but undetected in a given sample.

We earlier posed three questions with respect to Aravaipa Creek fishes and benthic invertebrates to better understand assemblage structure. Our analyses suggest the following:

(1)Long-term persistence of fishes was high, with no indications of gain or loss of species from at least 1943 through 1984. Short-term persistence was high in all areas, but less so in the lower reach where a trend of species addition was observed from 1963 to 1979. This is probably related to greater temperature and discharge extremes lower in the system. The upper and canyon reaches of Aravaipa Creek experience cooler summer water temperatures, and flooding probably has fewer impacts due to smaller watershed size higher in the system (Bruns and Minckley, 1980). The latter results in rela-

TABLE 7.—Analysis of benthic invertebrate assemblage stability using Kendall's Coefficient of Concordance (W)

Season	# Samples (years)*	# Taxa	W	P
All samples	26	12	.461	<.001
Winter	4	12	.632	<.005
Spring	4	12	.757	<.01
Summer	3	12	.775	<.01
Autumn	3	12	.709	<.025

* "Years" does not apply to the combined 26 samples, which covered a span of 40 months

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tively stable substrates in the upper system and more predictable populations of algae, macrophytes and invertebrates that serve as food for fishes (Minckley, 1981).

Long-term persistence of benthic invertebrates also is likely high in Aravaipa Creek, although our data cannot directly address this question. Short-term persistence is high unless frequent and intensive flooding occurs, whereupon repeated local extinctions and recolonizations occur.

(2)Stability of rankings was high for both assemblages; common taxa tended to remain common and rare taxa rare. However, actual numbers of individuals probably fluctuated greatly in both groups (Tables 1-3, 6). Fish population fluctuations may in part be attributed to intrastream movements to avoid adversity such as high summer temperatures (Siebert, 1980), or active selection of optimal conditions by individuals in "preferred" reaches of stream. Examples of the latter are *Pantosteus clarki*, which feeds by scraping periphyton from solid surfaces (Fisher *et al.*, 1981; Schreiber and Minckley, 1981) and thus remained most abundant within the canyon, and *Agosia chrysogaster*, which tends to avoid solid bottoms and cool water and "prefers" shifting sand substrates in warmer streams (Minckley and Barber, 1971; Kepner, 1982). It remained dominant in the lower section of Aravaipa Creek, was most abundant in the upper section after long periods of low flow (Minckley, 1981), and was typically least abundant in the hard-bottom, cool, canyon segment (Tables 1-3). Aquatic insect fluctuations may result from emergences (Jackson, 1984) or other biological events, but typically are attributed to stochastic phenomena (Fisher, 1983).

(3)The semipersistent, nonresistant invertebrate assemblage is resilient to flood disturbance. Taxa which are repeatedly reduced in number or apparently eliminated generally reappear in subsequent samples in densities approximating their former states (Minckley, 1981; Gray and Fisher, 1981).

When investigating temporal assemblage change, a single analytical tool (such as Kendall's W) or a single conceptual approach (such as an equilibrium/nonequilibrium dichotomy) restricts breadth of understanding and interpretation. For example, categorization of assemblages into equilibrium or nonequilibrium tends to obscure important biological features of the system that can only be appreciated through a combined quantitative/qualitative analysis. In this study, a strict concordance approach using Kendall's W would lead to a conclusion of stable assemblages unaffected by flooding. Such a simple categorization is misleading, since other analyses reveal major declines of benthic invertebrates in the latter part of the study, and minor changes in presence and absence of the fishes. It is only by examination of assemblages from a variety of perspectives, and with knowledge of pertinent environmental perturbations, that we can develop fuller understandings of community structure and dynamics.

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