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VARIABILITY AND DYNAMICS OF A DESERT STREAM COMMUNITY

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Abstract. Communities can be highly variable over a few years, but remain fairly constant over the long term. Evaluating measures and examining the variability associated with long-term change is useful because it increases our understanding of and our ability to predict responses to disturbances. We used long-term fish community data from Aravaipa Creek, Arizona, USA, a Sonoran Desert stream, to determine whether there had been long-term changes in the community composition, what measures best describe these shifts, and what environmental factors are correlated with the changes. Aravaipa Creek is an intrinsically variable system and one of the few remaining desert streams to support its complete historical assemblage of native fishes. Multivariate analyses illustrated important changes in composition of the native fish community that were not described by traditional measures of persistence and stability. In the early 1980s, changes in community composition were correlated with alterations in base flow, while more recent changes are likely associated with the presence of exotic species. Changes in stream morphology, hydrology, and climate have decreased flow variability, thereby increasing the likelihood of exotic establishment, and may have increased the downstream connection between Aravaipa Creek and the San Pedro River thus increasing the likelihood of repeated invasions by nonnative species. These results support previous research in intrinsically variable desert systems, which conclude that retention of high flow variability is important to conservation of the native fish community. In addition, although connectivity in aquatic lotic systems is important, isolation from large river systems teaming with exotics may be important in preserving these remnant native fish assemblages.

Key words: Aravaipa Creek; community composition; conservation; desert stream; exotics; fish; flow variability; measures of community change; Sonoran Desert, USA.

INTRODUCTION

In many systems, our ability to detect long-term change is anecdotal and based on relatively brief studies (e.g., Blaustein et al. 1994). Studies that span only a few years can produce a misleading picture of the variability of natural populations. Even studies that span more than one turnover of the population may underestimate natural variation because they fail to detect infrequent, large fluctuations in populations (Connell and Sousa 1983, Pimm and Redfearn 1988, McArdle et al. 1990). Understanding how populations respond to natural variation in a system (e.g., droughts and floods) and differentiating natural fluctuations from human impacts often require long-term studies (Pechmann et al. 1991). Examining how best to detect long-term patterns in assemblages and determining factors that influence change are key research needs in community ecology and conservation biology.

Desert streams offer an excellent system in which to test different indicators of long-term community change, because they are renowned for their intrinsic variability. Desert systems are characterized by extremes in conditions. Intense local rainstorms that produce flash floods are common in the Sonoran Desert. With flow changing several orders of magnitude over a period of hours, flash floods scour stream bottoms, increase turbidity, and can change water temperatures >15°C. In contrast, during periods of drought, water temperatures may exceed 40°C and pools and channels may become stagnant and overgrown with algae (Deacon and Minckley 1974).

In addition to such intrinsic variability, anthropogenic changes to desert stream systems are common. Specifically, native southwestern fish populations in many areas are declining primarily due to destruction and alteration of aquatic habitats and effects of introduced species (Minckley and Douglas 1991). Flow modification is one of the most widespread human disturbances in the stream environment (Fraser 1972, Ward and Stanford 1983). As discharge changes, stream substrate and cover are altered thus shifting physical habitat characteristics (i.e., water depth, current velocity, and substrate) and subsequently influencing fish community composition (Gorman and Karr 1978, Schlosser 1982*a*, *b*, Moyle and Vondracek 1985). Thus, alterations in stream base flow can be an important form of disturbance to fish communities in these systems (Bain et al. 1988, Holling and Meffe 1996). Although

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changes in flow have contributed to the decline of native fishes in western North America, it has been argued that the most serious threat is the invasion of exotic species (Minckley 1991). Changes in the flow regime may influence the presence of exotics and therefore the two factors may be correlated in time. For example, flash floods in these systems differentially remove the lentic-adapted nonnative species thereby contributing to the persistence of intact native fish communities; regulation of flood events increases the vulnerability of the native fish community to exotic species (Meffe 1984, Minckley and Meffe 1987).

We examined whether there were trends in a Sonoran Desert fish assemblage that had experienced changes in base flow, flash floods, and the introduction of exotics. We used a 30-yr database from Aravaipa Creek, Arizona, to examine several issues. First, we examined whether there was a long-term change in native species community composition, and which of several measures (persistence, concordance, time lag regression, or multivariate ordination) best described these changes. Second, we examined whether interannual variability in both the number and proportion of exotic species in the community was related to flow characteristics, specifically minimum flow, maximum flow, predictability of these flows, and/or variation in flow. Third, we examined whether we could differentiate the effects of the potential major influences on the system. For example, are the extremes of natural variation in the environment resulting in large shifts in the fish community? Can we differentiate community changes mediated by natural vs. anthropogenic factors? To explore these potential dependencies, we examined the correlation between floods (and scouring events), changes in base flow, and the presence of exotic species with changes in the native fish assemblage.

Methods

Study site

Aravaipa Creek has a drainage area of ~1500 km^2. This creek has historically been subdivided into "upper," "canyon," and "lower" reaches based on topography (Minckley 1981, Meffe and Minckley 1987). The last section is ephemeral for its lowermost 8 km at modal discharge; surface flows usually sink into the streambed before joining the San Pedro River at ~650 m elevation. The United States Bureau of Land Management manages a designated "Wilderness Area" within the canyon, and The Nature Conservancy owns much of the land upstream and downstream. However, the upper and lower reaches remain available for irrigated farming, pasturage, and domestic supplies. Pumping or diversion from the creek sometimes dries short segments (Ellingson 1980), although far less so today than in the past.

Fish habitat often is controlled by patterns of sediment erosion, transport, and deposition, which in turn are functions of precipitation, runoff, and bed load volume (Schlosser 1982*b*). Like most unregulated aridland streams, Aravaipa Creek is subject to intense flash floods, highly erosive events that have rapid onset and are short in duration. Modal discharge in Aravaipa Creek is ~3.4 m^3/s, but runoff can accumulate quickly and major floods are common.

Historically, the native southwestern fish assemblage is species poor: rarely more than five species occurred at any given locality in Sonoran Desert streams (Minckley and Deacon 1968, Minckley 1973). Compared with most Arizona stream systems, Aravaipa and its fishes are relatively undisturbed and protected. Aravaipa Creek is one of the last streams in the upper Sonoran Desert to sustain an intact diverse assemblage of native fishes. Seven native fishes inhabit the stream. These include two federally listed threatened species, loach minnow (*Tiaroga cobitis*) and spikedace (*Meda fulgida*), and five candidate species, roundtail chub (*Gila robusta*), desert sucker (*Catostomus clarki*), Sonora sucker (*Catostomus insignis*), longfin dace (*Agosia chrysogaster*), and speckled dace (*Rhinichthys osculus*). Historically, Aravaipa Creek was fairly well protected from introductions because of its seasonal isolation from the San Pedro River and propensity for flash flooding. However, during the 1980s nonnative fishes were encountered including fathead minnow (*Pimephales promelas*), green sunfish (*Lepomis cyanellus*), yellow bullhead (*Ameiurus natalis*), black bullhead (*Ameiurus melas*), common carp (*Cyprinus carpio*), western mosquitofish (*Gambusia affinis*), and largemouth bass (*Micropterus salmoides*) (Bettaso et al. 1995). The exotic red shiner (*Cyprinella lutrensis*) was first discovered in 1990 in the lower reach. *Cyprinella lutrensis* is of special concern as it has been implicated in the decline of several native southwest fishes (e.g., Rinne 1991, Douglas et al. 1994), replacing both *M. fulgida* and *T. cobitis* throughout substantial parts of their ranges (Minckley and Deacon 1968).

Sampling and data

W. L. Minckley, his students, and colleagues began sampling fishes of Aravaipa Creek in 1963. Sampling involved teams of from 2 to >15 persons using two sizes of double weighted seines, 1.8 × 1.2 m with 3.2-mm mesh and 4.6 × 1.2 m with 6.4-mm mesh. Because scouring events often rearrange habitat types in stream systems, sampling sites were not fixed. Instead, emphasis was placed on sampling habitat diversity within each reach. The available diversity of habitats was sampled each year in each reach. Thorough seining of ~200 m per site included repeated sweeps through open areas, probing under banks and around obstructions and vigorous substrate disturbance from upstream to downstream. Fishes usually were identified and counted at the site, although some were retained as vouchers deposited at Arizona State University. Monthly sampling of the system performed by the state between 1992 and

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1994 demonstrated peaks in juvenile abundance (pulses of recruitment) occurring from May through November (Bettaso et al. 1995). Although seining was done every year in the spring (March–April) and autumn (October–November), we chose to examine spring data to minimize the effects of recruitment events on community composition (Yant et al. 1984).

Although both gear and length of stream segment sampled were standardized, differences existed in survey crews and sampling motivation (e.g., collections for museum specimens vs. conservation monitoring). To overcome these potential issues, we analyzed the fish assemblage structure in terms of species richness (presence/absence) and proportional community composition (proportion of total abundance). In addition, we pooled collections among sites within reaches before calculating proportional community composition, so the data reflect proportional composition in each reach each year. This pooling increases confidence that our data set represents the underlying community composition because accuracy of proportional composition estimates increases as the total number of fishes sampled increases. Although sampling began in the early 1960s, we constrained our analyses to time periods with the most data, which included 1975–2000 for the upper and lower reaches and 1970–2000 for the canyon reach. Still there were a few years where not every stream reach was sampled.

We used U.S. Geological Survey (USGS) stream flow data from gauge station 09473000 (in the lower reach of Aravaipa Creek near Mammoth, elevation 716 m) to characterize water flow patterns (1965–1999) for Aravaipa Creek, which drains an area of 1409 km^2 above the gauge. We also obtained USGS peak flow data from the same gauge to estimate instantaneous peak flow exhibited by Aravaipa Creek during each calendar year.

Analyses

To understand changes in community structure over time we analyzed native fish assemblages from the three physiographic sections of Aravaipa Creek separately using four different quantitative measures. The first metric, persistence, is a measure of whether the same native species are present from one year to the next. Following Meffe and Minckley (1987), we generated persistence measures from an index of species turnover rates (T) calculated as $T = (C + E)/(S1 + S2)$. C and E are the number of species that colonized or were extirpated between sample periods, while $S1$ and $S2$ are the numbers of species present in each sample period (Diamond and May 1977, Jarvinen 1979). We averaged turnover rates of all adjacent years and an index of persistence was calculated as $1 - \text{mean } T$. This index ranges from zero (no persistence) to one (complete persistence).

Second, we examined stability of the species relative abundance rankings over the study period. Constancy in species rank abundances was tested using Kendall's W (Conover 1971), a nonparametric procedure that tests for overall concordance among multiple samples. The null hypothesis for W is that concordance of ranks is significantly different from random (if random, $W = 0$) and the magnitude of the concordance value indicates how constant the assemblage has been over time.

Third, we examined how community composition changed over time using a time lag regression analysis (see Collins 2000). We calculated the Euclidean distance between each possible pair of community assemblages. The higher the Euclidean distance the more dissimilar the community vectors. Then we conducted a linear regression of Euclidean distance against the square root of the time lag separating the samples. The square root transformation lessens the potential for the few data points at long lags to bias the regression.

In the final analysis, we used detrended correspondence analyses (DCA) and examined the temporal trajectories of native community composition. The most important information in this type of plot is the displacement or movement of points across time (Matthews 1996). At two possible extremes, an assemblage could remain in or move within a small area in multivariate space (indicating variability with no long-term directional shift in composition), or it could move progressively further away from the original condition (indicating a directional shift in composition). Multivariate plots have been used recently to assess changes in fish communities over long and short periods, before and after treatments, and between sites (e.g., Gelwick 1990, Meffe and Sheldon 1990, Edds 1993, Hansen and Ramm 1994, Matthews 1996).

For our second objective, we examined whether interannual variation in either the number of exotic species or their proportional contribution to total community composition (all species, native and exotic) was related to minimum flow, maximum flow, and/or variation in flow using Mantel tests (Legendre 1993). These analyses test for linear relationships in distance or difference matrices. In addition, we examined whether there was a difference in predictability of maximum and minimum flows before 1982 (before many exotics were common in Aravaipa Creek) and after 1981 (as exotics species became common and more abundant). We calculated predictability, and its two components constancy and contingency, as detailed by Colwell (1974). We obtained means and standard errors by using a jack-knifing technique where we calculated each index multiple times using all but one year of data (Weis and Schwartz 1988). We performed these analyses on the data from the lower reach because exotic species have been present the longest in this reach.

Our third objective was to examine whether hydrologic variables (base flow, scouring flow, flash floods) or the presence of exotic species altered the native fish assemblage structure in a way that is detectable given the variability in this system. To achieve this goal, we

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TABLE 1. Aravaipa Creek top ten daily discharges and peak flows from Tables 3–17 and 3–18 in Fuller (2000).

	Largest mean daily discharges		Largest instantaneous peak flows	
Rank	Date	Discharge (m^3/s)	Date	Discharge (m^3/s)
1	1 Oct 1983	453	2 Oct 1983	2006
2	2 Oct 1983	397	18 Dec 1978	459
3	18 Dec 1978	181	17 Dec 1967	434
4	11 Jan 1993	128	11 Jan 1993	368
5	19 Dec 1978	113	5 Jan 1995	253
6	19 Oct 1972	106	19 Oct 1972	232
7	5 Jan 1995	103	8 Jan 1993	222
8	8 Jan 1993	94	2 Mar 1991	192
9	2 Mar 1991	88	3 Mar 1970	158
10	20 Dec 1967	77	15 Feb 1995	149

used mean daily minimum flow from the hydrograph of USGS daily flow data (gauge 09473000) as an index to describe changes in base flow. To characterize potential effects of high flow events, we calculated instantaneous peak flow, number of years since a major flooding event, and number of years since a scouring event. To examine the magnitude of a major flooding event, we obtained USGS peak flow data from the same gauge to estimate the instantaneous peak flow exhibited by Aravaipa Creek during each calendar year. Because floods may alter habitat characteristics, such as stream bank vegetation and bottom type, we calculated number of years since major flood event using historic flood events described in Table 1. A hydrologic study in Aravaipa Creek that classified evidence of scouring events to be change in bed forms, change in location of riffles and rapids, loss of over-bank vegetation, and/or change in stream pattern with stream flow, found no evidence of these habitat changes with daily mean discharges below 23 m^3/s (800 cfs; Fuller 2000). Thus we calculated number of years since a scouring flow event using the 23 m^3/s criterion. Finally we examined whether exotic species may be affecting the native fish assemblage. We calculated proportion of the total community composed of exotic species for any given year. For presence/absence in each reach, we differentiated between years since the estimated arrival of exotics and those prior to their establishment.

We assessed associations between community dissimilarity and environmental variation by first examining whether we could describe the changes in native species assemblage by statistically distinguishing general species groupings and if so, what environmental variables predicted these clusters. We clustered the data and used classification and regression trees to examine which (if any) predictor variables could be used to differentiate these species groupings. We conducted hierarchical agglomerative cluster analyses with the unweighted group averaging linkage method (Pielou 1984, Manly 1994) and tested the clusters with permutation procedures (Mielke 1984, 1991, Biondini et al. 1988). Multivariate analyses were performed using PC-ORD 4.0 (McCune and Mefford 1999). Finally, we used classification and regression trees (Breiman et al. 1984) to examine whether the clustered groups reflect differences in any of the environmental predictor variables. Classification and regression tree analyses were performed using the S-plus 2000 software package (MathSoft, Seattle, Washington, USA).

RESULTS

Patterns of stream flow

Flow in Aravaipa Creek was highly variable. Over the past 34 years, mean daily discharge spanned more than four orders of magnitude (Fig. 1). Mean minimum flow increased nearly fourfold from 0.08 m^3/s (2.3 cfs) between 1965 and 1977 to 0.30 m^3/s (10.7 cfs) between 1978 and 1999. After 1978, base flow increased and the seasonal cycle was dampened (Fig. 1). Thus, recent years exhibit higher and more stable flows than past flows. During this period several flash floods occurred (Fig. 1). Between 1970 and 1999, the system experienced several periods of high discharge (Table 1). Onset of these floods was rapid, and duration was short. For example, in 1983, daily mean flow increased from 1.9 m^3/s (67 cfs) to 453.4 m^3/s (16 000 cfs) within 2 days and by the fifth day daily mean flows were back to normal.

Overview of changes in community composition

Community composition of Aravaipa Creek varied through time. In all reaches variation in the relative proportion of *Agosia chrysogaster*, *Meda fulgida*, and *Catostomus clarki* dominated the major changes in community composition (Fig. 2). *Catostomus insignis*, *Tiaroga cobitis*, *Gila robusta*, and *Rhinichthys osculus* were less abundant and constituted a minor portion of the total community. Although every reach experienced shifts in species relative abundance, only the lower reach exhibited declines in species richness resulting from the rarity of *M. fulgida* in more recent years (Fig. 2).

In the upper reach, exotic species (primarily, *Lepomis cyanellus*) were uncommon and did not contribute >0.5% of the total community. Few exotic species

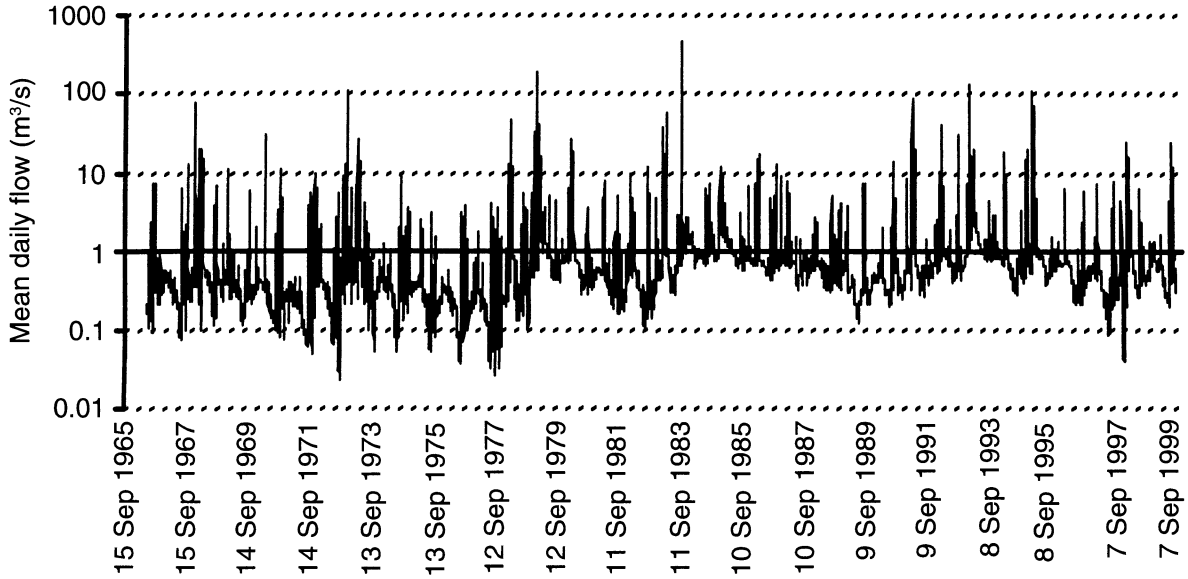

FIG. 1. Mean daily stream flow in Aravaipa Creek, Arizona, as measured by USGS gauge station 09473000 in the lower reach. Note log scale on the *y*-axis.

were captured in the canyon reach (including, *L. cyanellus*, *Ameiurus natalis*, and *Cyprinella lutrensis)* and did not contribute >7% to the total community composition in any year. In the lower reach, exotic species have been present since the early 1960s. Both the number of different species and the proportional contribution of exotics increased around 1983 (Fig. 3). Since the early 1980s, eight exotic species (listed in *Methods: Study site*) have been present and their percentage contribution to the community has varied between 0% and 30% depending on the year (Fig. 3).

Measures of community change

Given this variability in fish community structure, we evaluated different measures that describe changes in the native fish community structure. Persistence measures were all >0.9, indicating high persistence in the Aravaipa Creek fish assemblage. The fish assemblage in the upper reach was most persistent, whereas the assemblage in the lower reach was least persistent (Table 2). Fish species rankings in all sections were significantly concordant, as measured by Kendall's W (Conover 1971; Table 2). Even though Aravaipa Creek fish assemblages were significantly concordant, the value for the upper site ($W = 0.48$) was fairly low, while the canyon and lower sites had high (>0.70) concordance values.

Time lag regression analyses revealed evidence of directional change in fish community composition in two of the three reaches. In both the upper and canyon reaches, vectors of fish community composition grew increasingly different as time lags increased (Fig. 4). The upper reach had changes that were both the most pronounced (steepest slope) and most directed (highest R^2).

Additional evidence for community change came from examination of the vector diagram in the multivariate ordinations. In upper and canyon reaches, detrended correspondence analysis (DCA) vectors demonstrated similar community shifts between the 1970s, 1980s, and 1990s. *Agosia chrysogaster* dominated the community composition in the 1970s. The 1980s composition was more evenly distributed across all species. Both *A. chrysogaster* and *M. fulgida* constituted a larger proportion of the community in the 1990s (Figs. 5 and 6). The upper reach two-dimensional ordination explained 80% of the variation (axis 1, 58% and axis 2, 22%). *Agosia chrysogaster* and *M. fulgida* were inversely correlated with axis 1 (0.80 and −0.87, respectively). Three species were correlated with the second axis; *A. chrysogaster* (−0.70), *C. clarki* (0.78), and *C. insignis* (0.85; Fig. 5). The 1970s, which featured a high proportion of *A. chrysogaster* and low proportions of *M. fulgida*, aggregated in the right side of the ordination. Sampling dates from the 1980s, with low proportions of *A. chrysogaster* and higher proportions of *C. clarki* and *C. insignis* grouped on the upper left side of the ordination. Most dates from the 1990s were near one another because of the relatively high proportions of both *A. chrysogaster* and *M. fulgida* present (Fig. 5). Similar shifts were seen in the canyon reach (Fig. 6); a two-dimensional ordination explained 89% of the variation (axis 1, 45% and axis 2, 44%). *Agosia chrysogaster*, *G. robusta*, and *C. clarki* were correlated with axis 1 (0.79, −0.71, −0.86, respectively). *Meda fulgida* and *A. chrysogaster* were inversely correlated with axis 2 (0.88, −0.66, respectively).

The downstream reach did not exhibit a directional pattern; instead the assemblage structure returned over time to an earlier state. Similar native species assem-

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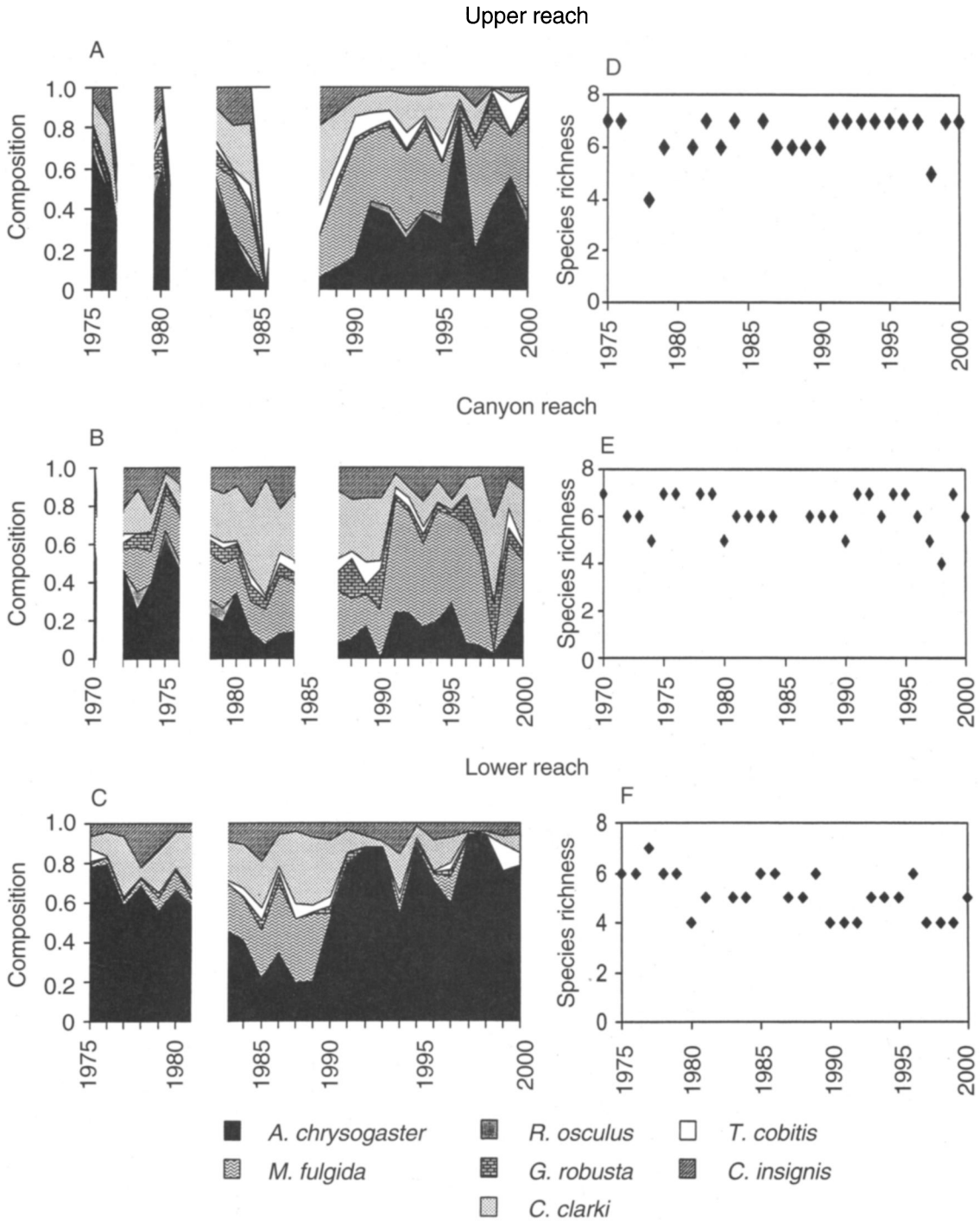

FIG. 2. Community structure of the native fish community in Aravaipa Creek, Arizona. (A–C) Proportional contribution of the abundance of each native species to total native fish abundance for each reach every year sampled. White vertical bars indicate no data. (D–F) Native species richness vs. year sampled. A decline in native species richness occurred in the lower reach.

blages occurred in the 1970s and 1990s (Fig. 7). Variation in the downstream reach community composition was primarily explained by the first axis (88% of the variation, with axis 2 explaining only 2% of the variation). *Agosia chrysogaster*, *M. fulgida*, and *C. clarki* were associated with the first axis (0.99, −0.94, −0.80, respectively). Time vectors demonstrated similar assemblages in the 1970s and 1990s overlapping on the

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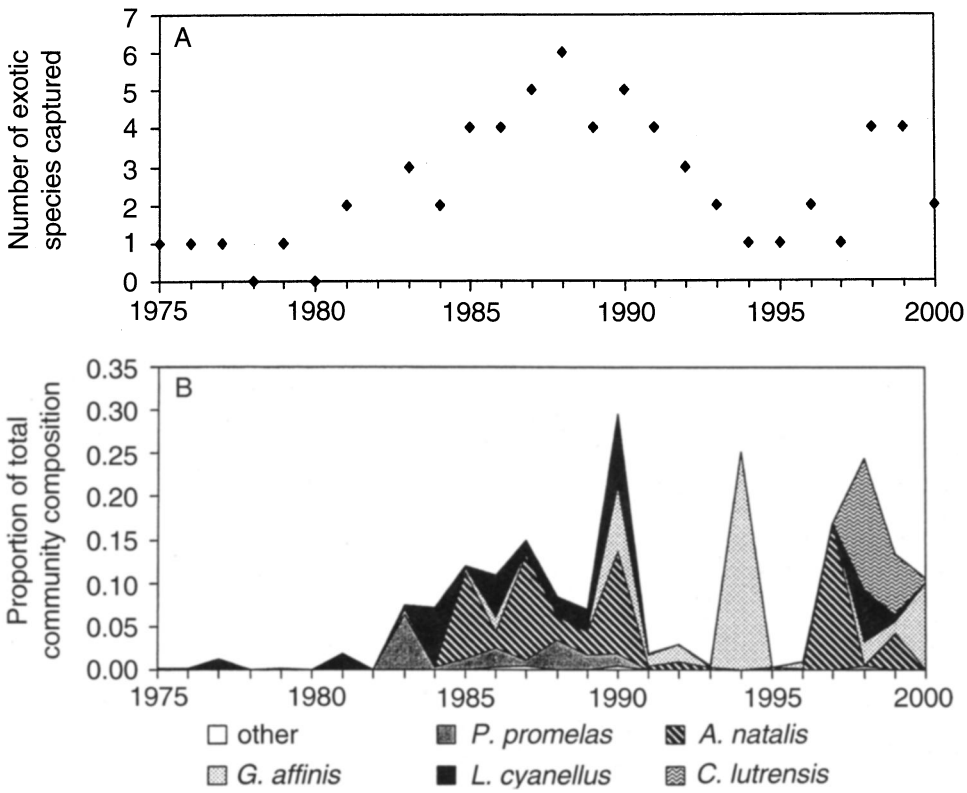

FIG. 3. (A) Time trend of exotic fish species richness in the lower reach between 1975 and 2000. (B) Time trend of the proportion of total species abundance composed of different exotic species between 1975 and 2000 in the lower reach of Aravaipa Creek, Arizona.

left side of the ordination (high proportion of *A. chrysogaster*, low proportions of *M. fulgida* and *C. clarki*) while the 1980s separated toward the right side with lower proportions of *A. chrysogaster* (Fig. 7).

Exotics and flow

Exotic species contributed a higher proportion of community composition in years after variability in flow was lower (Fig. 8a), and a higher number of exotic species were present after years with low flow variability (Fig. 8b); however, these results were not significant. These relationships were heavily influenced by two years with high variability, high peak flows, and a low number and proportion of exotic species. We did not find any significant results or trends between the number or proportion of exotic species and minimum daily discharge. Predictability of maximum and minimum flow increased from 0.48 (SD = 0.01) and 0.60 (SD = 0.01) in the early time period (pre-1982) to 0.50 (SD = 0.01) and 0.68 (SD = 0.01) in the later time period (post-1981). The rise in predictability over the study period was driven by increases in the constancy component of the predictability index. Constancy in maximum flow increased from 0.24 (SD = 0.01) to 0.29 (SD = 0.06) and constancy in minimum flow increased from 0.44 (SD = 0.01) to 0.55 (SD = 0.01). Although predictability significantly increased between the early (pre-1982) and later (post-1981) time periods, these increases were small and their ecological importance is equivocal.

Environmental correlates with native fish composition

We next examined which environmental factors may explain the observed changes in community composition. Significant clusters were found in all reaches. As all native species were present most years, these groups are described by the changes in relative abundance of the species. Because there were temporal trends in community composition, we ran categorical and regression tree analyses with and without year as a predictor variable to determine which year distinguished the clusters and to examine whether any of our environmental variables (e.g., minimum flow, time since flood, presence/absence of exotic species) could distinguish the groups. The upper reach clustered into two groups separating years with higher proportions of *A. chrysogaster* and lower proportions of *M. fulgida* from other years. The tree model separated the groups using year (1982) as a predictor variable with a good fit (residual mean deviance 0.35, 2/22 misclassifications). Without year in the model, minimum flow

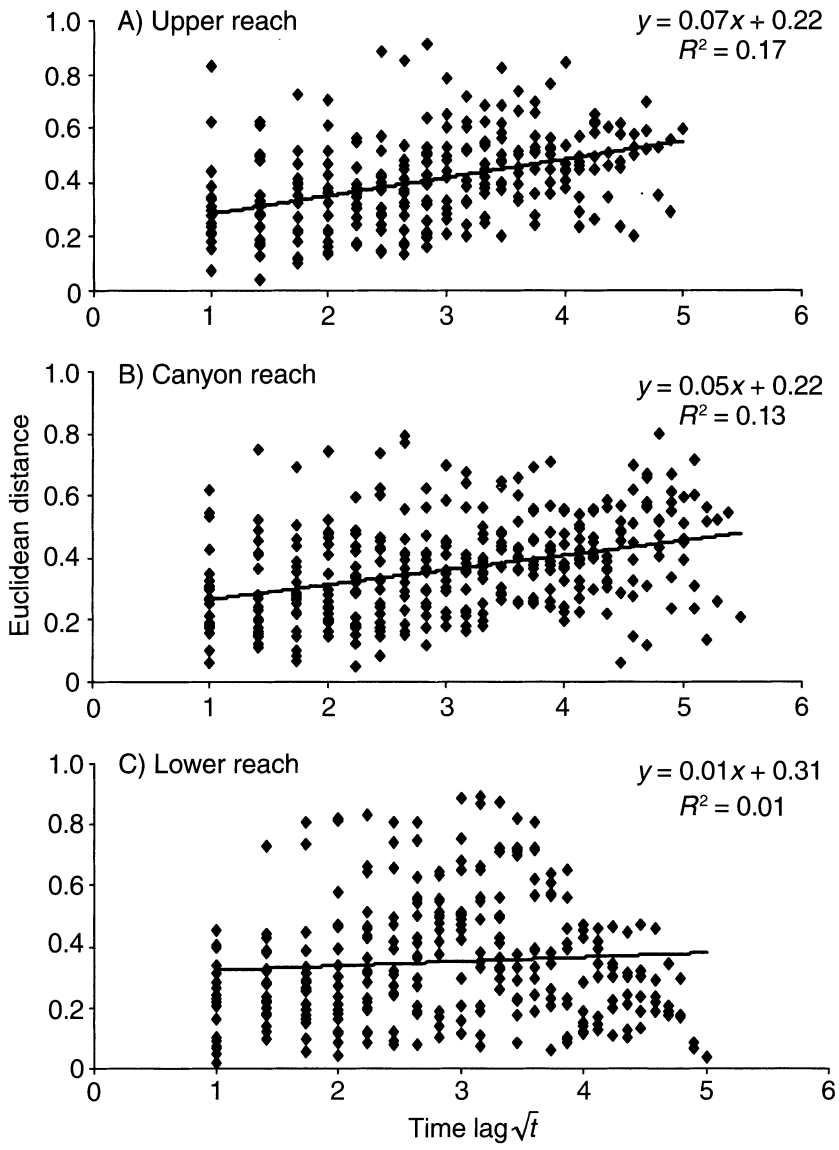

FIG. 4. Time lag regression analyses for spring survey data characterizing directional changes in community composition over time for three sampled reaches of Aravaipa Creek, Arizona. Regressions indicate significant ($P < 0.05$) long-term directional change for (A) upper and (B) canyon reaches, but not for (C) lower reach.

(<0.25 m^3/s or 8.7 cfs) was the best predictor variable (residual mean deviance 1.02, 5/22 misclassifications). The canyon reach data were separated into two significant clusters separating years with higher proportions of *M. fulgida* and lower *A. chrysogaster* from the rest of the data. The best predictor variable was year (breaking the data set between 1990 and 1991, residual mean deviance 0.26, 1/26 misclassifications). Without year,

TABLE 2. Summary of community change analyses for the fish communities of Aravaipa Creek, Arizona, USA.

Stream section	Year (no.)	Species (no.)	Persistence	W	Time lag regression	DCA results
Upper	22	4–7	0.96	0.48	directional change	directional change
Canyon	26	4–7	0.95	0.70	directional change	directional change
Lower	24	4–7	0.92	0.78	no change	change followed by return to earlier state

Notes: From left to right, columns are number of years of data, range in the number of species captured per year, persistence measures, Kendall's rank concordance values (W; all $P < 0.001$), time lag regression results, and patterns in multivariate analyses.

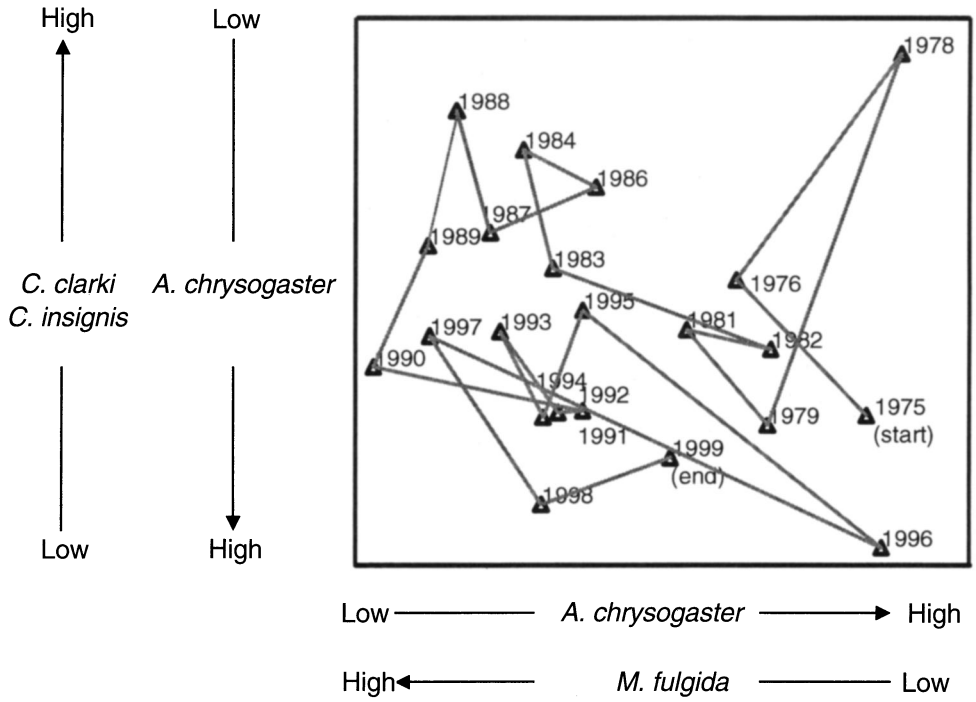

FIG. 5. DCA plot of the upper reach fish community composition through time. The native fish community has changed during the 1970s, 1980s, and 1990s; changes were primarily driven by the relative abundances of *Agosia chrysogaster* and *Meda fulgida*.

the tree model that included proportion of exotics in the community (<0.02), minimum flow (<0.19 m^3/s or 6.6 cfs), and presence/absence of exotics explained the most variance (residual mean variance 0.84, 4/26 misclassifications). The downstream reach data set also divided into two groups separating years with higher proportions of *A. chrysogaster* and lower *M. fulgida* from years with lower proportions of *A. chrysogaster* and higher *M. fulgida* and *C. clarki*. The first group included data from before 1982 and after 1989, while the second included data from the period between those dates (residual mean deviance 0, 0/24 misclassifica-

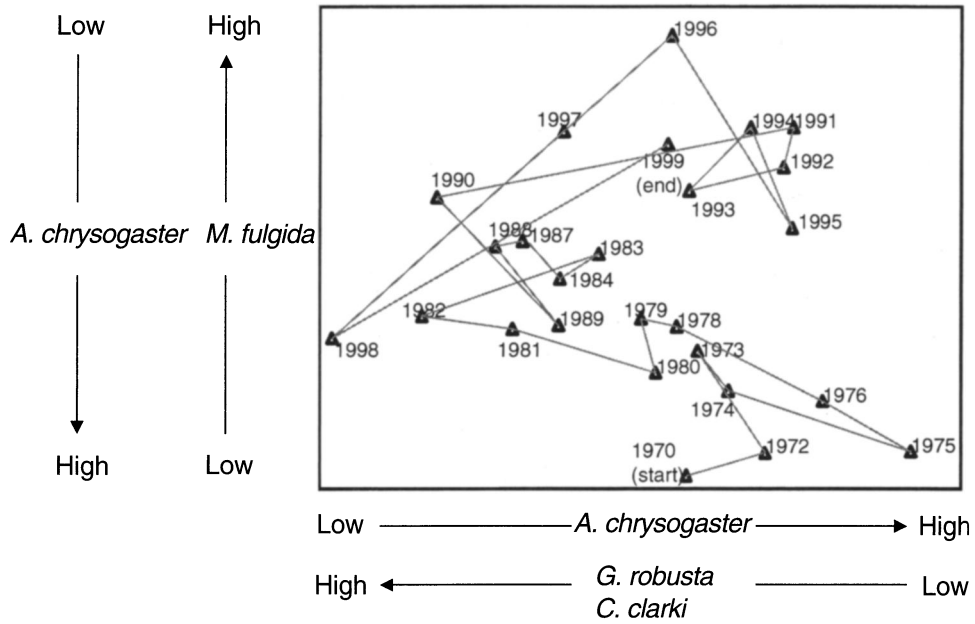

FIG. 6. DCA plot of the canyon reach fish community composition through time.

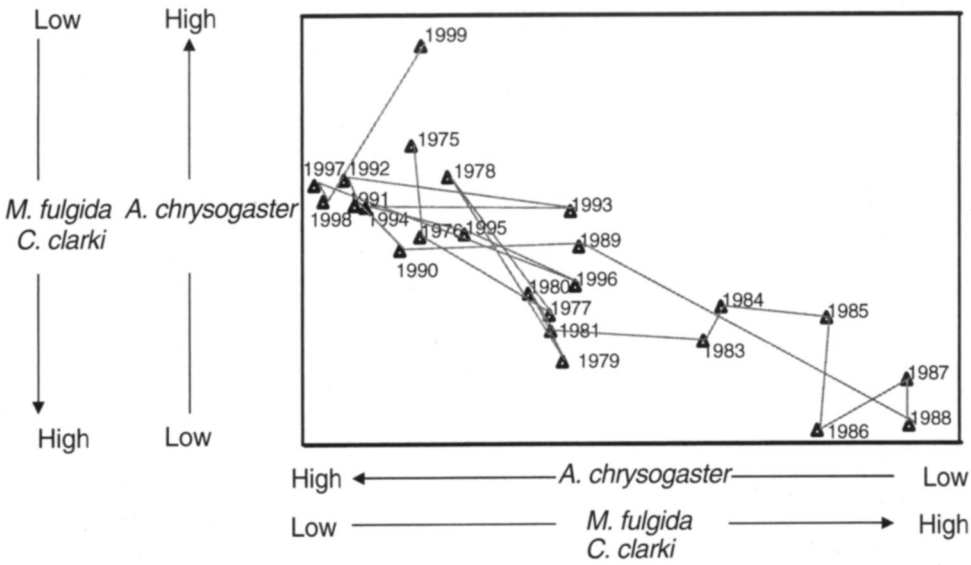

FIG. 7. DCA plot of the lower reach fish community composition through time. Changes in the native fish community are cyclic and primarily driven by inverse patterns in *Agosia chrysogaster* and *Meda fulgida* over time.

tions). Without year, both the proportion of exotic species (<0.07) and first occurrence of *C. lutrensis* (presence/absence) were in the final model and explained all of the variance (residual mean deviance 0, 0/24 misclassifications).

DISCUSSION

Measures of community change

The variety of indices used to evaluate community change not only incorporate different information, but

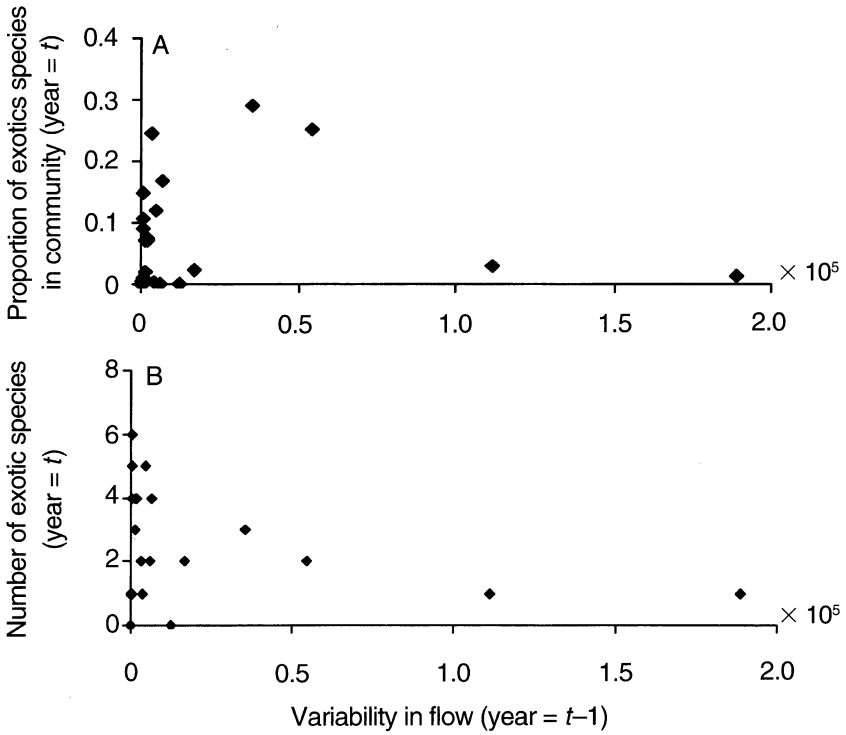

FIG. 8. Relationships between exotic species and flow variability in the lower reach of Aravaipa Creek between 1975 and 1999. (A) Proportion of community composed of exotics in the spring vs. variability in flow from the previous year. (B) Number of different exotic species present vs. variability in flow from the previous year.

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would lead investigators to disparate conclusions. Persistence and concordance are two of the most commonly used indices of stream fish community change (e.g., Grossman et al. 1990, Matthews 1996). Persistence of the native fish community was high, implying that there have been few changes in the presence of native fish species from 1965 to 1999. These results are typical for stream fish assemblages (Grossman et al. 1990) and similar to earlier analyses (1943–1983) from this system (Meffe and Minckley 1987). The lower reach had the lowest persistence (implying the highest rate of native species turnover). This reach experiences the greatest temperature fluctuations and discharge extremes, and the highest proportion of exotics. Canyon and upper reaches experience cooler summer temperatures, and flood events may have lesser impacts because watersheds are smaller higher in this system and the stream width is more constrained through the canyon (Bruns and Minckley 1980). Although persistence is useful in examining the continued existence of a species in a system, it is influenced by the detection of rare species over time and does little to anticipate or predict future loss. Concordance values were significant for all reaches, but only high (>0.70) for the canyon and lower reaches. The upper reach concordance value was lower (0.48) and primarily a function of a large increase in the rank abundance of *M. fulgida* and a comparable decrease in *C. clarki* over the study period. Concordance measures have been criticized as too simplistic (Ebeling et al. 1990), difficult to interpret (Grossman et al. 1990), and sensitive to continued low abundances of rare species (Grossman et al. 1982, Rahel et al. 1984). In examining long-term data sets for conservation concerns, persistence and concordance measures are too coarse to be useful.

As expected, as we increase the resolution of our measures, we are more likely to detect community change (Rahel 1990). Results from time lag regression analyses and time vectors of multivariate plots both indicated a temporal shift in community composition. Time lag regression demonstrated shifts in upper and canyon reaches that are demonstrated in the multivariate plots driven primarily by changes in the proportion of *M. fulgida* and *A. chrysogaster* in the assemblage. In contrast, the ability of community changes in the lower reach to be detected by the time lag regression were confounded by the community shift in the 1990s back to an assemblage structure similar to the 1970s; an assemblage with high proportions of *A. chrysogaster* and low proportions of *M. fulgida*. Since time lag regression assumes a linear relationship in community dissimilarity over time, it did not detect changes in the lower reach. This pattern of the native fish assemblage changing then returning to a previous state was described only by the time vectors of multivariate plots. Our results support the conclusions of Matthews (1996) that there is no one simple quantitative tool for the detection of change, but that an array of statistical investigations is necessary to explore changes in fish species assemblages.

Exotics and flow

Native southwestern fishes have persisted in highly fluctuating streams for thousands of years. Stabilization of flows by dams in systems that previously experienced flash flooding has resulted in easier colonization and establishment by invasive species (Meffe 1984, Minckley and Meffe 1987). Effects of floods and high flow variation may inhibit the establishment of exotics and select for communities predominated by native species (Minckley and Meffe 1987). Although not significant, both the decrease in number of exotic species and in the proportion of the community composed of exotics with increasing flow variation driven by a few years of very high peak flow support this theory. Unfortunately, with proportional data we cannot differentiate whether this trend results from increasing absolute abundance of native species or decreasing abundance of exotics. However, previous work in desert stream systems (e.g., Minckley and Meffe 1987), examination of our raw data, and the trend in number of exotic species would suggest these trends are caused by a decrease in exotic species and their abundances during times with high variation in flow. Although the rise in constancy of maximum and minimum flow between the early and later years of this study was small, it may have increased the likelihood of survival for those exotics that did enter the system.

In addition to flow changes, morphological changes occurred in Aravaipa Creek during the early 1980s. The large 1983 flood rearranged channel morphology downstream at the confluence of Aravaipa Creek and the San Pedro River (Fuller 2000). In addition to the changes in channel characteristics, changes in the flow regime since 1983 have resulted in a shift in the frequency distribution of flows toward more sustained, higher flows (Fig. 9). Likely as a result of both changes in morphology and flow, the downstream connection between Aravaipa Creek and the San Pedro River, previously occurring only in years with high runoff, has become commonplace in winter (P. Marsh, *personal communication*). Increased connectivity with the San Pedro River increases the likelihood of exotic species entering Aravaipa Creek.

Changes in the native fish assemblages

Similar to the findings of Meffe and Minckley (1987), we did not detect a direct effect of large flash floods (1978, 1983, or 1993) on the native fish assemblage. In systems where floods are common, native fish assemblages typically appear resilient to the flood disturbances unless the populations are otherwise stressed or very rare (Collins et al. 1981, Matthews 1986, Meffe and Minckley 1987).

Evidence suggests that both changes in base flow and introduction of exotics are altering the Aravaipa

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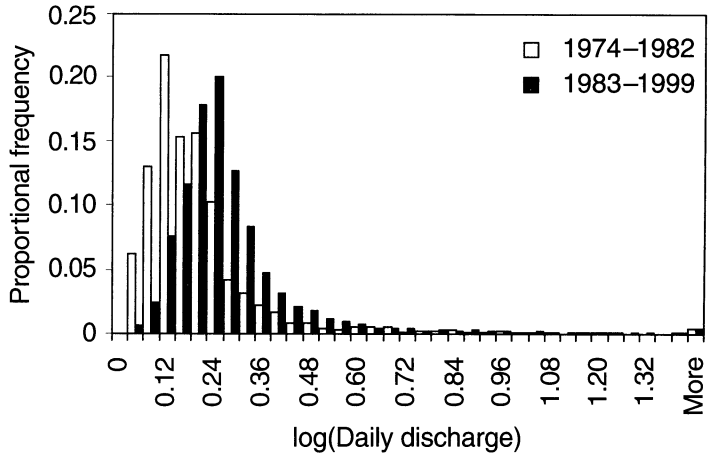

FIG. 9. Proportional frequency distribution of the log daily mean discharge (original units of m^3/s) in the lower reach of Aravaipa Creek, Arizona (USGS gauge station 09473000), grouped between 1974–1982 and 1983–1999.

Creek native fish community. Mean annual base flows for the last 21 years (1978–1998) were more than twice the values in 1967–1977. The increase in daily mean minimum flow was probably a result of both an increase in winter precipitation starting in 1978, and a change in land use associated with lessened farming and groundwater-dependent irrigation (Fuller 2000). The 1978 flood removed sediment and downcut the creek; this change in geomorphology also could have resulted in increased flow velocities. In the upper and canyon reaches, mean daily minimum flow was the best predictor of community shifts. Although cluster analyses broke the time series at 1982, examination of the data indicates that declines in *A. chrysogaster* began in the late 1970s. Similar community changes associated with base flow have been documented previously in Aravaipa Creek and Sonoita Creek, Arizona. These include increases in *R. osculus* and decreases in *A. chrysogaster* populations associated with substantial precipitation and increasingly persistent flow (Barber and Minckley 1966, Minckley 1981).

No change in the hydrograph (such as a decrease in mean minimum flow) occurred that could explain the resurgence of *A. chrysogaster* during the 1990s. A potential mechanism to explain this increase in *A. chrysogaster* would be if the 1983 flood had altered habitat (e.g., decrease vegetation and increase erosion and sediment supply) that then required a recovery period before a large year class was produced. By 1993, canyon sections exhibited formation and revegetation of bars associated with the creek's recovery after the 1983 flood (Fuller 2000). Unfortunately there are no quantitative habitat measures over this time period with which to examine this hypothesis.

The synchrony of similar fish community changes in the early 1980s throughout the entire creek system indicates that the forcing is probably a system-wide phenomenon, such as a change in hydrology. In contrast, the 1990s community shifts differed among reaches; upper and canyon sites were predominated by *A. chrysogaster* and *M. fulgida* while the lower site composition was dominated by *A. chrysogaster* alone. The deviation of the lower reach community composition changes compared with the entire system indicates a unique driving factor associated with the lower reach. This difference is a result of the lower reach not experiencing the same continued increase in *M. fulgida* as the canyon and upper reaches. *Meda fulgida* are historically found throughout the system (Minckley 1981), thus the absence of *M. fulgida* in the lower reach as the population increased throughout the rest of the creek is unusual and a serious concern because of its threatened status. The composition of the lower reach begins to diverge from that of the rest of the system in 1990, the year with the highest proportion of exotics and the first appearance of *C. lutrensis*. Previous studies suggest that *T. cobitis*, another threatened species, may also do poorly in the presence of exotics. However we did not detect a decrease in the proportional contribution of *T. cobitis* to the fish assemblage in the lower reach. The abundance of this species was typically low, and thus has little influence on proportional composition data. This constraint is one of many limitations of using proportional data.

Although Aravaipa Creek is an intrinsically variable system with flash floods and temperature extremes, community composition changes were not a result of environmental extremes but instead were due to chronic changes in the system, specifically changes in base flow and the presence of exotics. Synchrony of changes in separate reaches helps differentiate potential forces driving community changes. Community changes in the early 1980s were likely a result of base flow changes. More recent community changes and future risks for native species are likely associated with exotics. Some evidence suggests that low flow variability and connection with the San Pedro River were both important in facilitating entry of exotic species into the system and their continued persistence.

Habitat fragmentation constitutes a serious threat to aquatic biological diversity and understanding its consequences for persistence of native populations and

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communities remains a daunting challenge for conservation biologists. But when exotics are widespread, we also need to reconsider our general assumption about the universally beneficial role of connectedness. Even though fragmentation may historically have been a key contributor to native fish losses in the region (Fagan et al. 2002), isolation may now be critical for protection of some remnant native fish assemblages. Threatened with exotic species, conservation of remnant desert native fish communities requires isolation that makes invasions by nonnative species less likely plus maintenance (or restoration) of the natural flow regimes that make persistence of exotic species difficult.

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