FISH POPULATION RESPONSE TO VARIANCE IN STREAM DISCHARGE, ARAVAIPA CREEK, ARIZONA

by

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ABSTRACT

Recent developments in ecological theory have identified dynamical processes as key components to ecosystem integrity. Natural disturbance is one such process that may be essential to ecosystem maintenance. Under the maintenance paradigm, communities that have evolved with disturbance regimes should show resilience to disturbance events.

Spatial variance of the Aravaipa Creek fish populations was compared to variance in creek discharge on two temporal scales, from long- (decades) and short-term (months) studies. The hypothesis that patterns of spatial variance, if present, followed patterns of variance in discharge or discharge-related phenomena was supported by long-term data. The short-term data suggest that recruitment of some species tracks discharge-related disturbance events and patterns.

Sediment transport and deposition are determined by magnitude, intensity and frequency of disturbance events; spatial heterogeneity and availability of habitats in Aravaipa Creek thus are maintained. Fish populations appear to track these events through spatial responses, demonstrating resilience.

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INTRODUCTION

Waterless Deserts and Deserted Waters.—Many of the first reactions to the phrase "desert fishes" are nervous laughter accompanied by suggestions that such a phrase is oxymoronic. Fishes nonetheless exist in North American deserts and other arid lands, often abundantly where permanent water occurs. The evolutionary history of native Western American fishes involves persistence under severe conditions. As regional warming progressed through Tertiary times, ever-increasing aridity culminated after the last glaciation into present deserts (Axelrod, 1979). Aquatic communities evolved along with this climatic trend (Miller, 1981; Resh *et al.*, 1988) and exploit available water to "boom" in wetter years, and decline or "bust" during drought (Minckley, 1973; Poff and Ward, 1989).

Human modifications and over utilization of water resources have drastically altered these aquatic systems. Many natural waters are diverted, impounded, or pumped dry. Extensive fragmentation of habitat has exacerbated local extinctions, since populations that vary widely in numbers often reach levels too low for recovery (Pimm, 1991; Schoener and Spiller, 1992) and there is no opportunity for populations to recolonize. Human impacts that continue to reduce water availability cause vast reductions in species' geographic ranges and population sizes, and thus in regional biodiversity. Introduced species have replaced natives in altered habitats, and where native fishes remain, their populations are increasingly small and often nearing extirpation (Minckley and Meffe, 1987; Minckley *et al.*, 1997).

Species that fluctuate dramatically in numbers, from minor to substantial percentages of a community over time, are a dilemma for conservation managers. This is especially true of Western American fishes, many of which are Federally listed under the Endangered Species Act of 1973 (as amended). High-variance populations are addressed by theory, but due to an inability to replicate conditions in unpredictable environments, it is difficult to apply theory to management (Hilborn, 1992). This is especially the case of highly variable, "boom or bust" desert streams where a population or species may be in jeopardy, or even considered extinct for years or decades, then reappear (Marsh *et al.*, 1990; Knowles *et al.*, 1995). Others may in fact disappear permanently.

Temporal and spatial variance are two types of environmental variance that describe population fluctuations. Temporal variance in fish populations is the difference in abundance on a relative time scale. Spatial variance is differential distribution in abundance among available habitats. However, environmental variance may not always be clearly of a single type, as it is common for temporal and spatial variance to interact. I examined long-term (decades) data on fishes (Minckley, unpubl.) and stream discharge [U.S. Geological Survey (USGS), various dates] for Aravaipa Creek, Graham and Pinal counties, AZ. Acquisition of a shorter-term (months) data set for the same place, allowed me to examine high-variance populations and their spatial responses to discharge and discharge-related variables at two temporal scales. Original hypotheses were: The community showed no pattern of spatial variance (H_0); and patterns of spatial variance, if present, followed patterns of variance in discharge or discharge-related phenomena (H_1).

Study Area.—Aravaipa Creek is one of the last perennial tributaries to the San Pedro River to support a diverse assemblage of native fishes. The system is thus of singular importance as a refugium for a fauna otherwise fast disappearing, and critical as a point of reference in assessment of regional ecological change (Rolston, 1991; Landres, 1992).

Headwaters of Aravaipa Creek are in a broad watershed lying among the Pinaleño, Santa Teresa, and Galiuro mountains in Graham County (Fig. 1). The perennial section rises from unconsolidated sediments of its bed at 1050 m above mean sea level and flows northwest ("eastern reach"). Its floodplain funnels progressively into a narrow "canyon reach" with pronounced gradient, cutting west between the Galiuro and Santa Teresa mountains into Pinal County. The canyon's 18 km length has vertical rock walls rising more than 250 m above the stream. Canyon widths rarely exceed 100 m, and sometimes constrict to less than 20 m. The creek then flows southwest for 12 km, to turn west through a gradually widening floodplain for another 10 km ("western reach"). At modal discharge, the remaining segment is ephemeral for 8 km, where surface water disappears into deep alluvium before its confluence with the San Pedro River at 650 m above mean sea level (Simons, 1964; Cooke and Reeves, 1976; Minckley, 1981).

The U.S. Bureau of Land Management (BLM) manages a Wilderness Area within the canyon reach, and The Nature Conservancy (TNC) owns much of the land both up- and downstream of the Wilderness. Both agencies have instream-flow water-rights to maintain baseflows in the system for conservation purposes. The eastern and western reaches are further used for limited farming and pasturage; ground water is pumped or the creek diverted for irrigation, at times drying short segments (Ellingson, 1980).

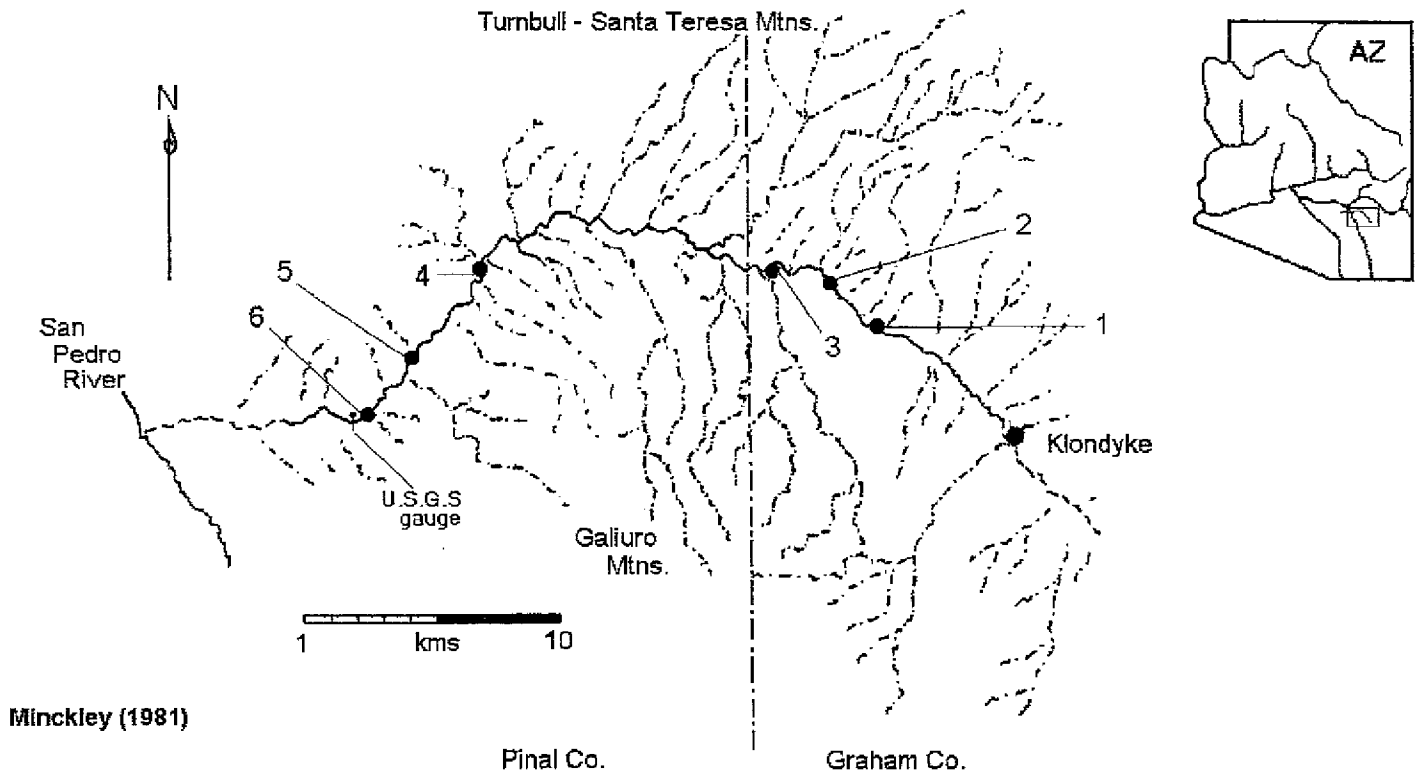


Figure 1. Map of Aravaipa Creek, Pinal and Graham counties, AZ, depicting sampling sites 1&2 in the eastern reach; sites 3&4 in the canyon reach; and sites 5&6 in the western reach.

Fishes and Fish Habitats.—Seven native fishes, five cyprinids (minnows) and two catostomids (suckers), inhabit the system. Four of the minnows are small-bodied, short-lived species (longfin dace, Agosia chrysogaster; spikedace, Meda fulgida; speckled dace, Rhinichthys osculus; and loach minnow, Tiaroga cobitis). One minnow (roundtail chub, Gila robusta) and both catostomids (Sonora sucker, Catostomus insignis; and desert sucker, Pantosteus clarki) are long-lived and large-bodied.

Stream habitats are a product of the physical characteristics of each reach and the magnitude and pattern of recent flooding (Gorman and Karr, 1978; Matthews, 1986; Sedell *et al.*, 1990). Distribution of habitats helps determine distribution of fishes according to their requirements. Agosia chrysogaster thrive in lower-elevation, hot, shallow, sand-bottomed reaches. Meda fulgida are more numerous in pools and eddies. Rhinichthys osculus are primarily over coarse substrates, often associated with freshly scoured riffles and turbulent margins. Tiaroga cobitis are in similar places. Catostomus insignis and G. robusta occupy deep undercuts and debris piles; P. clarki live in more open pools and riffles where periphyton is abundant. Most species can be found in all segments of the creek, depending on time of year and population sizes. The latter are highly variable, and some trends have been hypothesized: Large-bodied fishes are capable of moving great distances (Siebert, 1980; Williams, 1991); small-bodied fishes also move, and strong habitat requirements tend to segregate them spatially (Barber and Minckley, 1966; Minckley, 1973, 1981) contributing to apparently well-defined niche space (Schreiber, 1978; Schreiber and Minckley, 1981; Vives and Minckley, 1990). Additional biological information for native fishes is summarized in Table 1.

Table 1. Habitat summary for adult native fishes in Aravaipa Creek, Arizona (Barber and Minckley, 1966, 1983; Minckley, 1973, 1981; Schreiber and Minckley, 1981).

Species[1/]	gradient	preferred substrate	cover	depths	habitat type	reproduction and other notes
AGCH	low	sand, silt	algae, debris	shallow	glides, sandy runs, moderate riffles, pools	digs spawning pits in sand; omnivorous and opportunistic
GIRO	low-high	generally fine	cutbanks, debris, roots, shade	deepest available	corners, backwater, pools	spawns over gravel(?), young in margins near cover; feeds on algae, invertebrates, fishes
RHOS	low-moderate	gravel, cobble, sand	riffles, streamside plants	moderate to shallow	riffles, edges, glides, runs	spawns over clean, post-flood gravel; feeds on benthic invertebrates
TICO	low-moderate	rubble, cobble, gravel	rubble, riffles	shallow	turbulent riffles	nests under rubble in cavities; feeds on riffle-dwelling invertebrates
MEFU	moderate-low	cobble, gravel, sand	riffles, submerged algae and debris	moderate to shallow	shear zones, pools near swift riffles	spawns over coarse sand and gravel; feeds on drifting invertebrates
CAIN	moderate-low	sand, silt, gravel	cutbanks, roots, debris, depth in pools	deep to moderate	pools, undercuts, shade	spawns on gravel riffles, young in channel braids; feeds on invertebrates
PACL	high-low	rubble to gravel	cutbanks, roots, debris, depth in pools	moderate to shallow	pools, riffles, undercuts, shade	spawns on gravel riffles, young in channel braids; feeds on periphyton scraped from large substrates

[1/] AGCH=*Agosia chrysogaster*, GIRO=*Gila robusta*, RHOS=*Rhinichthys osculus*, TICO=*Tiaroga cobitis*, MEFU=*Meda fulgida*, CAIN=*Catostomus insignis*, PACL=*Pantosteus clarki*

Eight non-native species have been recorded. Non-natives almost certainly affect the native species and community, but to what degree is unknown. Greater abundances occur in the western reach, with dispersal to the eastern reach limited by winter floods and frequent spates of summer monsoons which remove non-natives from the high-gradient, constrained canyon reach. Natives do not appear to be displaced by flooding, at least as adults (Minckley and Meffe, 1987; Meffe and Minckley, 1987).

MATERIALS AND METHODS

Field Operations.—Sampling methods and general localities selected in 1964 for long-term studies were also applied for the short-term data set. Two sites in the three stream reaches (Appendix A), visited twice annually (spring and autumn) since 1964 (Minckley, unpubl.), were sampled monthly from March 1991 to February 1993. All sampling has been by two sizes of seines, 1.8- x 1.2-m with 3.2-mm mesh, and 4.6- x 1.2-m with 6.4-mm mesh, each with double-weighted leadlines. Vigorous and thorough coverage of at least 200 linear meters of creek per site included kicking the substrate from up- to downstream, probing beneath cut-banks and around obstructions, and sweeping through open-water areas. Seining distance was standardized when feasible to twice the length of seine in use. Fishes in each haul were identified, counted, and life stages were combined for the long-term data. Fish were recorded as adults or juveniles (Table 2) for the short-term data set. Daily mean discharges were obtained from USGS as recorded at a downstream (western reach) gaging station (Fig. 1).

Data Analyses.—Coefficient of variation (CV) for the long-term data set was used to estimate annual spatial variance for each fish species among reaches. Coefficient of variation in the short-term data set represents monthly spatial variance. As noted, long-term data are for all life-history stages combined; short-term data were treated the same way or separated by adult and juvenile classes for specific analyses. Coefficient of variation of stream discharge was calculated from daily mean discharge to represent annual variance for the long-term data and monthly variance for the short-term data.

Table 2. Estimated total lengths at sexual maturity for native fishes of Aravaipa Creek, Arizona, used in field collections as criteria for recording as "juvenile" vs. "adult" (Minckley, pers. comm.).

Species	Total length (mm)
TICO	38
AGCH, MEFU, RHOS	45
PACL	125
CAIN, GIRO	150

Coefficient of variation was used to demonstrate the amount of variation independent of the mean within data sets; because small (often zero) sample sizes are common for some species, the unbiased estimator for small sample sizes was used following Sokal and Rohlf (1981). When zeros occur in samples CV is a better measure of variance, over the more commonly used standard deviation of the logarithms of the population densities, because data do not require transformation and thus are not sensitive to zeros (McArdle *et al.*, 1990).

I used the Distance Weighted Least Squares (DWLS) algorithm (Wilkinson *et al.*, 1992, following McLain, 1974) to smooth fluctuations around temporal trends in CV. Distance Weighted Least Squares uses a least squares technique when fitting a line, where neighboring values on the scatterplot are weighted more than distant or outlier values. Weighting contributes to an emphasized curve rather than an approximated straight line usually obtained by least squares (McLain, 1974; Trexler and Travis, 1993).

Second-order regression analyses (Neter *et al.*, 1990; Wilkinson *et al.*, 1992) were used on curves to compare spatial variation of fishes to patterns of variance in discharge. Statistical analyses and graphs were generated with Systat for Windows, version 5.05, and Sigma Plot for Windows, version 2.01.

RESULTS

Raw abundances in the long-term data set were plotted using Tukey box plots to emphasize the variability and general lack of central tendencies of fish populations (Appendix B). Raw numbers from long-term data are plotted as histograms to review distributions among creek reaches and population characteristics over years (Appendix C). Each plot represents an individual species with regard to abundances by stream reach in each segment of the stacked bars; equivalent sample periods (spring and autumn only in 1991-93) are included from the short-term data set. In some years, variations indicate intensity of sampling, often reflecting experience of field assistants or other sampling bias. Nonetheless, short-term data generally coincide with long-term ranges, with only M. fulgida and T. cobitis differing greatly. Short-lived fishes show more year-to-year variance, whereas abundances of long-lived fishes remain relatively consistent over longer periods of time.

Raw data for daily mean discharges showed highly variable trends over the long-term data collecting period (Fig. 2). Annual modal discharge and annual weighted average of daily discharges also are presented (Fig. 3) to elucidate the sequence of changes and trends. Baseflows appear to have elevated after floods of 1978-79, began returning to pre-1978 conditions until the flood of 1983, elevated again, then began to return to lower volumes over the past few years. Elevated baseflows may be explained by reduced irrigation due to conservation actions and because channel incision precluded use of diversions for a time after major floods.

Figure 2. Daily mean discharge, $m^3 \cdot s^{-1}$ (common log scale), plotted over consecutive days within the period of Minckley's long-term fish collection records. USGS Gaging Station 09473000, Aravaipa Creek, AZ.

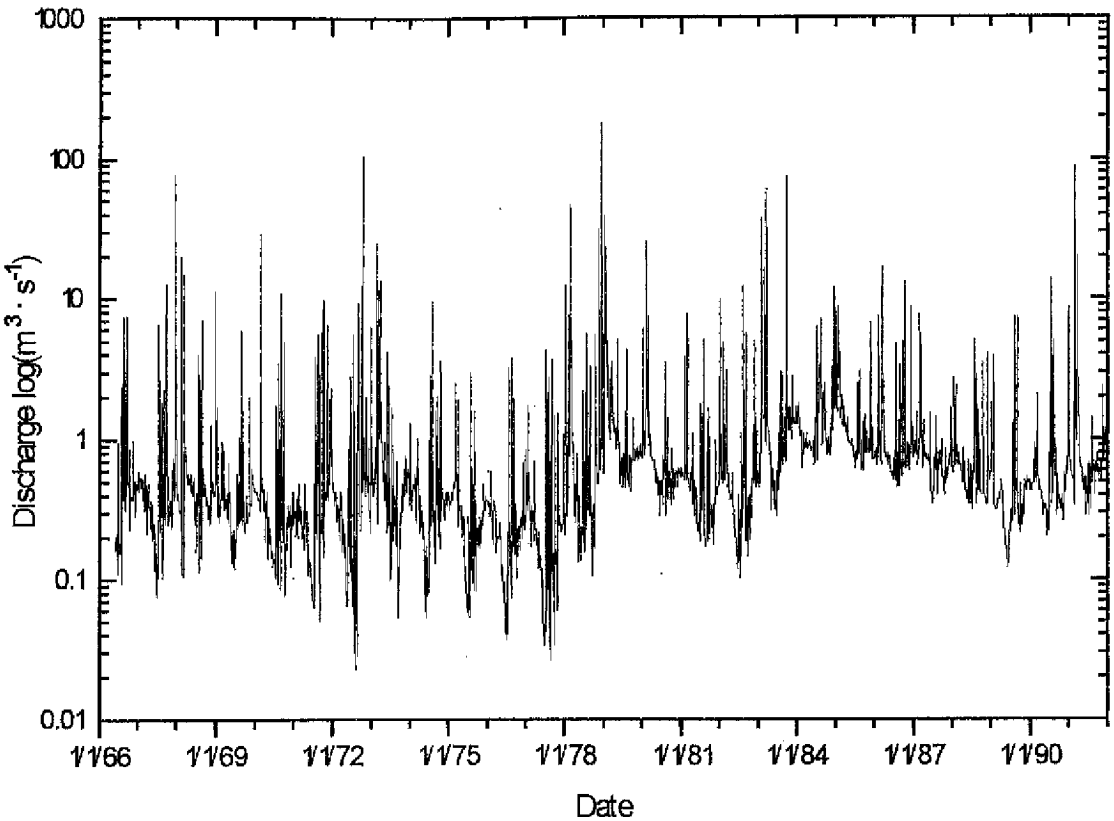
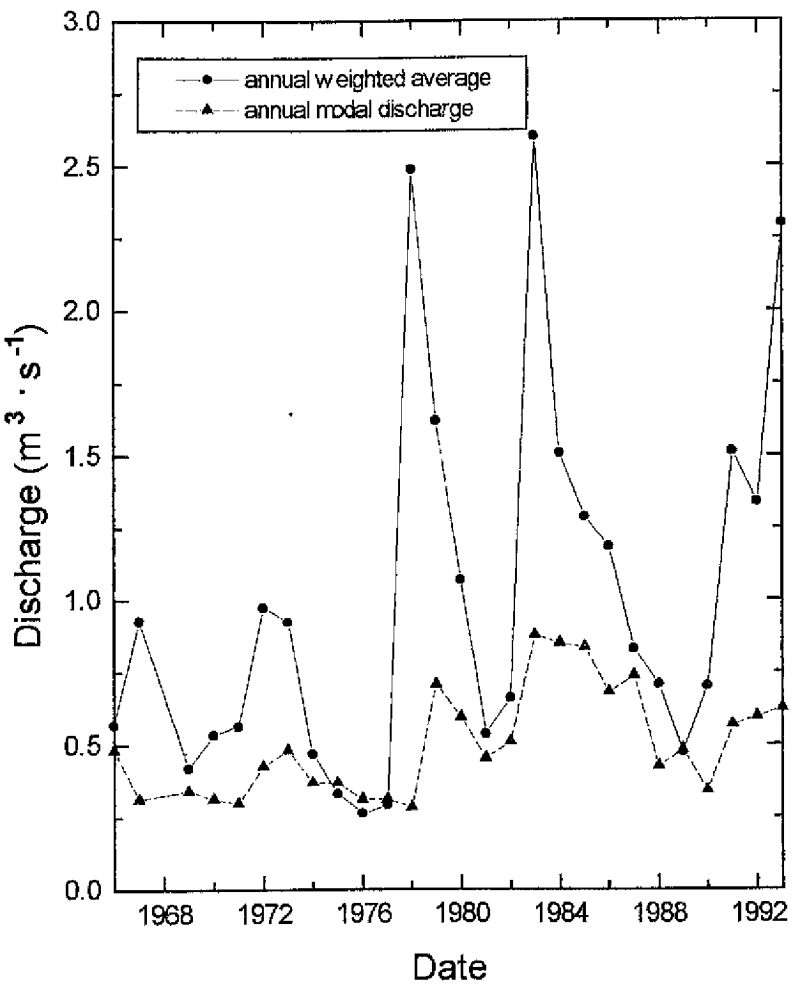


Figure 3. Annual modal discharge and annual weighted average of daily discharge, $m^3 \cdot s^{-1}$, plotted over consecutive days within the period of Minckley's long-term fish collection records. USGS Gaging Station 09473000, Aravaipa Creek, AZ.

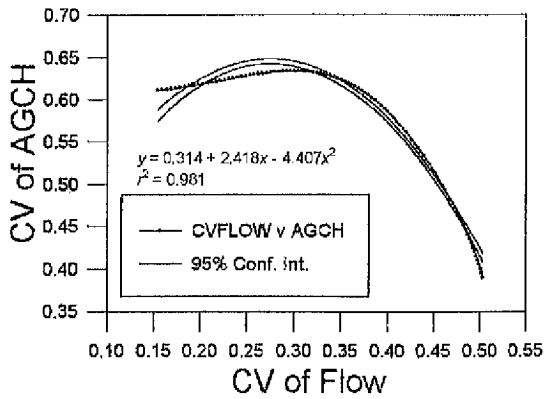


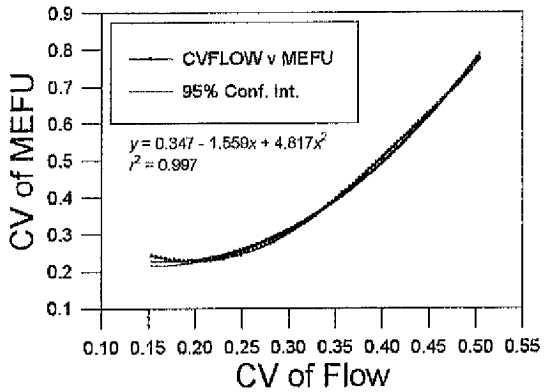
Regression analyses of smoothed CV for fish populations and stream discharges resulted in highly significant correlations. In several of the species, as variance in discharge increases population sizes increasingly differed among reaches (Fig. 4, positive slope), at least until a threshold is reached. This apparent "threshold response" is best explained as a point where each species reaches a level of maximal response to discharge variance and reverts to previous values of spatial variance, *i.e.*, more uniformly distributed among reaches (Fig. 4 - negative slope). Levels that decline beyond "threshold" may indicate radical change in habitat conditions or flood displacement of populations.

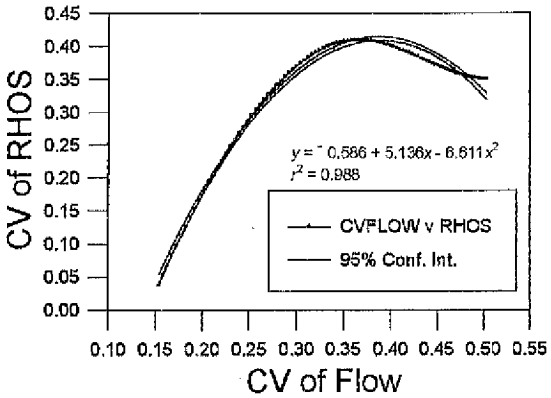
Rhinichthys osculus and T. cobitis respond similarly, with nearly identical "threshold" values and slopes. The two catostomids and M. fulgida are notable in exhibiting strong positive slopes with little or no "threshold" response. Responses of A. chrysogaster and G. robusta exhibit the greatest departures. The former seems to have an early "threshold," as discharge variance increases their spatial variance decreases (*i.e.*, they become more evenly distributed). Even though spatial variance in the chub is strongly influenced by discharge variance, its pattern of response is so different from other species that other, unmeasured variables must be coming into play.

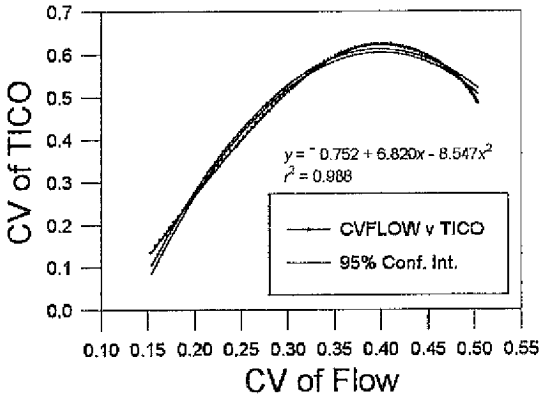
Short-term data were analyzed similarly but by using a monthly temporal scale. Range of variance for both discharge and fishes is greater than on the long-term scale. Results for A. chrysogaster and G. robusta (Fig. 5) show the greatest departure from long-term data. For the remainder, discharge values falling within the range of the long-term population data are similar to results of the long-term analyses. Outside that range, short-term responses typically extend in the same directions implied by the long-term data.

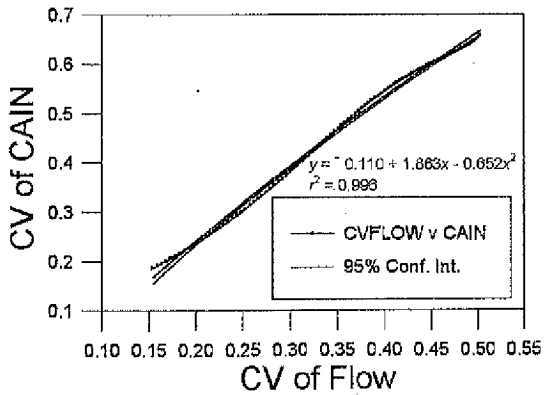
Figure 4. Polynomial regression results for Minckley's long-term data set, where CV of individual fish species among stream reaches was regressed on CV of annual stream discharge (flow), Aravaipa Creek, AZ. The model statement, coefficient of determination ($p \leq 0.001$), and 95% confidence intervals are included on each graph.

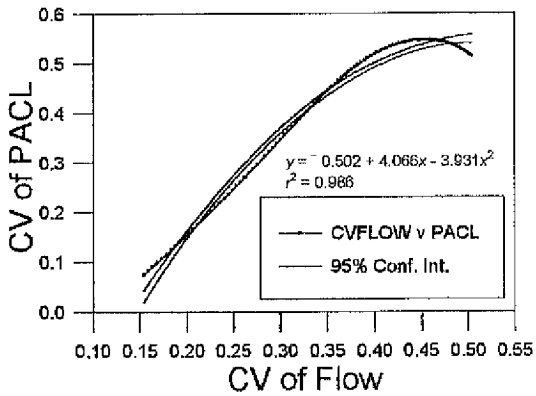

CV of AGCH
CV of Flow
y = 0.314 + 2.418x - 4.407x²
r² = 0.981
CVFLOW v AGCH
95% Conf. Int.


CV of MEFU
CV of Flow
CVFLOW v MEFU
95% Conf. Int.
y = 0.347 - 1.559x + 4.817x²
r² = 0.997


CV of RHOS
CV of Flow
y = ⁻0.586 + 5.136x - 6.611x²
r² = 0.988
CVFLOW v RHOS
95% Conf. Int.


CV of TICO
CV of Flow
y = ⁻0.752 + 6.820x - 8.547x²
r² = 0.988
CVFLOW v TICO
95% Conf. Int.


CV of CAIN
CV of Flow
y = ⁻0.110 + 1.863x - 0.652x²
r² = 0.998
CVFLOW v CAIN
95% Conf. Int.


CV of PACL
CV of Flow
y = ⁻0.502 + 4.066x - 3.931x²
r² = 0.986
CVFLOW v PACL
95% Conf. Int.

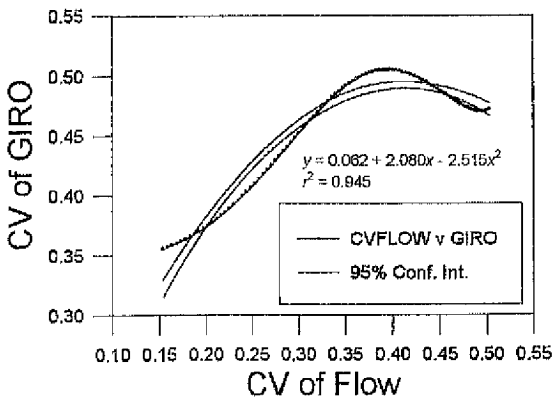
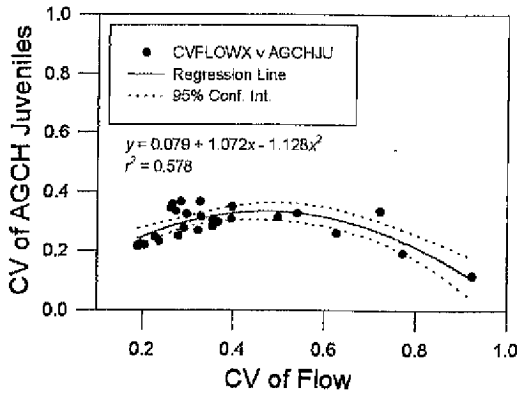
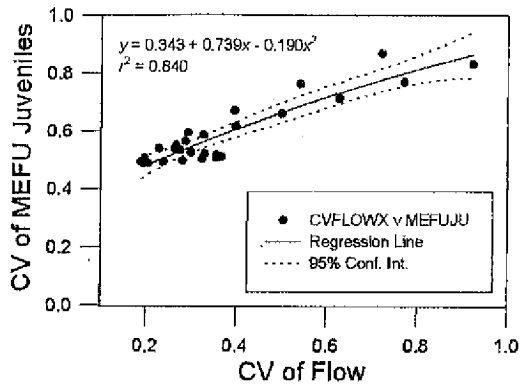
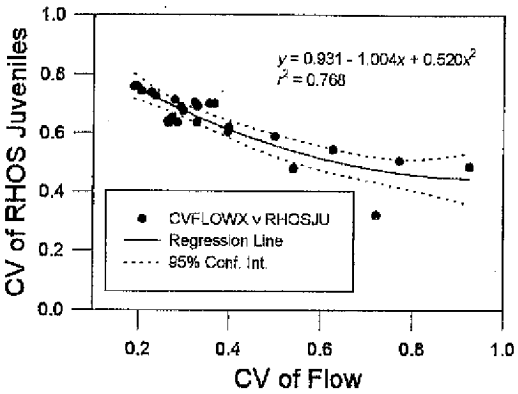
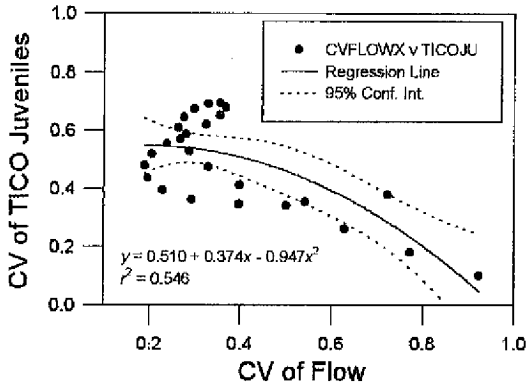

CV of GIRO
CV of Flow
y = 0.062 + 2.080x - 2.515x²
r² = 0.945
CVFLOW v GIRO
95% Conf. Int.

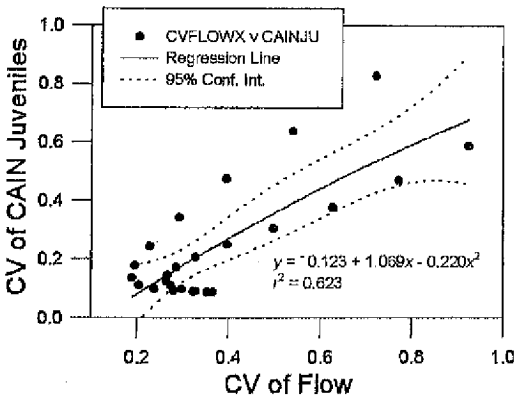
Figure 5. Polynomial regression results for short-term data set, where CV of individual fish species among stream reaches was regressed on CV of monthly stream discharge (flow), Aravaipa Creek, AZ. The model statement, coefficient of determination, and 95% confidence intervals are included on each graph.

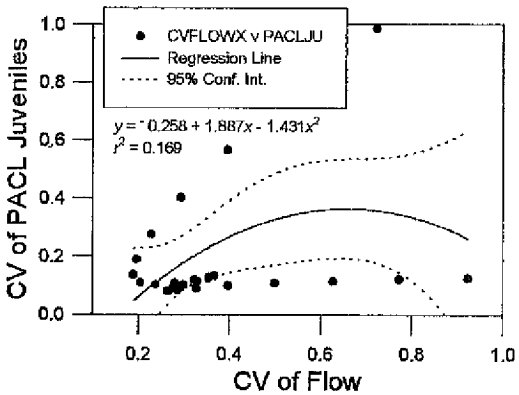

CVFLOWX v AGCHJU
Regression Line
95% Conf. Int.
y = 0.079 + 1.072x - 1.128x²
r² = 0.578
CV of AGCH Juveniles
CV of Flow

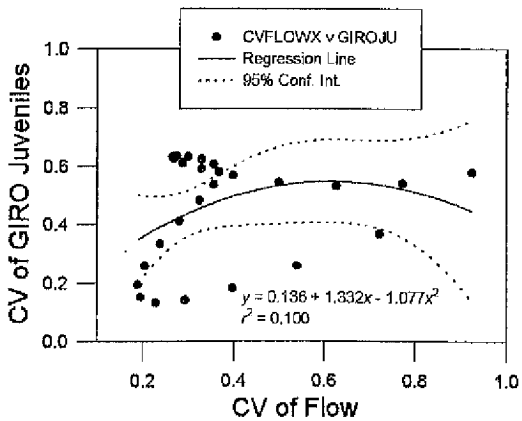

y = 0.343 + 0.739x - 0.190x²
r² = 0.840
CVFLOWX v MEFUJU
Regression Line
95% Conf. Int.
CV of MEFU Juveniles
CV of Flow


y = 0.931 - 1.004x + 0.520x²
r² = 0.768
CVFLOWX v RHOSJU
Regression Line
95% Conf. Int.
CV of RHOS Juveniles
CV of Flow


CVFLOWX v TICOJU
Regression Line
95% Conf. Int.
y = 0.510 + 0.374x - 0.947x²
r² = 0.546
CV of TICO Juveniles
CV of Flow


CVFLOWX v CAINJU
Regression Line
95% Conf. Int.
y = -0.123 + 1.069x - 0.220x²
r² = 0.623
CV of CAIN Juveniles
CV of Flow


CVFLOWX v PACLJU
Regression Line
95% Conf. Int.
y = -0.258 + 1.887x - 1.431x²
r² = 0.169
CV of PACL Juveniles
CV of Flow

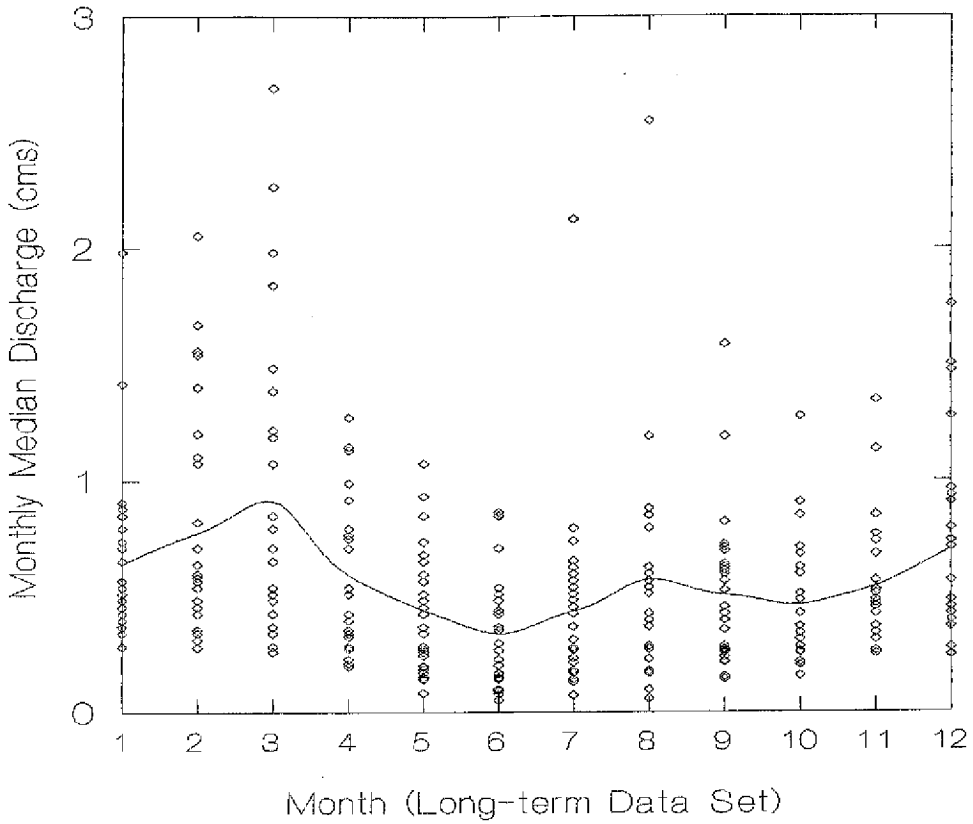

CVFLOWX v GIROJU
Regression Line
95% Conf. Int.
y = 0.136 + 1.332x - 1.077x²
r² = 0.100
CV of GIRO Juveniles
CV of Flow

Polynomial regression of results of the short-term data (Fig. 5) are not, however, as statistically robust as in the long-term data set. The cyclical nature of the population data suggests that temporally-driven variables acting within the seasonal scale influence population responses. Cycles of precipitation and streamflow, sediment sorting, and life-history phenomena may play such roles, as discussed below.

Median flows for long- and short-term data sets in Figure 6 illustrate the bimodal annual hydrograph. Winter discharges contribute greater variance in both magnitude and time. Summer monsoons influence the hydrograph to a lesser degree, but still provide measurable effects. Median flows in the short-term data set closely resemble ranges and patterns of the long-term data.

When raw abundances of adult and juveniles in the short-term data set are plotted with CV of discharge, population recruitment appears to track the hydrologic cycle after a relatively short lag-time (Fig. 7). To further test this hypothesis, adult and juvenile class data were subjected to polynomial regression analyses after temporal-shift treatments were applied. In temporal-shift treatments, stream discharge CV data were shifted back 1-3 months for "pre"; forward 1-3 months for "post"; "null" indicates time-zero. A backward shift ("pre") in time was used to detect responses that might be independent of CV of stream discharge; a forward shift ("post") in time was used to detect responses that might indicate a lag response to CV of stream discharge. Coefficients from polynomial regressions indicate the correlation between CV of adult/juvenile fishes and CV of stream discharge at different points in the temporal shift treatment. Figure 8 depicts these values graphically on the temporal shift scale.

Figure 6. Median values for daily mean discharge plotted over consecutive months within period of Minckley's long-term fish collection records and short-term fish survey. USGS Gaging Station 09473000, Aravaipa Creek, AZ.


Monthly Median Discharge (cms)
0
1
2
3
1 2 3 4 5 6 7 8 9 10 11 12
Month (Long-term Data Set)

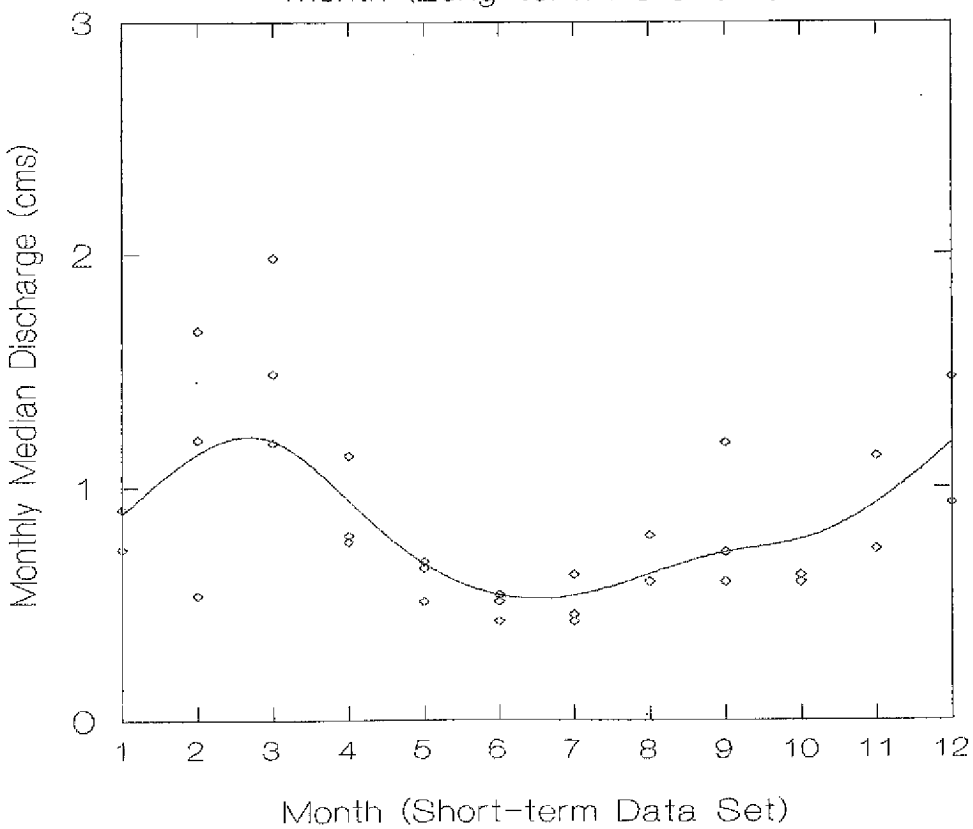
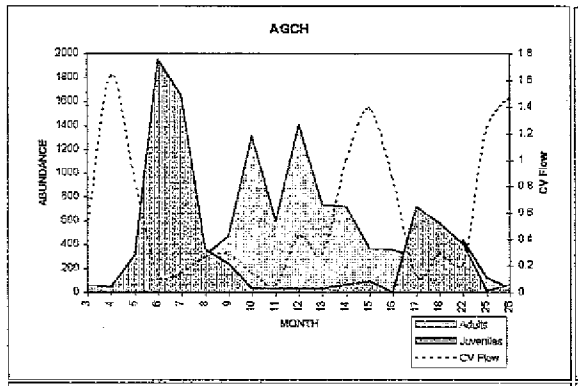
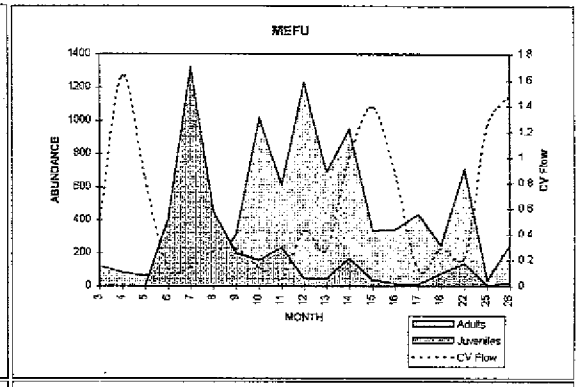
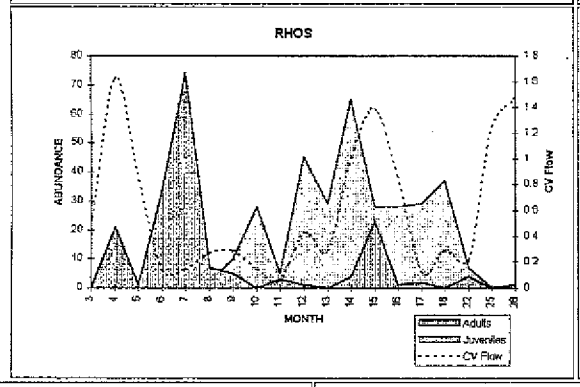
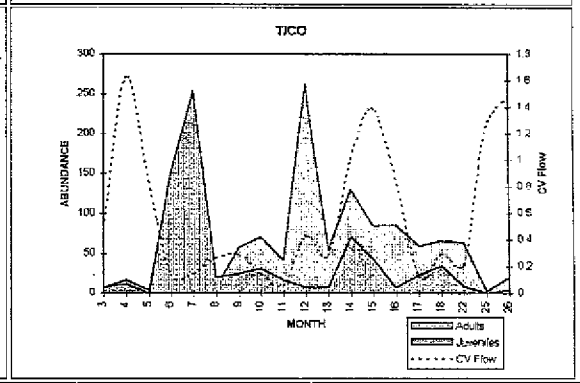

Monthly Median Discharge (cms)
0
1
2
3
1 2 3 4 5 6 7 8 9 10 11 12
Month (Short-term Data Set)

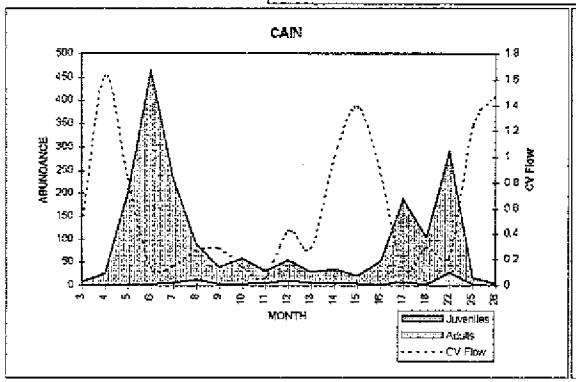
Figure 7. Graphs depicting population fluctuations of adult and juvenile fishes in the short-term data set. Coefficient of variation of monthly stream discharge (flow) is included for showing population correlation with discharge-related variables, Aravaipa Creek, AZ.

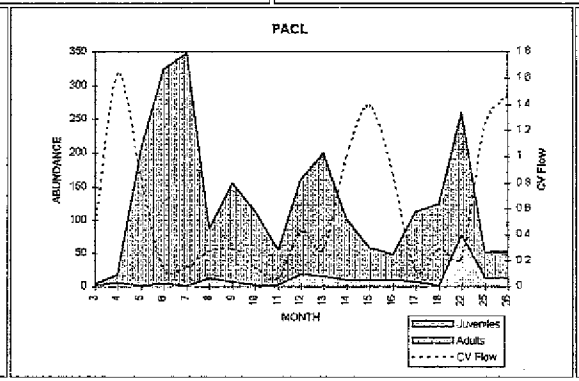

AGCH
ABUNDANCE
CV Flow
MONTH
Adults
Juveniles
CV Flow


MEFU
ABUNDANCE
CV Flow
MONTH
Adults
Juveniles
CV Flow


RHOS
ABUNDANCE
CV Flow
MONTH
Adults
Juveniles
CV Flow


TICO
ABUNDANCE
CV Flow
MONTH
Adults
Juveniles
CV Flow


CAIN
ABUNDANCE
CV Flow
MONTH
Juveniles
Adults
CV Flow


PACL
ABUNDANCE
CV Flow
MONTH
Juveniles
Adults
CV Flow

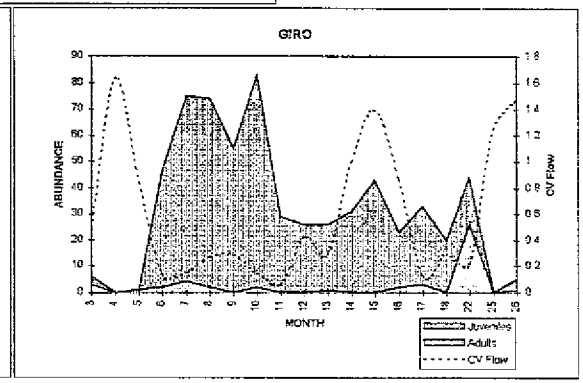
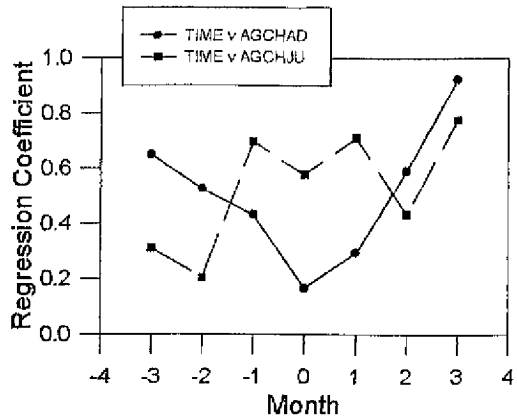
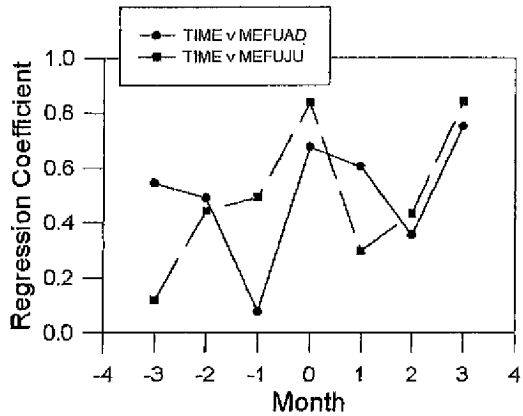
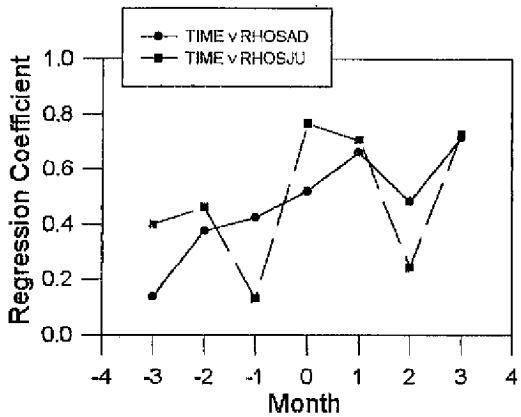
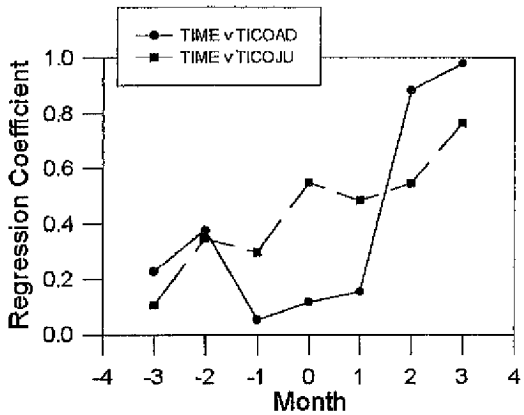

GIRO
ABUNDANCE
CV Flow
MONTH
Juveniles
Adults
CV Flow

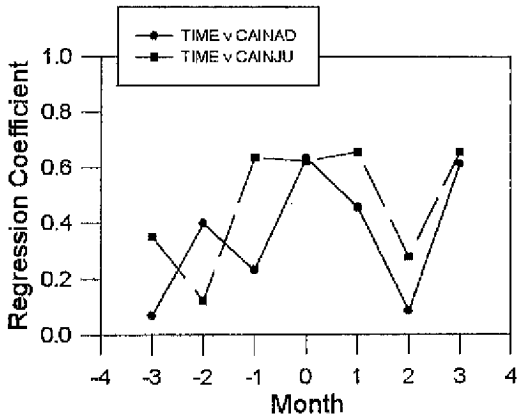
Figure 8. Graphs illustrating temporal-shift treatments of adult and juvenile fishes in the short-term data set. Negative numbers on the x-axis (Month) represent a backward temporal-shift; positive numbers represent a forward shift. Results were derived from polynomial regression of CV of individual fish species (after temporal-shift treatment) among stream reaches on CV of monthly stream discharge, Aravaipa Creek, AZ.

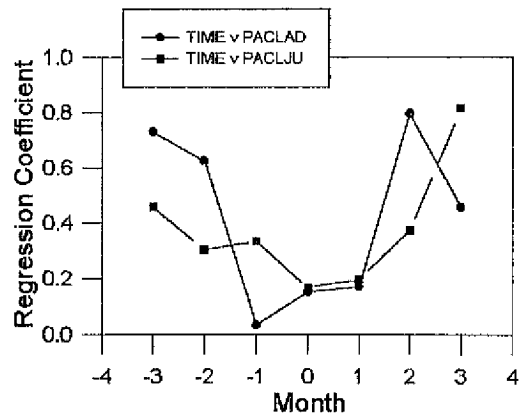

TIME v AGCHAD
TIME v AGCHJU
Regression Coefficient
Month

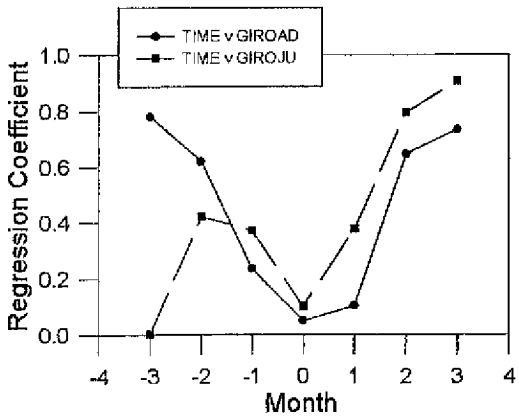

TIME v MEFUAD
TIME v MEFUJU
Regression Coefficient
Month


TIME v RHOSAD
TIME v RHOSJU
Regression Coefficient
Month


TIME v TICOAD
TIME v TICOJU
Regression Coefficient
Month


TIME v CAINAD
TIME v CAINJU
Regression Coefficient
Month


TIME v PACLAD
TIME v PACLJU
Regression Coefficient
Month


TIME v GIROAD
TIME v GIROJU
Regression Coefficient
Month

The temporal-shift treatments indicate that differential responses exist among life-history stages in Aravaipa Creek fishes. Agosia chrysogaster, T. cobitis, P. clarki, and G. robusta adults elicit more immediate negative response to increased variance in discharge by becoming uniformly distributed among reaches in the creek. Meda fulgida, R. osculus, and C. insignis adults appear to be unaffected by immediate increases in variance of discharge, with positive responses possibly indicated. Spatial variance in all juvenile fishes is more pronounced after a three-month lag period when variance in stream discharge begins to decline. Small-bodied fishes show a net increase in response after three months, while large-bodied fishes generally return to previous values. A two-month lag period is the approximate time it takes for newly recruited fishes to be "catchable" by seine after hatching. Rhinichthys osculus adults and T. cobitis juveniles increase steadily to a maximal response, independent of variance in stream discharge.

DISCUSSION

Patterns of spatial variance exist in Aravaipa Creek and spatial variance of fish populations is related to variance in stream discharge. The alternative hypothesis thus is supported.

Spatial variance in the short-term data set supports the functional relationships exhibited in the long-term data set. Patterns of spatial variance seem to explain much of the temporal variance in fish populations, and spatial variance is largely related to variance in discharge or discharge-related phenomena. Spatial variance in fish populations, habitat preferences, and recruitment response, may ultimately be determined by habitat heterogeneity (Schlosser, 1987). In Aravaipa Creek, heterogeneity is maintained by annual cycles of variance in discharge, *i.e.*, magnitude, duration, and frequency of flood events.

Abiotic Determinants.—Fish habitats in streams like Aravaipa Creek are controlled primarily by patterns of sediment degradation, transport, and deposition, which in turn are functions of bedload volume and patterns of precipitation and runoff (Minckley, 1981; Schlosser, 1982; Graf, 1988). Annual precipitation at Klondyke (upstream of the eastern reach) averages 39 cm, half of which is in summer (Simons, 1964; Ellingson, 1980). The area experiences strongly bimodal annual precipitation and resulting streamflow. Cyclonic winter rains are prolonged over several days or weeks, separated by a springtime drought from convective summer monsoons consisting of short, violent downpours of a few hours at most (Bruns and Minckley, 1980; Aldridge and Hales, 1984; Pearthree and Baker, 1987; Roeske *et al.*, 1989). An autumn drought completes the annual cycle.

Modal discharge for the long-term data set is approximately 0.34 $m^3 \cdot s^{-1}$. Runoff can accumulate rapidly and major flooding is common. However, discharge exceeded 60 $m^3 \cdot s^{-1}$ five times at 5–8-year intervals between 1964 and 1993 (Fig. 2). One major flood (>85 $m^3 \cdot s^{-1}$) occurred during the short-term study in March 1991. Other high discharges in winter through early spring and summer of 1992 approached 28 $m^3 \cdot s^{-1}$. High-gradient, physically-constrained reaches like the central canyon transport high sediment loads during floods (Twenhofel, 1942). As a result, these reaches have higher proportions of exposed or embedded, large-particle debris and bedrock. Wider floodplains with lower gradients promote deposition of massive amounts of finer sediments (Graf, 1988) that predominate in eastern and western reaches.

Long periods of "normal" flow, including low intensity, low-volume floods (Fig. 6) transport fine sediments into and through the canyon *via* both suspension and saltatory action. Pools are leveled and interstices of coarser sediments are filled. Sediment sorting occurs on riffles and runs during heavy freshets of summer monsoons, but this tends to be localized to near a particular cloudburst. Winter runoff, by far, dictates pattern and complexity of habitat for the year. Habitats will be more spatially permanent if heavy flooding produces adequate turbulence from large obstructions (*e.g.*, canyon walls, bedrock, roots of large trees) to scour deep pools and armor riffles with heavy boulders, cobble and rubble (Twenhofel, 1942; Burkham, 1970b; Heede, 1980).

Flood events, which tend to surge in volume due to variation in inputs contributing to the whole, transport comparable surges of sediments (cobble, gravel, and sand) that deposit where the stream widens, gradient flattens, or velocity and turbulence decrease for

some other reason (Twenhofel, 1942; Hereford, 1992; Gordon *et al.*, 1992). Dams formed by these deposits cause water to back up, break into braids, and meander until lower-elevation channels cut through them (Burkham, 1970a; Heede, 1980). If permanent enough, such areas develop high primary productivity since braids are often shallow and exposed to direct sun. Braided matrices provide excellent nurseries for larval and juvenile fishes. Larvae also are protected from aquatic piscivores by shallowness and space until sediments are sorted to re-establish a single, wetted channel. By then, juveniles are large enough to evade most native predators (Turner *et al.*, 1994).

John (1963) and other workers have suggested that photoperiod and temperature, along with flooding, may be important as cues for late summer-early autumn spawning by desert fishes. It seems evolutionary consistent, however, for them to use water immediately after it becomes available, especially after moderate to heavy floods have scoured substrates, deepened pools, and deposited sediment dams appropriate for larval nurseries (Haynes *et al.*, 1984; Nesler *et al.*, 1988; Tyus and Karp, 1989).

Short-lived species in Aravaipa Creek seem to have a strong positive response to floods or flood-related phenomena, but weaker responses to other environmental cues. Agosia chrysogaster thrive when habitats are relatively homogenous, becoming far more numerous when finer sediments predominate. Their response to discharge variance was not as strong as some other species in the long-term data set, but short-term data show a positive response to decline (recovery phase) of the flood hydrograph (Fig. 7). Minckley (1981) and Kepner (1982) indicated that biannual or multiannual spawning was typical in apparent response to flooding or flood scour. John (1963) suggested that spawning by R.

osculus tracked photoperiod and floods in both spring and late summer in small mountain streams, but a reproductive cue consisting of both increasing (spring) and decreasing (late summer) photoperiod is difficult to accept. John (1963) found ripe males in late summer of drought years, however, and stated that flooding was required to elicit successful reproduction. John (1964) recorded downstream displacement of R. osculus after a summer flash flood, with a subsequent recruitment effort. Fresh-scoured substrate may provide a stimulus to initiate spawning by R. osculus (Mueller, 1984). Vives and Minckley (1990) reported autumnal spawning of T. cobitis in Aravaipa Creek twelve days after a late monsoonal spate. Barber *et al.* (1970) detected no correlation of photoperiod and gonadal cycles in M. fulgida in Aravaipa Creek, and Minckley (1981) reported species with mature gonads for much of the year and with a later major spawning season than other short-lived species. I found tuberculate M. fulgida in breeding colors through late summer (but not always as distinctly so as in spring) and spawning after summer floods was evidenced by individuals <15 mm long caught in autumn.

Long-lived species also may exhibit spatial responses to floods and flood-related phenomena. Catostomus insignis, P. clarki, and G. robusta require deeply scoured pools, undercuts, and root- and debris-masses, that are established/maintained in years of heavy flooding especially in the canyon segment. Siebert (1980) observed canyon-bound migration of these fishes during months when higher temperatures and lower stream discharges appeared to limit habitat suitability elsewhere. However, pool depth and overall volume may determine sedentary or vagile activity patterns (Bestgen *et al.*, 1987). Williams (1990) did not observe canyon-bound migration and suggested that habitat

heterogeneity and complex responses related to floods and drought might provide necessary cues. Highly variable discharges did not occur during Williams' 1989-90 census. Sediment distribution is more uniform and fewer scoured habitats are available in Aravaipa Creek when variance in discharge is low, therefore, migration is more likely to be statistically undetectable. Alternatively, years of high-variance in stream discharge will maintain an abundance of scoured habitats in Aravaipa's canyon segment and migration will be conspicuous, as evidenced in Siebert's 1978-79 census.

Disturbance: A Driving Ecosystem Element.—Minckley (1981) reported Aravaipa as having one of the largest "standing crops" of fishes known. I suggest the heterogeneous nature of the system promotes a higher carrying capacity than would normally be expected, thus reducing negative, density-dependent effects (Ricklefs, 1979; Resh *et al.*, 1988; Rosenzweig, 1996). When summer floods redistribute or allow redistribution of fishes, new resources are available to juveniles that spring from adults with rapid reproductive response to flooding. Monsoonal freshets usually arrive in time to allow distribution of larvae into newly scoured, previously unavailable places (Ricklefs, 1979; Denslow, 1985). Decreasing negative density-dependent factors occur in periods of low flow; it is unlikely that fishes would reproduce when in these stressed, crowded conditions. Because summer freshets are regular events, these species may have developed appropriate (exploitative) adaptive responses to floods (Karr and Freemark, 1985; Mayr, 1988). Floods also redistribute adults prior to spawning so related individuals in isolated pools are less likely to mate.

Coefficient of variation plots of short-term data (Fig. 5) indicate that spatial variance is correlated with discharge variance, yet there are indications that considerable temporal influence exists as well. The short-term data reflect more temporal than spatial heterogeneity, which may be a result of the importance of scale in translating response to disturbance regimes (Karr and Freemark, 1985). Dynamics on one scale may determine stasis on another scale (White and Pickett, 1985). The problem with using the same analyses for both long- and short-term data sets is that more temporal variance is inherent in the latter. Temporal variance on this scale may be contributed by annual cycles (*e.g.*, daylength, temperature, rainfall), life-history attributes, localized spatial disturbances, nutrient input, and other variables.

Highly resilient species can track environmental variance more closely than less resilient species; variance in populations thus can be associated with annual cycles (Schlosser, 1982; Pimm, 1984, 1991). Therefore, highly resilient species could be responding to variables other than those being tested (in this case, variance in discharge) (Hilborn, 1992). Fine-scale responses [days or weeks; *e.g.*, the recruitment responses reported by John (1964), Kepner (1982), and Vives & Minckley (1990)] were not, however, evident in the short-term component of my study. Further subdivision of age/size classes of juvenile/larval fishes might have been helpful.

Historic and current human influences in the Aravaipa Creek system are very similar to PRESS experiments (Bender *et al.*, 1984; Yodzis, 1988; Pimm, 1991) that provide information on population resistance. The long-term data set could be used along with records of human actions to detect changes over time (Ives, 1995), but further

analyses would be necessary to effectively dissect out any deterministic effects. For example, channelization, and recent implementation of instream-flow water-rights may be creating conditions to which the fish community has or will respond. It might be helpful in this regard to review the long-term data set at the short-term scale, especially considering that significant habitat and population changes occurred during the period. The long-term data set would be useful in separating temporal and spatial variance seen on the short-term scale, and information on temporal variance would be particularly helpful in determining community and population equilibrium conditions.

Management Implications.—Strong seasonal and spatial variation among species colonizing disturbance patches is probably typical of many communities, and is especially evident in species-rich communities (Denslow, 1985). Spatial variance must not, however, be confused with temporal variance in management decisions and actions. Temporal variance must be fully understood to distinguish normal levels from those which may indicate jeopardy (Landres, 1992); long-term data sets are useful in determining trends and in recognizing deviation. As populations approach drastic levels of temporal variance like those reported by Marsh *et al.* (1990) and Knowles *et al.* (1995), where a species remains undetected for decades before they appear or reappear, it must be nearing extirpation. Small populations are at greater risk of not recovering from dramatic population fluctuations or major catastrophes (Pimm, 1991; Mangel and Tier, 1994). These populations vary between few and essentially zero in "boom-and-bust" cycles where cycling too close to zero might be fatal (Pimm, 1991; Schoener and Spiller, 1992). With

extreme temporal variance, extinction can even occur in relatively large populations (Mangel and Tier, 1994).

Spatial variance in populations increases with increasing habitat heterogeneity. Habitat heterogeneity is reduced or absent when frequency and amplitude of the annual hydrograph is below average (Sedell *et al.*, 1990). Because homogeneous conditions may essentially consist of only a single large habitat, species diversity may be reduced by density-dependent effects that decrease options and opportunities for alternative life-history strategies to be expressed (Lomnicki, 1978). Further, in Aravaipa Creek, more homogeneous habitat conditions are created by channelization and bank stabilization, which both are being applied by government agencies. Natural channel dynamics could be better achieved without artificial structure, which would increase habitat heterogeneity (Stalnaker, 1981; Gordon *et al.*, 1992; Leopold, 1994). In other streams, hydrologic processes have become more homogeneous *via* human alterations that have brought about irretrievable changes to whole ecosystems.

Water use by humans in the American Southwest has essentially produced a chronic drought cycle for aquatic systems. Many fish populations thus have been maintained at low levels for decades. Connectivity between habitats and basins is lost through fragmentation, and local extirpations have reduced regional population sizes. Human-induced trends toward homogenized environments provide ideal conditions for establishment of exotic species that further increase local extirpation (Turner, 1974; Pimm, 1991; Minckley *et al.*, 1997). Current rates of environmental degradation may never permit recovery of species needed for healthy ecosystems. The 30-year data set for

Aravaipa Creek allows definition of adaptation of its fishes to, and dependence upon, a variable hydrologic cycle. It therefore must be emphasized that disturbance regimes are crucial to maintain if those remaining indigenous species are to survive in a functioning ecosystem.

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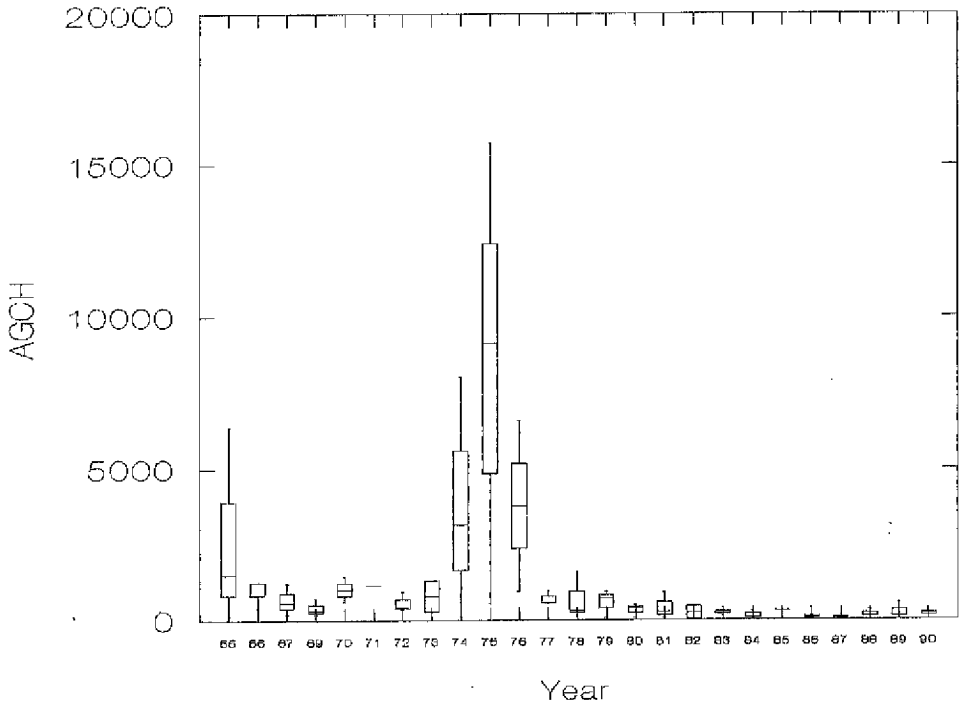
APPENDIX A

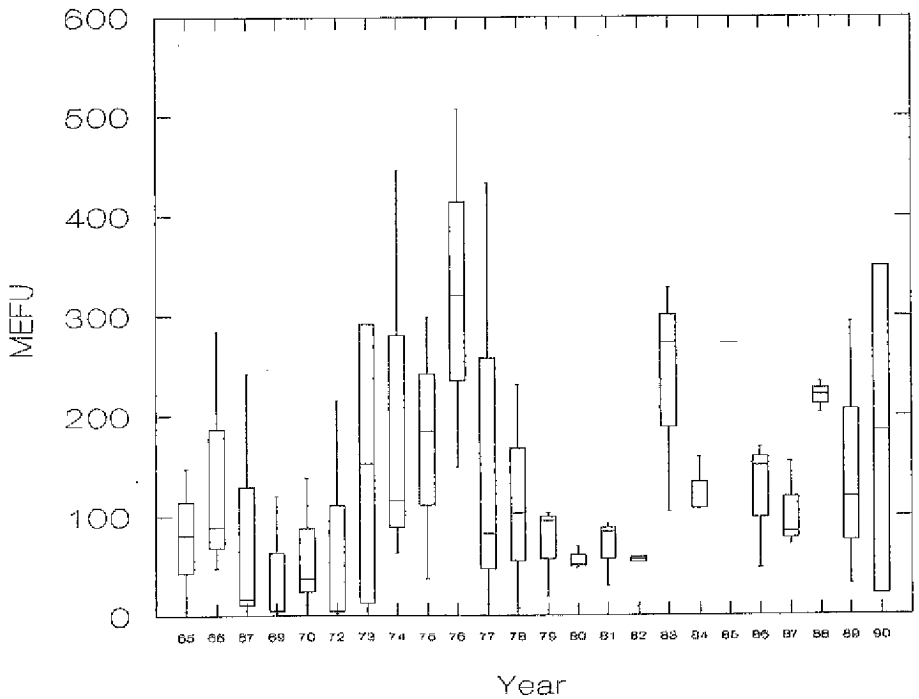
SAMPLE-SITE MAP-COORDINATES FOR LONG- (BARBER AND MINCKLEY, 1966) AND SHORT-TERM DATA SETS, ARAVAIPA CREEK, AZ.

Sample-site coordinates	Long-term data	Short-term data
T-7S R-16E S-11 NE1/4	√	
T-7S R-17E S-8 NW1/4	√	√
T-6S R-17E S-34 CENTER	√	√
T-6S R-17E S-26 SW1/4	√	
T-6S R-17E S-23 SE1/4	√	
T-6S R-17E S-24 NW1/4	√	√
T-6S R-18E S-18 NW1/4	√	
T-6S R-18E S-17 NE1/4	√	
T-6S R-18E S-15 NE1/4	√	
T-6S R-18E S-24 SE1/4	√	
T-6S R-18E S-24 E1/2	√	
T-6S R-19E S-19 CENTER	√	√
T-6S R-19E S-20 NW1/4	√	
T-6S R-19E S-21 SW1/4	√	√
T-6S R-19E S-27 W1/2	√	√

APPENDIX B

TUKEY BOX PLOTS OF RAW ABUNDANCES OF FISHES IN THE LONG-TERM DATA SET (MINCKLEY, UNPUBL.), ARAVAIPA CREEK, AZ.


20000
15000
10000
5000
0
AGCH
65 66 67 69 70 71 72 73 74 75 76 77 78 79 80 81 82 83 84 85 86 87 88 89 90
Year


600
500
400
300
200
100
0
MEFU
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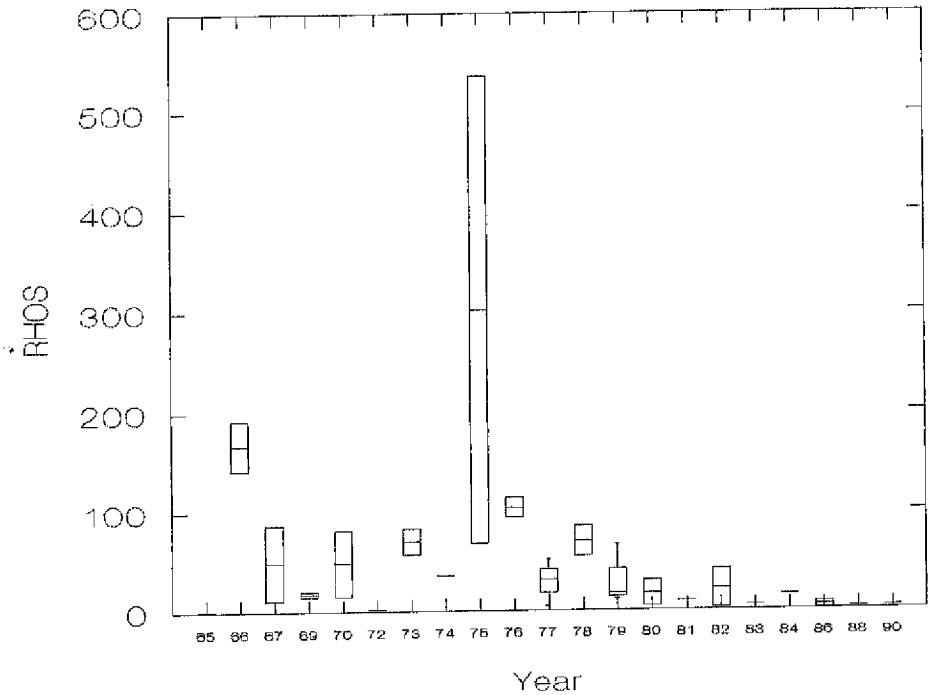
Year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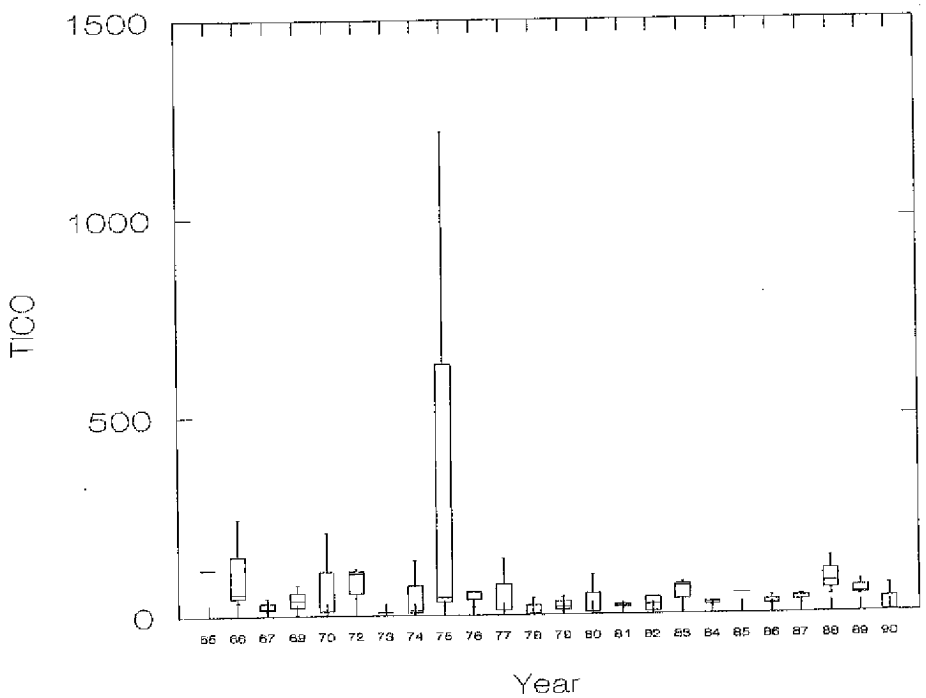
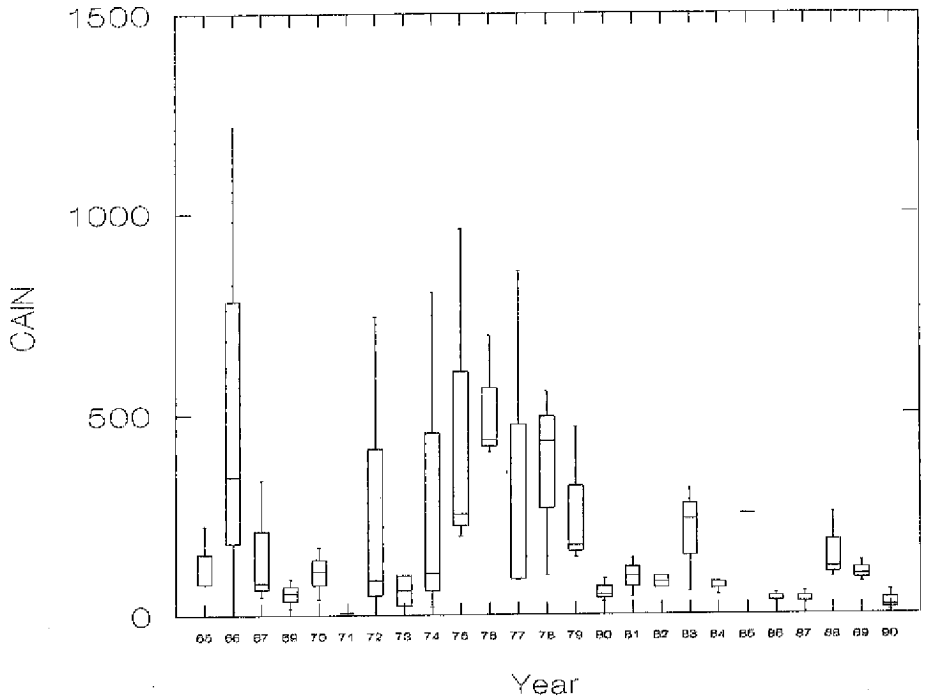
500
400
300
200
100
0
RHOS
65 66 67 69 70 72 73 74 75 76 77 78 79 80 81 82 83 84 86 88 90
Year


1500
1000
500
0
TICO
66 67 69 70 72 73 74 75 76 77 78 79 80 81 82 83 84 85 86 87 88 89 90
Year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1000
500
0
CAIN
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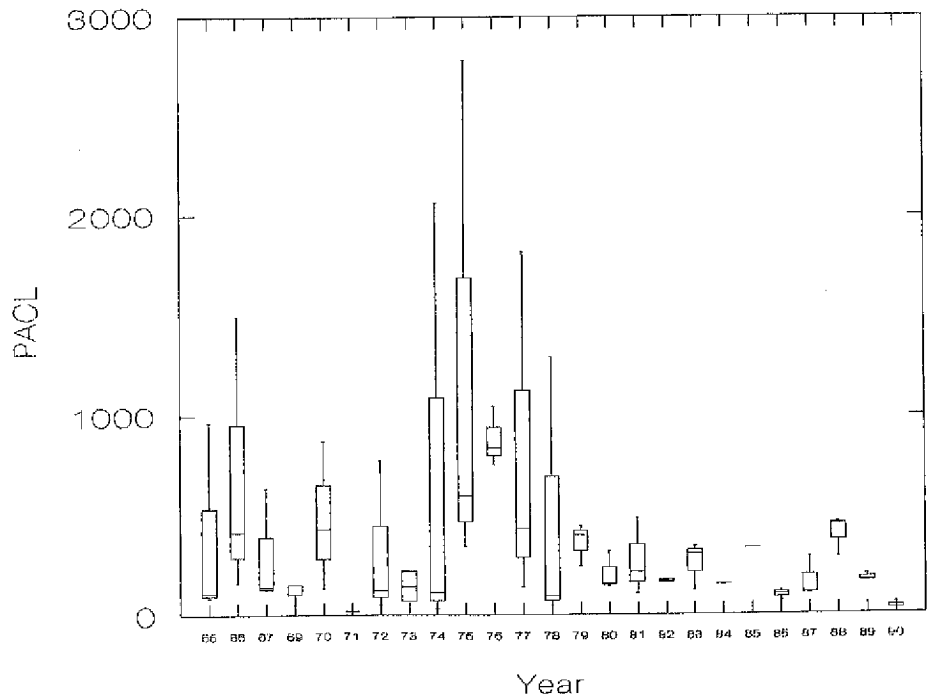
Year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2000
1000
0
PACL
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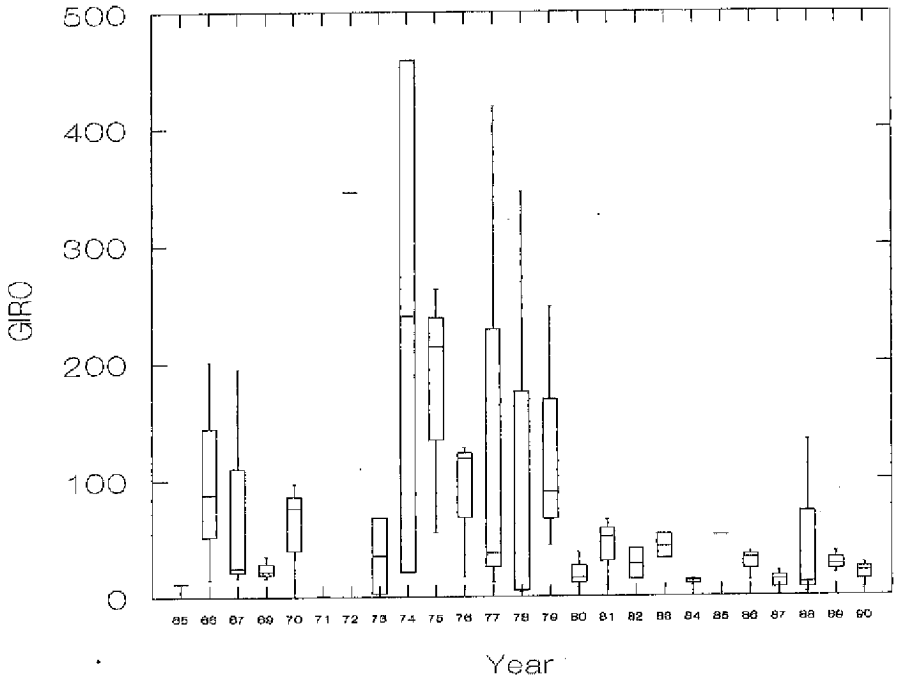
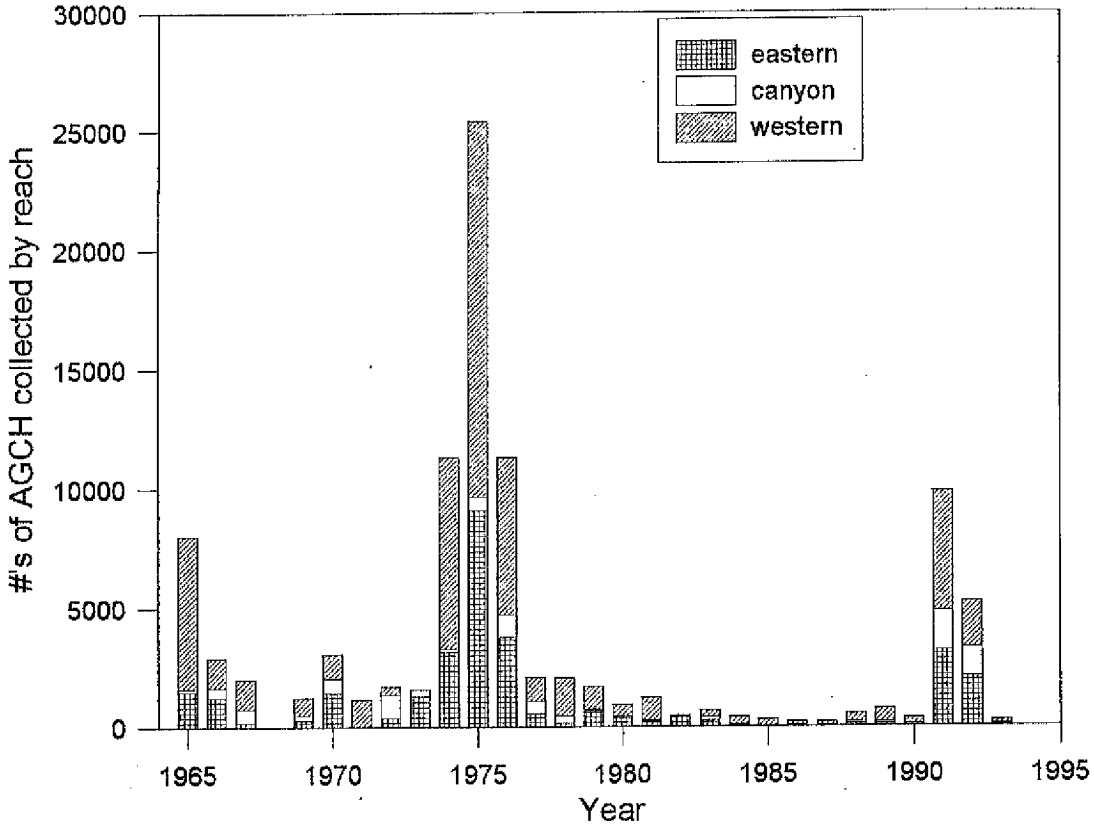
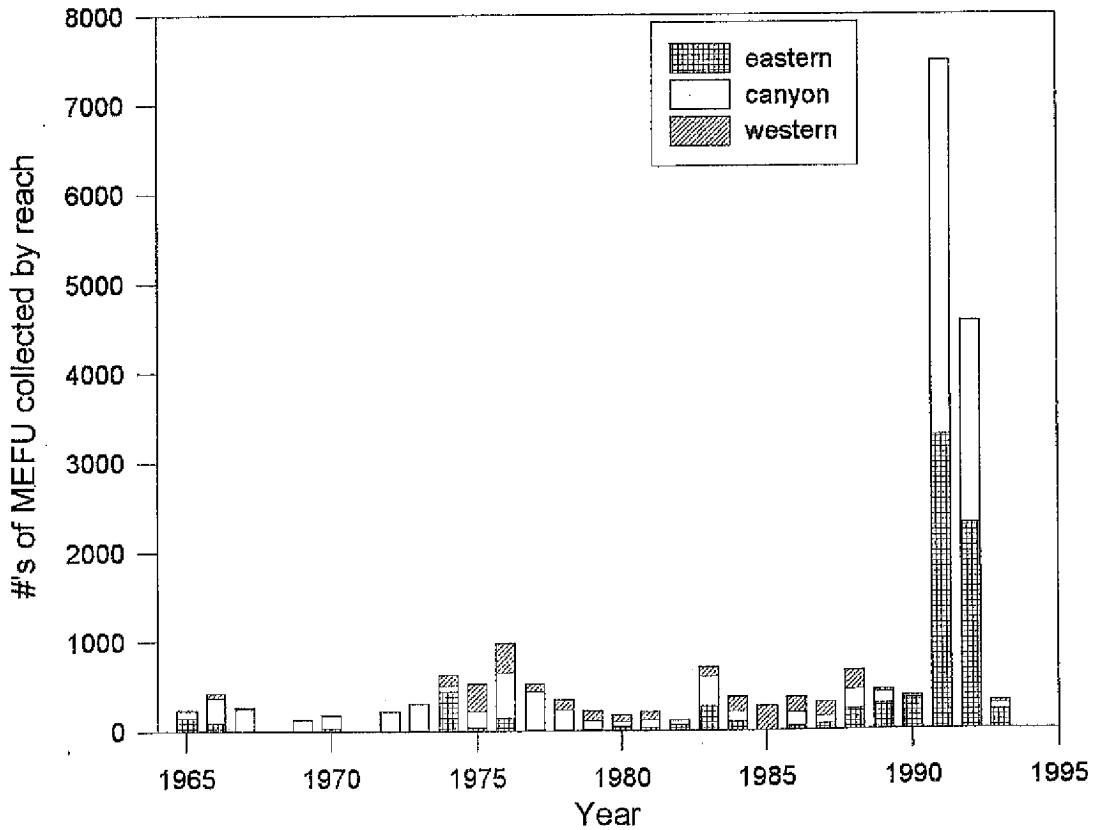
Year


500
400
300
200
100
0
GIRO
65 66 67 69 70 71 72 73 74 75 76 77 78 79 80 81 82 83 84 85 86 87 88 89 90
Year

APPENDIX C

HISTOGRAMS OF RAW ABUNDANCES OF FISHES, BY REACH, IN THE LONG-TERM DATA SET (MINCKLEY, UNPUBL.), ARAVAIPA CREEK, AZ.


30000
25000
20000
15000
10000
5000
0
#'s of AGCH collected by reach
eastern
canyon
western
1965
1970
1975
1980
1985
1990
1995
Year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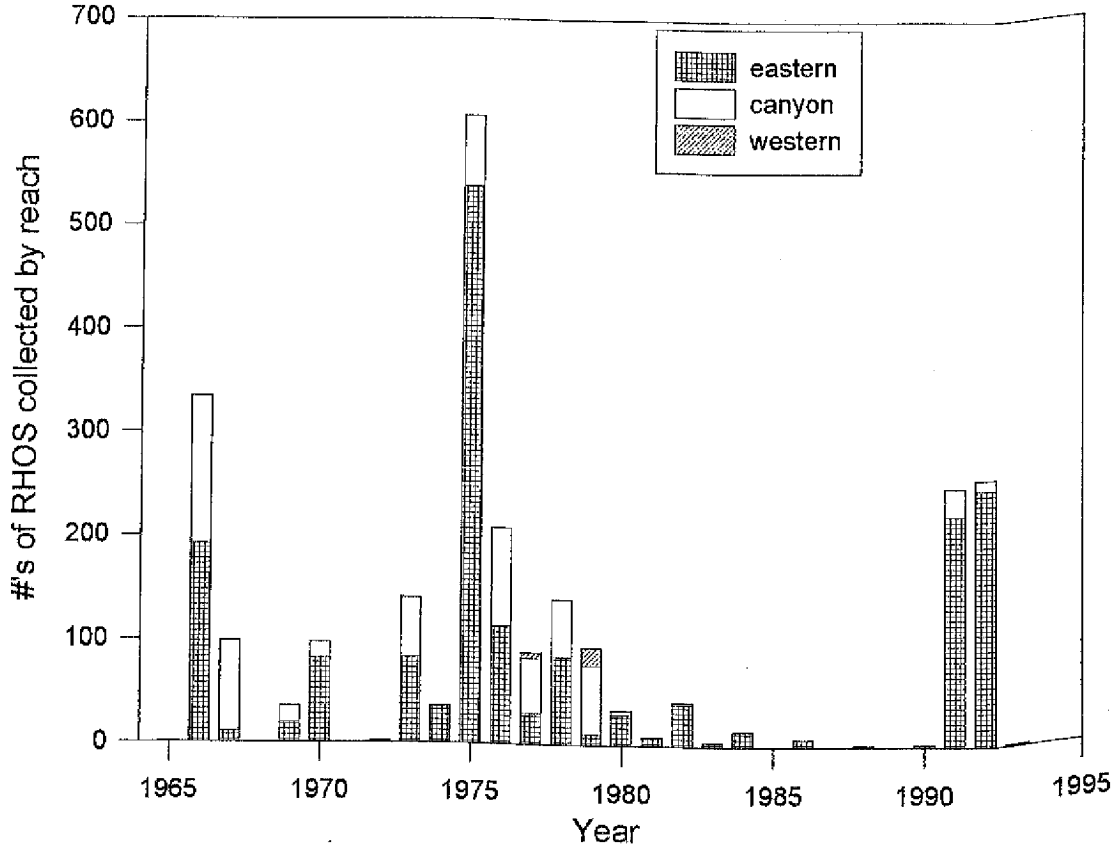
7000
6000
5000
4000
3000
2000
1000
0
#'s of MEFU collected by reach
eastern
canyon
western
1965
1970
1975
1980
1985
1990
1995
Year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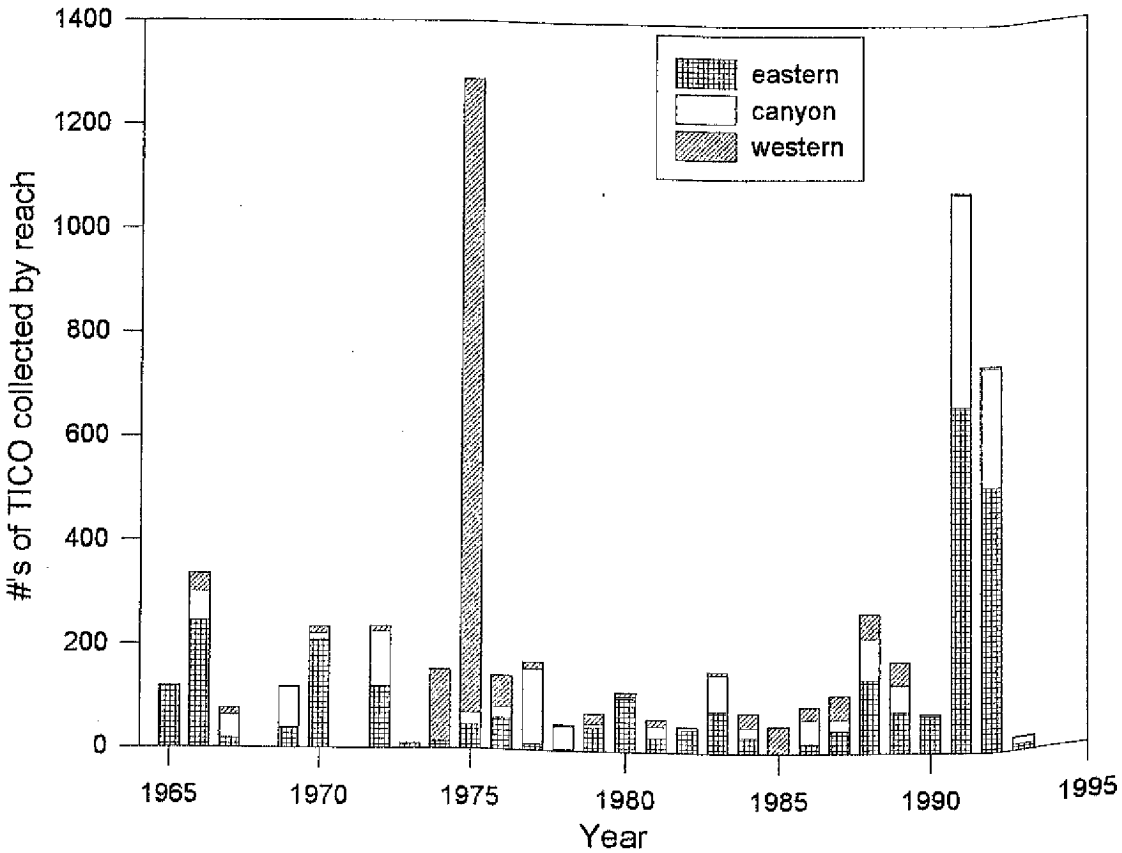
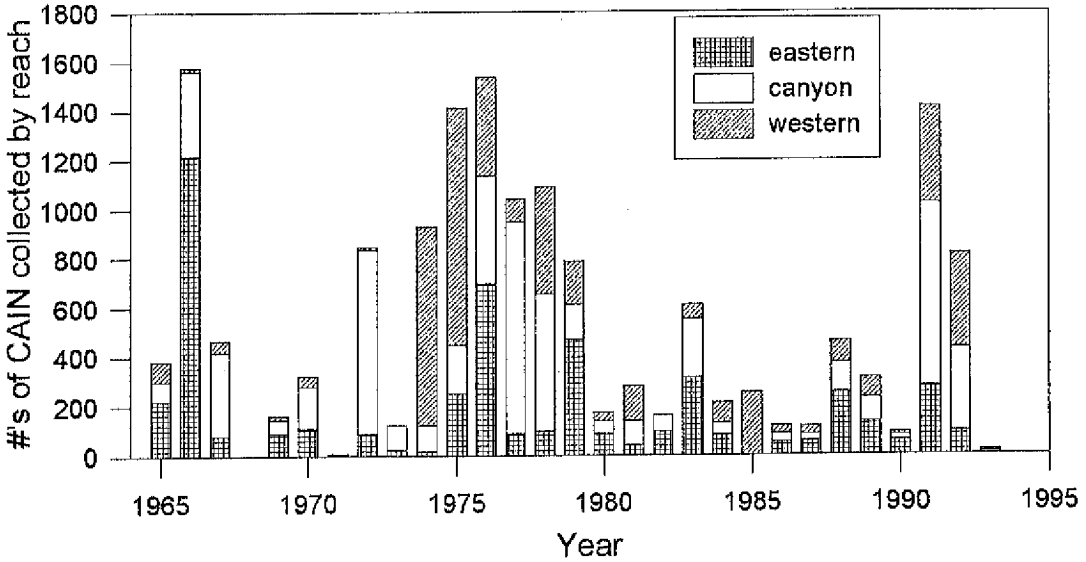
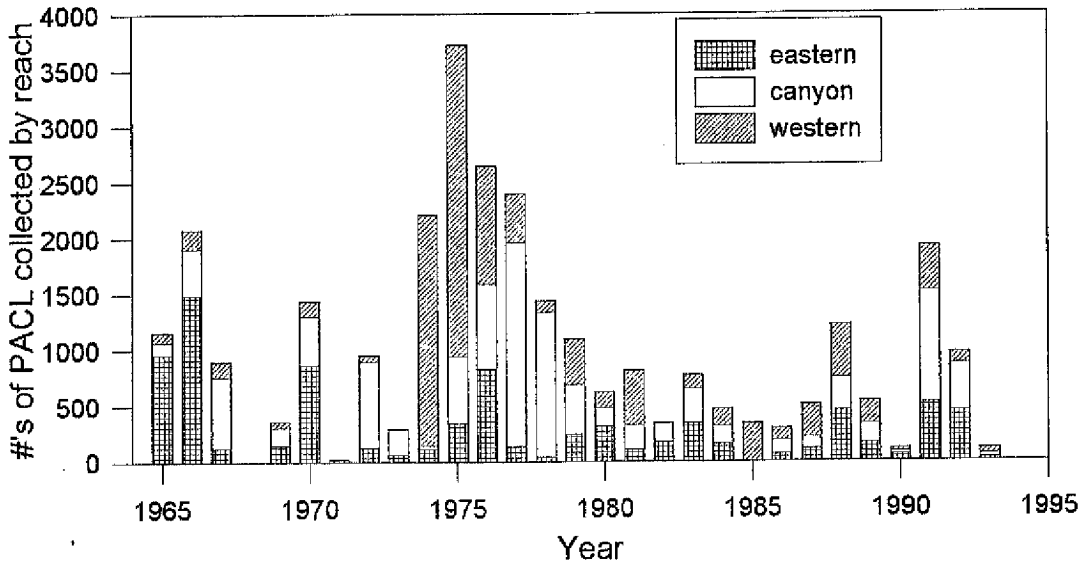
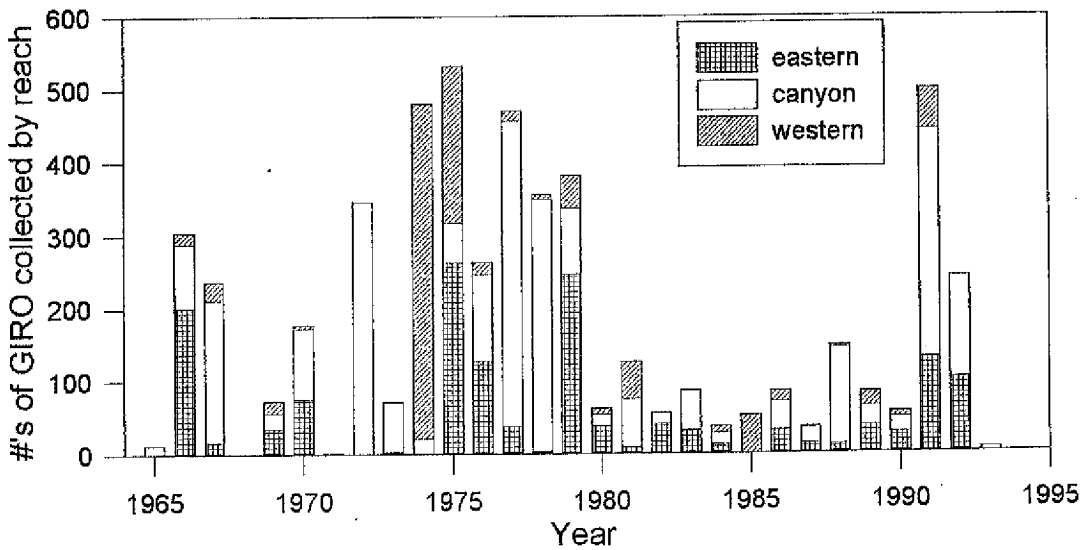
600
500
400
300
200
100
0
#'s of RHOS collected by reach
eastern
canyon
western
1965
1970
1975
1980
1985
1990
1995
Year


1400
1200
1000
800
600
400
200
0
#'s of TICO collected by reach
eastern
canyon
western
1965
1970
1975
1980
1985
1990
1995
Year


#'s of CAIN collected by reach
1800
1600
1400
1200
1000
800
600
400
200
0
1965
1970
1975
1980
1985
1990
1995
Year
eastern
canyon
western


#'s of PACL collected by reach
4000
3500
3000
2500
2000
1500
1000
500
0
1965
1970
1975
1980
1985
1990
1995
Year
eastern
canyon
western


#'s of GIRO collected by reach
600
500
400
300
200
100
0
1965
1970
1975
1980
1985
1990
1995
Year
eastern
canyon
western