

NATURAL FLOW REGIMES, NONNATIVE FISHES, AND NATIVE FISH PERSISTENCE IN ARID-LAND RIVER SYSTEMS

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Abstract. Escalating demands for water have led to substantial modifications of river systems in arid regions, which coupled with the widespread invasion of nonnative organisms, have increased the vulnerability of native aquatic species to extirpation. Whereas a number of studies have evaluated the role of modified flow regimes and nonnative species on native aquatic assemblages, few have been conducted where the compounding effects of modified flow regimes and established nonnatives do not confound interpretations, particularly at spatial and temporal scales that are relevant to conservation of species at a range-wide level. By evaluating a 19-year data set across six sites in the relatively unaltered upper Gila River basin, New Mexico, USA, we tested how natural flow regimes and presence of nonnative species affected long-term stability of native fish assemblages. Overall, we found that native fish density was greatest during a wet period at the beginning of our study and declined during a dry period near the end of the study. Nonnative fishes, particularly predators, generally responded in opposite directions to these climatic cycles. Our data suggested that chronic presence of nonnative fishes, coupled with naturally low flows reduced abundance of individual species and compromised persistence of native fish assemblages. We also found that a natural flow regime alone was unlikely to ensure persistence of native fish assemblages. Rather, active management that maintains natural flow regimes while concurrently suppressing or excluding nonnative fishes from remaining native fish strongholds is critical to conservation of native fish assemblages in a system, such as the upper Gila River drainage, with comparatively little anthropogenic modification.

Key words: *climate cycles; disturbance regime; drought; fish assemblage stability; Gila River, New Mexico (USA); introduced species; native fish conservation.*

INTRODUCTION

Increasing human populations have escalated demands on water resources in arid lands, and water acquisition has left few arid-land river systems unmodified (Minckley and Deacon 1991). Concurrent with physical modifications has been widespread introduction and establishment of nonindigenous aquatic species (e.g., Fuller et al. 1999, Schade and Bonar 2005). This combination of unnatural stressors has led to declines of native fish assemblages throughout arid lands (Miller et al. 1989, Kingsford 2000, Olden and Poff 2005) and prompted considerable discussion into how these declines might be halted, if not reversed (Tyus and Saunders 2000, Minckley et al. 2003, Clarkson et al. 2005, Mueller 2005, Anderson et al. 2006). Prominent among proposed conservation strategies is restoration or maintenance of natural flow regimes (Poff et al. 1997, Bunn and Arthington 2002, Richter et al. 2003). In addition to the inherent value of retaining natural fluvial processes, natural flow regimes are believed essential for

maintenance or restoration of native aquatic communities (Bunn and Arthington 2002, Lytle and Poff 2004, Propst and Gido 2004). With a natural flow regime it is expected that streams retain those attributes with which native fauna evolved and thus are necessary to maintain robust, healthy populations. A natural flow regime also should be less likely to provide conditions suitable for establishment of nonnative organisms that evolved in systems with different suites of biotic and abiotic attributes (Minckley and Meffe 1987, Baltz and Moyle 1993, Marchetti and Moyle 2001, Lytle and Poff 2004). Others contend (e.g., Tyus and Saunders 2000), however, that maintenance of a natural flow regime is not sufficient to ensure retention of native fish assemblages or depletion of nonnative organisms.

Understanding the context within which invasive species effects are detrimental to native populations is a major challenge for ecologists (Parker et al. 1999). Despite considerable advances in ecologists' understanding of linkages between natural flow regimes and maintenance of native fish assemblages, few studies have characterized the dynamics of native fish assemblages in systems where nonnative invaders are the only, or primary, unnatural disturbance. The lack of such research can be attributed to the paucity of physically

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unmodified river systems (e.g., Vitousek et al. 1997), which are particularly scarce in arid regions with high human water demands. Even in the few systems where human-caused modifications are minimal, but nonnative fishes are present, decoupling the influence of environmental factors from those imposed by nonnative fishes is daunting (Bunn and Arthington 2002). It is particularly difficult to test if the proliferation of nonnative species is in direct response to environmental factors or the decline in native species (or both). Addressing such questions requires establishment of reference or baseline conditions with data obtained across a substantial portion of the range and habitats occupied by species and over a sufficient time to include reasonably anticipated variation in natural abiotic and biotic conditions that each native species might encounter during at least two complete generations (Stoddard et al. 2006).

Negative interactions of nonnative salmonids with native galaxids or salmonids via hybridization, competition, or predation have been well documented in unregulated streams (Behnke 1992, Crowl et al. 1992, Fausch et al. 2001). Effects of nonnative fishes in naturally flowing warmwater streams are generally believed to be negative, but their extent and magnitude are less explicitly demonstrated. For example, in Aravaipa Creek, an unregulated tributary of the San Pedro River in southeast Arizona, native fishes have persisted, despite the presence of several nonnative fishes (e.g., red shiner *Cyprinella lutrensis*, yellow bullhead *Ameiurus natalis*, and green sunfish *Lepomis cyanellus*; Eby et al. 2003). Although Eby et al. (2003) documented a decline in proportion of native fishes in lower reaches of Aravaipa Creek, it was not apparent whether the shift was a consequence of negative interactions or colonizing nonnatives from the San Pedro River. Moyle et al. (2003) reported negative impacts of an alien predator (redeye bass, *Micropterus coosae*) in the Cosumnes River, California, that had a quasi-natural flow regime; however, several tributary impoundments diminished summer flows, and this, as well as other human-induced changes, was suggested as equally important factors. Pusey et al. (2006) reported negative effects of a piscivorous gudgeon (sleepy cod, *Oxyeleotris lineolatus*) above a mainstem impoundment on the Burdekin River, Australia, but again, this system was potentially influenced by human activity. Additional elucidation of the complex manner in which natural flows mediate the interactions of native and nonnative fishes might be facilitated by examining change in fish assemblages across multiple spatial and temporal scales in an undisturbed river system.

The upper Gila River in southwest New Mexico, USA, largely undisturbed by anthropogenic activities provided a rare opportunity to assess and characterize the extent to which a natural flow regime in an arid-land system mediated structure and persistence of native fish assemblages that were concurrently under pressure from nonnative fishes. Most of its forested upper watershed is

in federal ownership and on these lands human use is largely confined to low-impact outdoor recreation, dispersed livestock grazing, and sparse human settlement. In valley reaches of downstream portions, human influences are somewhat greater, but limited mainly to seasonal water diversion for small tracts of irrigated agriculture, livestock grazing, and scattered dwellings.

Our study began in 1988 with a primary purpose of monitoring fish assemblages at six locations to characterize factors that influenced the stability (i.e., resistance and resilience, sensu Connell and Sousa 1983) of native warmwater fish assemblages. Nonnative species that might prey upon or compete with native fishes were present in the drainage, and several had been implicated in decline of at least one species, *Gila robusta* (Bestgen and Propst 1989). Within this overarching purpose, we intended to (1) test if there were long-term directional changes in fish assemblage structure across the six locations, (2) characterize the response of native and nonnative fishes to attributes of a natural flow regime, and (3) characterize the effect of nonnative fishes on stability of native fish assemblages. We predicted that annual variation in native fish assemblage structure would be associated with annual variation in the flow regime, that native fish assemblages would not change appreciably (despite pressures by nonnative fishes) in a natural flow regime setting, and that evidence of native and nonnative fishes interactions would be most apparent during years with low flows.

METHODS

Study area

Six sample sites were established in the upper Gila River drainage in southwest New Mexico (Fig. 1) and represented a gradient from small- to medium-sized streams within a landscape having relatively low-impact local land uses. One site was located on Tularosa River (1817 m elevation), the smallest stream, in a valley where dispersed livestock grazing was the primary human activity on federal and private lands of the timbered (mainly piñon-juniper) watershed. The San Francisco River site (1433 m) was near the village of Glenwood, downstream of a broad valley used for livestock grazing and irrigated agriculture, and upstream of a low-head irrigation diversion dam. A site was located on each of the East, Middle, and West forks of the Gila River; the Middle Fork (1733 m) and West Fork (1737 m; see Plate 1) sites were near the downstream terminus of each river, but the East Fork site (1876 m) was near the stream's origin. Watersheds of each were almost entirely within federal lands, much of which was in the Gila and Aldo Leopold Wildernesses and almost completely unaffected by human activity except dispersed livestock grazing in the East Fork Gila River drainage. For most of their courses, each flowed through canyons and narrow valleys with forested uplands (primarily ponderosa pine, piñon, and juniper). The site on the mainstem Gila River (1359 m) was near the middle of a broad

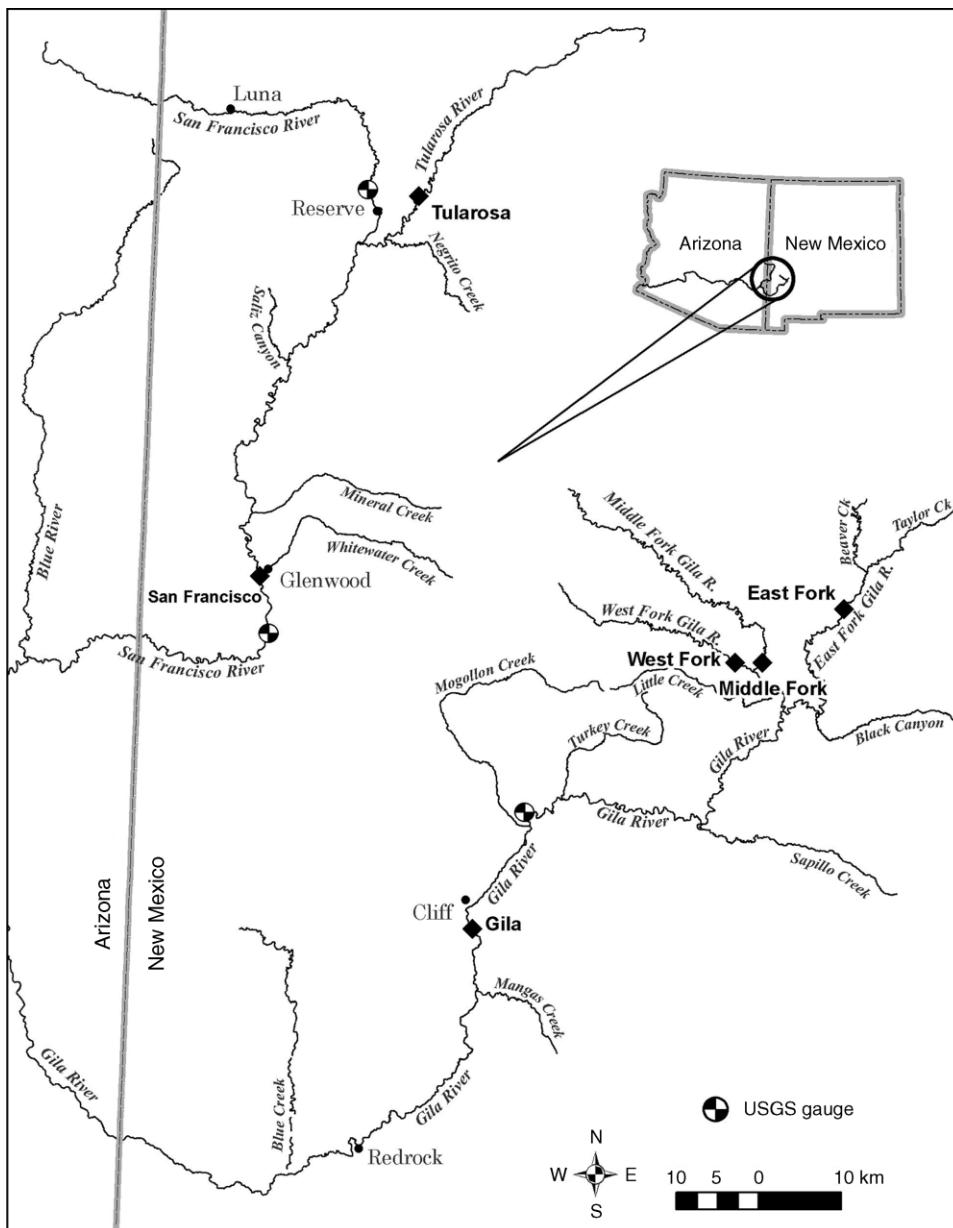


FIG. 1. Upper Gila River drainage in southwest New Mexico, USA. Locations of permanent study sites are indicated by black diamonds, and USGS stream gauging stations are denoted with surveyor's symbols.

valley where irrigated agriculture and livestock grazing were the predominant land uses, and while still quite rural, human settlement increased during our study. Uplands in the vicinity of this site, the most removed from headwaters, were largely privately owned grasslands.

Precipitation and hence stream discharge in the upper Gila River drainage was quite variable within and across years (Thomas and Pool 2006; Fig. 2a). During our study, mean daily discharge in the Gila River near Gila (USGS gauge 9430500) normally ranged from 1 to 8 m³/s (mean = 5.17 m³/s). Mean daily discharge was

greatest in March or September in 9 of 19 years and least in June or July in 16 of 19 years. Floods, ≥ 50 m³/s mean daily discharge, were infrequent, but occurred in 8 of 19 years. All floods were in August, September, November, February, or March. Maximum mean daily discharge never exceeded 25 m³/s, but twice, from September 1999 through December 2005. Our study period included both relatively wet and dry periods. When compared to the period of record for the Gila River near the Gila gauging station (October 1927 to present), median daily discharge exceeded the historical median in all but two years between 1988 and 1998 (Fig. 2b). In contrast, from

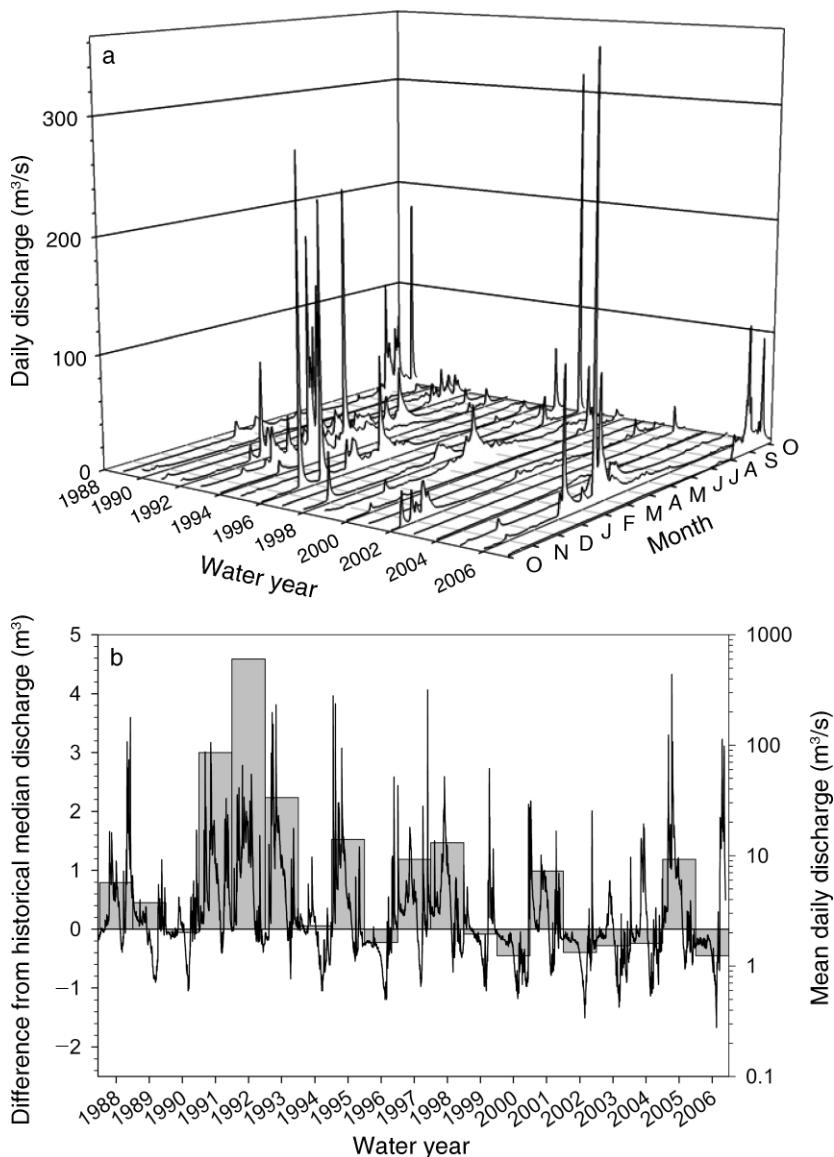


FIG. 2. (a) Mean daily discharge of Gila River near the Gila USGS gauge (94305000) September 1988 through October 2006 and (b) mean daily discharge (September 1988 through October 2006; note log scale) contrasted with annual median discharge difference from period of record median discharge (year \times median discharge minus period of record median discharge [$2.066 \text{ m}^3/\text{s}$] = difference [$\pm \text{m}^3/\text{s}$]).

1999 through 2006, median daily discharge exceeded the historical median in only 2001 and 2005. These hydrologic patterns were generally consistent across the region. Unregulated Aravaipa Creek and Verde River (upstream of Clarkdale) in Arizona experienced similar wet and dry periods between 1988 and 2006 (Table 1). While specific hydrologic attributes varied, the general outline was similar across sites in that small floods were more frequent during the wet period (1988 through 1998) than dry (1999 through 2006), particularly in Gila River and Aravaipa Creek. Extreme low flow events were not substantially more frequent during the dry than wet period, except in Gila and Verde rivers.

Sampling methods

Sampling occurred each year during October through early November. Elevated flows precluded sampling at Gila site in 2000 and San Francisco in 2006. Access was denied to East Fork in 1996 and San Francisco in 2000. Discharge at time of sampling was not associated with estimated total fish densities across years for all sites ($P > 0.1$). Seines ($3.0 \times 1.2 \text{ m}$, 3.2-mm mesh) and backpack electrofishers (12 or 24 V) were used (either singly or in combination with seine) to obtain specimens. Typically, sampling crews consisted of three to five individuals, with D. L. Propst or J. A. Stefferud always

TABLE 1. Hydrologic attributes of Gila River drainage in Arizona and New Mexico, USA, at selected USGS gauging stations.

USGS gauge	Watershed area (km ²)	Mean annual discharge (m ³ /s)		Discharge CV		No. extreme low flows
		1988–1998	1999–2006	1988–1998	1999–2006	1988–1998
San Francisco at Reserve	906	0.74	0.39	2.38	2.85	56
San Francisco at Glenwood	4281	3.39	2.06	2.67	3.32	57
Gila near Gila	4828	6.17	3.81	2.23	3.11	16
Aravaipa near Mammoth	1391	1.12	0.79	3.71	11.26	28
Verde near Clarkdale	9073	5.17	3.97	4.46	4.36	49

Notes: Watershed area is that provided by USGS for each gauge. Hydrologic attributes were calculated (default settings) using Index of Hydrologic Alteration software, version 7 (The Nature Conservancy 2006).

present. Sampling was done in a manner to collect all species and size classes likely present at a site and to yield realistic estimates of assemblage structure. All mesohabitats (e.g., riffle, riffle eddy, run, and pool) present were sampled; uncommon habitats (e.g., debris pools) tended to be sampled more completely than common (e.g., run). Mesohabitats were defined by lateral location, water velocity, flow pattern (e.g., laminar, circular, and turbulent), depth, substrate, and cover. Sampling began at the downstream terminus of a site and proceeded upstream, mesohabitat by mesohabitat. After sampling a mesohabitat, nonnative individuals were retained and native fishes were identified, enumerated, and released. Removal of comparatively few nonnatives (typically <25 individuals of each species present) once a year was not deemed likely to influence overall assemblage structure or species interactions. In addition, all sites were open to movement of nonnatives from adjacent stream reaches. Following fish collection, habitat measurements (one length and several width, depth, and water velocity) were made in each mesohabitat sampled. Substrate was visually classified as silt, sand, gravel, cobble, or boulder/bedrock at each depth measurement point.

Discharge data were obtained from U.S. Geological Survey gauging stations: San Francisco River near Reserve (9442680), San Francisco River near Glenwood (9444000), and Gila River near Gila (data *available online*).⁵ Only the San Francisco River near Glenwood and Gila River near Gila gauges were proximate to study sites. We assumed for analyses that the San Francisco River near Reserve generally reflected flows in the Tularosa River and the Gila River near Gila gauge did the same for each Gila River forks site. Data from Aravaipa Creek near Mammoth (09473000) and Verde River near Clarkdale (09504000) USGS gauges were used for regional comparisons.

Analyses

Assemblage trends.—Because multiple analytical methods can yield different insights into patterns of long-term change, we attempted to gain consensus by evaluating our data with multiple approaches. Spear-

man's rank correlations were used to detect trends in abundance rank of species over time at each site. Temporal change in $\log(x + 1)$ total native and nonnative fish densities (number of individuals per species per total area sampled) at each site was also assessed with correlation analysis. Persistence was used to characterize turnover (Minckley and Meffe 1987, Eby et al. 2003) and calculated as $T = (C + E)/(S_1 + S_2)$, where C and E are the number of species that colonized or were extirpated between sample periods, while S_1 and S_2 are the number of species present in each sample period (Diamond and May 1977).

Two approaches were used to test for a directional change in the fish assemblage within the study period. First, a Mantel test (Mantel 1967) was used to test for a significant association between a distance matrix that represented time between samples (years) and a matrix representing assemblage similarity between sample dates. We used both Bray-Curtis and Jaccard's similarity indices to represent quantitative and qualitative attributes of assemblage structure, respectively. The Mantel tests provided a correlation coefficient (Mantel statistic, r) and test of significance between triangular matrices (Jackson and Somers, 1989). Observed r values were compared to 10 000 random permutations of the data to determine the probability that observed patterns were randomly generated. All calculations were made with the NTSYS version 2.10 (Applied Biostatistics, New York, New York, USA). Second, we used principal components analysis (PCA) to visualize the temporal variation in fish-assemblage structure at the six study sites and identify species driving that variation. PCA is an indirect gradient analysis that assumes linear relationships among species, which is appropriate for evaluating temporal variation within a site and where high levels of species turnover are not expected. We chose this method over other approaches (e.g., nonmetric multidimensional scaling) because they yielded similar results, and eigenvalues from the PCA could be directly compared with those from constrained ordinations to evaluate factors driving patterns of assemblage change. Species that occurred <5 years at a site were excluded from this analysis. Eigenvalues and site scores for PCA were calculated using CANOCO software, version 4.5 (ter Braak and Smilauer 2002).

⁵ (<http://waterdata.usgs.gov/nwis/sw>)

TABLE 1. Extended.

USGS gauge	No. small floods	
	1988–1998	1999–2006
San Francisco at Reserve	8	5
San Francisco at Glenwood	7	5
Gila near Gila	8	1
Aravaipa near Mammoth	7	1
Verde near Clarkdale	6	5

Drivers of assemblage change.—Hydrologic regime, local habitat characteristics, and abundances of nonnative fish species were evaluated for associations with native assemblage structure. Hydrologic regime was characterized using daily discharge records from USGS gauges, and we partitioned the water year (1 October–30 September) into pre-spawn, spawn, and post-spawn periods (Table 2). Attributes of discharge quantity and variability were summarized using Indicators of Hydrologic Alteration software, version 7 (Richter et al. 1996, The Nature Conservancy 2006). Of the 66 attributes generated by this analysis, we identified 16 variables that, based upon documented life history attributes of the species of interest, were likely to affect fish assemblages at our study sites. To control for colinearity among these 16 variables, PCA was used to summarize variation across years in these variables. We summarized physical habitat by maximum depth, percentage fines (sand and silt substrates), and proportional frequency of three main habitat types (pools, riffles, and runs). Finally, we summed densities of nonnative predators (smallmouth bass *Micropterus dolomieu*, yellow bullhead, brown trout *Salmo trutta*, and rainbow trout

Oncorhynchus mykiss) and nonnative competitors (red shiner *Cyprinella lutrensis* and western mosquitofish *Gambusia affinis*) and used these as predictor variables.

Redundancy analysis (RDA) was used to characterize associations between native fish assemblage structure and potential abiotic and biotic drivers at each site. A Monte Carlo simulation was used to select variables that were significantly associated with assemblage structure. One thousand simulations were run and variables that significantly contributed to variance explained in the RDA >10% of the time (e.g., $P < 0.10$) were included in the analysis. Analyses were conducted using CANOCO software, version 4.5 (ter Braak and Smilauer 2002).

To characterize factors associated with nonnative predators, we used stepwise multiple regression to evaluate the relationship between environmental variables and total densities of nonnative predators at the six sites. Independent variables that described flow attributes (i.e., PCA axis scores) and habitat were the same as those used in the RDA. The criterion to enter independent variables was $P < 0.05$ and probability to remove independent variables was $P > 0.10$.

Because there were multiple years of severe drought in the region during our study (Fig. 2), we tested the relationship between consecutive years of below-median flows and densities of both small-bodied native fishes (longfin dace *Agosia chrysogaster*, spikedace *Meda fulgida*, speckled dace *Rhinichthys osculus*, and loach minnow *Tiaroga cobitis*) and nonnative predators with correlation analysis. We hypothesized that short-lived, small-bodied native species would respond negatively to multiple years of low flow because they are presumably less capable of rebounding after two or more failed or greatly diminished year classes. Nonnative predators

TABLE 2. Environmental correlates used in regression models to predict densities of native fishes at permanent sites in the Gila River drainage, New Mexico.

Environmental attribute	Ecological relevance
Pre-spawning hydrology (November–February)	
Median discharge	amount of habitat
Maximum daily	inter-day variation
High flood pulses	faunal displacing and channel forming
Spawning hydrology (March–April)	
Median discharge	amount of habitat
Minimum daily	spawning habitat reduction or loss
Maximum daily	modify stream morphology; eggs and larvae displacement
Baseflow index	current conditions vs. record norm
High flood pulses	disrupt spawning
Reversals	spawning disruption; egg exposure
Post-spawning hydrology (May–October)	
Median discharge	amount of habitat
Minimum daily	increased competition or predation
Maximum daily	modify stream morphology
Baseflow index	current conditions vs. record norm
Low flood pulse events	disrupt nonnative spawning
High flood pulse events	disrupt nonnative spawning; displace nonnative eggs or larvae
Biotic interactions	
Nonnative predator abundance	mortality of natives through consumption or behavioral shifts
Nonnative small-bodied abundance	competition for resources and predation of larval native fishes

TABLE 3. Fishes collected and number of occurrences at six annually sampled permanent sites in Gila and San Francisco drainages, New Mexico, USA, 1988–2006.

Species	East Fork (18)	Middle Fork (19)	West Fork (18)	Gila (18)	Tularosa (19)	San Francisco (17)
Native						
Longfin dace, <i>Agosia chrysogaster</i>	12	9	16	17	19	15
Headwater chub, <i>Gila nigra</i>	16	14	11			
Roundtail chub, <i>Gila robusta</i>				1		
Spikedace, <i>Meda fulgida</i>	5	6	16	17		
Speckled dace, <i>Rhinichthys osculus</i>	3	9	18		19	17
Loach minnow, <i>Tiaroga cobitis</i>	5	11	12	17	14	17
Sonora sucker, <i>Catostomus insignis</i>	18	19	18	18	19	17
Desert sucker, <i>Pantosteus clarki</i>	18	15	17	18	18	17
Nonnative						
Common carp, <i>Cyprinus carpio</i>				2		
Red shiner, <i>Cyprinella lutrensis</i>				9		
Fathead minnow, <i>Pimephales promelas</i>	4	3		2	5	4
Yellow bullhead, <i>Ameiurus natalis</i>	6	19	2	6		
Channel catfish, <i>Ictalurus punctatus</i>	2			1		
Chihuahua catfish, <i>Ictalurus</i> sp.	9					
Flathead catfish, <i>Pylodictus olivaris</i>				3		
Rainbow trout, <i>Oncorhynchus mykiss</i>		5	13		1	5
Brown trout, <i>Salmo trutta</i>		2	12			
Western mosquitofish, <i>Gambusia affinis</i>	15	11	3	16	10	6
Brook stickleback, <i>Culaea inconstans</i>					1	
Green sunfish, <i>Lepomis cyanellus</i>	2	3		2		
Smallmouth bass, <i>Micropterus dolomieu</i>	14	19	6	5		
Largemouth bass, <i>M. salmoides</i>	3			3		2

Note: The number of years a site was sampled is indicated in parentheses in the column headings.

were hypothesized to increase in abundance during low-flow periods because they are less likely to experience displacing-flow pulses during extended periods of low flow.

RESULTS

Assemblage trends

Collectively, the six sites supported seven native and 14 nonnative fish species, but occurrence varied among sites (Table 3). In 1988, longfin dace, loach minnow, Sonora sucker *Catostomus insignis*, and desert sucker *Pantosteus clarki*, were common to all sites. Speckled dace occurred at all but the Gila site. Spikedace was present at each Gila forks and Gila site and headwater chub *Gila nigra* was found only at the Gila forks sites. Western mosquitofish was the most widespread nonnative fish and found at all sites. Fathead minnow *Pimephales promelas* was found at all sites but West Fork. Yellow bullhead and smallmouth bass were found at all Gila River drainage sites, but not at either San Francisco River drainage site. Rainbow trout was found in both drainages, but most individuals were likely stocked. Naturalized brown trout was found almost exclusively at the West Fork site. Red shiner, common carp *Cyprinus carpio*, channel catfish *Ictalurus punctatus*, and flathead catfish *Pylodictus olivaris* were found only at Gila site. Other nonnative fish species were irregularly collected and never represented by more than a few individuals. Brook stickleback *Culaea inconstans* was the only nonnative species collected (one specimen at

Tularosa) that had not been documented prior to 1988 in the upper Gila River drainage.

By the end of our study, the San Francisco site retained its full native fish complement and nonnative fishes remained a rarity. Among its native fish species, only longfin dace declined in abundance (Table 4). Other than an occasional fathead minnow or western mosquitofish, nonnative fishes were not found at the Tularosa site, but loach minnow was possibly extirpated. Density of speckled dace, however, increased over time at the site. Fish assemblage persistence at these two sites was higher than that of all others and neither Bray-Curtis nor Jaccard's indices indicated assemblage-level change at either site (Table 5).

Fish assemblage changes at the Gila forks sites were largely because native species declined (Fig. 3). At the end of the study, no fork site had the full suite of native fishes present at the beginning. At these sites, lack of change in density by a native species was the exception. With the exception of headwater chub at West Fork, Sonora sucker at Middle and West forks, and desert sucker at West Fork, each native species declined at each site. Nonnative smallmouth bass increased in density at East and Middle forks and yellow bullhead was regularly found at Middle Fork site. Rainbow trout was the only regularly collected nonnative at West Fork site, and it declined over time (almost certainly because autumn and spring stocking in the vicinity of the site ceased in 1996). Assemblage persistence was lower for these sites than all others and similarity index comparisons yielded significant differences.

TABLE 4. Nonparametric trend analysis (Spearman's rank correlation) of species densities at six sites in the Gila-San Francisco River drainage, New Mexico.

Species	Tularosa	San Francisco	East Fork	Middle Fork	West Fork	Gila
Longfin dace	0.200	-0.600*	-0.376	-0.746*	-0.546*	0.377
Headwater chub			-0.625*	-0.490*	0.377	
Spikedace			-0.526*	-0.661*	-0.817*	-0.285
Speckled dace	0.688*	-0.116		-0.749*	-0.759*	
Loach minnow	-0.824*	-0.132	-0.275	-0.760*	-0.730*	0.277
Sonora sucker	0.074	0.210	-0.721*	0.274	-0.414	0.016
Desert sucker	0.304	0.317	-0.489*	-0.602*	-0.088	0.295
Western mosquitofish		0.203	0.109	0.264		0.124
Yellow bullhead				0.179		
Chihuahua catfish			0.078			
Rainbow trout		0.152		0.249	-0.711*	
Brown trout					0.159	
Smallmouth bass			0.694*	0.775*		0.010

Note: Asterisk indicates significance ($P \leq 0.05$).

From 1988 through 2006, the fish assemblage at the Gila site did not change, as evidenced by similarity and persistence index values. All native fishes present at the beginning of the study were found in 2006 and density of none declined over time (and this was the only site at which no native fish species declined). Although a greater number of nonnative fish species was collected over the course of study at the Gila site than any other, they were never regularly collected at the site or represented by more than a few (<25) individuals.

Results from the PCA summarizing variation of fish assemblages across time also illustrated changes in native fish densities, in that the three Forks sites showed patterns of directional change (Fig. 4). This was verified with Mantel tests, which showed significant changes in the fish assemblage structure using both qualitative and quantitative indices of similarity (Table 5). In general, collections in the late 1980s and 1990s were characterized by higher incidence and densities of native fishes, whereas collections in the 2000s were characterized by relatively high densities of nonnative predators and fewer occurrences of natives. Of the three Forks sites, the greatest concordance between time and assemblage similarity was at Middle Fork. Although there was not a notable temporal trend in the fish assemblage structure at San Francisco and Tularosa, species loadings for native and nonnative fishes were inversely correlated, which contrasted with Gila, where nonnative predators and competitors were positively associated with natives.

Correlates with hydrology and mesohabitat

PCA of hydrologic variables at the three gauging stations summarized annual variation in the hydrologic regime (Tables 6 and 7). The first five principal components explained >86% of the variation in hydrologic variables across years at each of the three gauging stations. Variable loadings from the first two axes were also similar across stations, indicating consistent regional trends in flow patterns. For example, the first axis summarized variation across years based on variables associated with total annual discharge (AnnualQ) at all stations and explained 42.7–46.7% of the variation in hydrologic indices across years. The second PCA axis explained between 19.7% and 20.6% of the variation across years and generally contrasted variables associated with high flows during the post-spawn period and those associated with low flows during pre-spawn. The remaining PCA axes varied across sites and represented mean discharge or variance in discharge during the different time periods relative to spawning of native fishes.

Redundancy analysis illustrated the associations between native fish assemblage structure, hydrology, densities of nonnative species, and habitat availability (Fig. 5). However, no single explanatory variable was found to be a strong driver of native fish assemblage structure across all sites. Hydrologic variables associated with mean annual discharge (AnnualQ) were positively related to the abundance of native fishes at the three Forks sites, a pattern primarily driven by high flows in

TABLE 5. Summary of similarity and persistence indices of six fish assemblages in upper Gila River drainage, New Mexico.

Site	Bray-Curtis		Jaccard's		Persistence
	Mantel's r	P	Mantel's r	P	
Tularosa	0.089	0.171	-0.130	0.094	0.966
San Francisco	0.128	0.095	-0.066	0.218	0.972
East Fork	0.234	0.018	-0.373	0.002	0.884
Middle Fork	0.564	0.001	-0.709	0.001	0.842
West Fork	0.382	0.002	-0.346	0.002	0.901
Gila	-0.097	0.179	-0.019	0.418	0.963

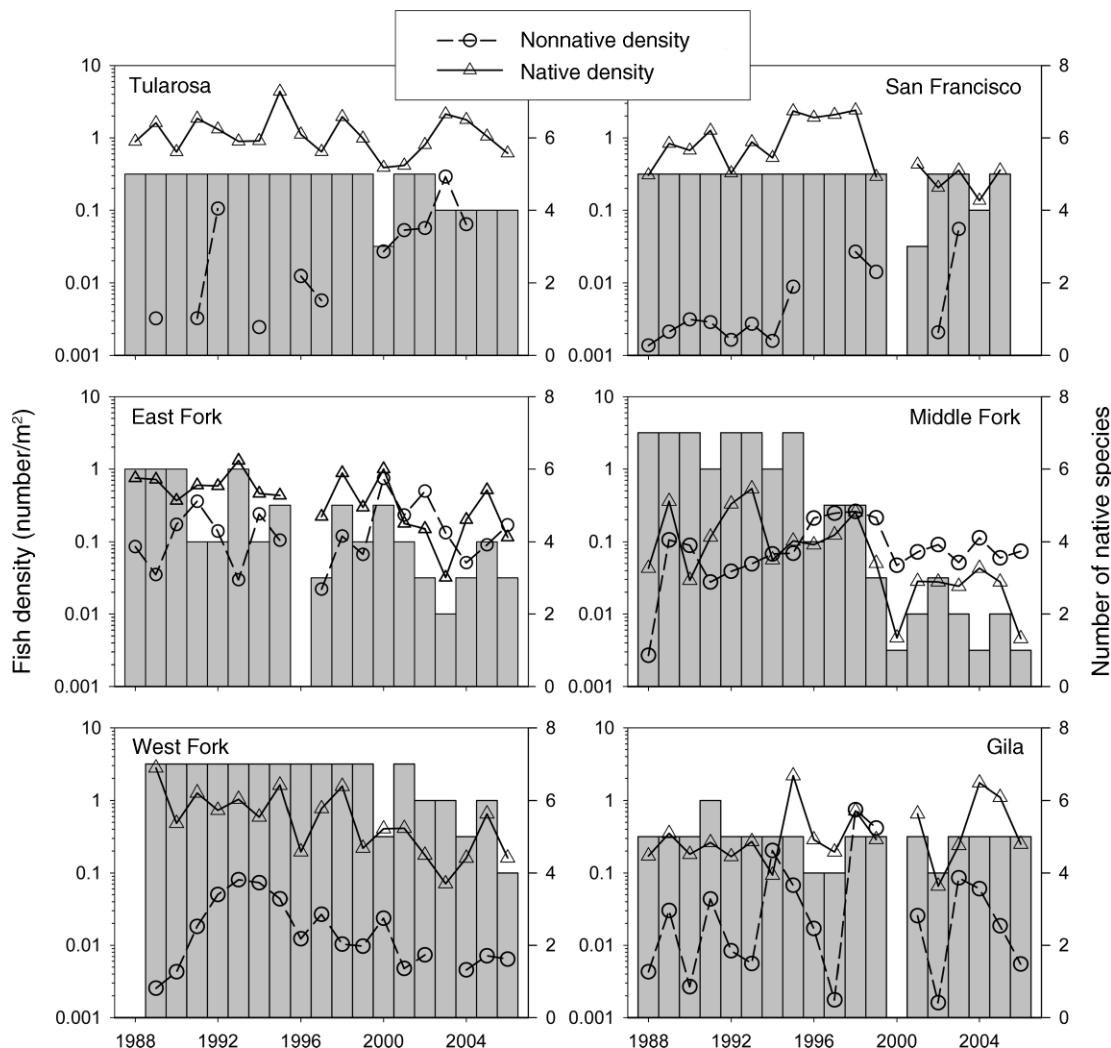


FIG. 3. Density of native and nonnative fishes and number of native fish species (gray bars) at each upper Gila River drainage site, New Mexico, USA, 1988 through 2006. Note the log scale.

1991 through 1993. In addition, high densities of native fishes were associated with high post-spawn flow variables at Gila and San Francisco. Densities of nonnative species were associated with variation in native fish assemblages at Middle Fork and East Fork. Nonnative predator density was positively associated with Sonora sucker and headwater chub, but negatively associated with other native fishes at Middle Fork. Nonnative competitors were positively associated with spinedace at East Fork. Habitat measurements associated with increased proportion of pool habitat (percentage pool, percentage fines, decreased maximum depth) were correlated with native fish assemblage structure at five sites, and were usually negatively associated with densities of small-bodied nonnative fishes. Only West Fork showed no association between native fish assemblage structure and habitat.

Densities of nonnative predators were accurately predicted with a stepwise regression model at five of

the six sites (Table 8). The only site without a significant trend was Tularosa. Nonnative densities were generally greatest during years with low flows and increased abundance of pool habitats. The strongest models occurred at East Fork and San Francisco, where nonnative predator density was positively associated with high flows during pre-spawning and low flows during spawning of natives.

Our hypothesis that density of small-bodied natives would decline with consecutive years of below-median flows was supported at the West Fork, Middle Fork, and San Francisco sites (Fig. 6). The lack of response at the East Fork site was the consequence of high density of longfin dace in 2000, following two consecutive years of low flows. In contrast to our hypotheses, nonnative predator densities did not increase with consecutive years of below-median flows, and declined at the West Fork site (and that likely caused by cessation of rainbow trout stocking).

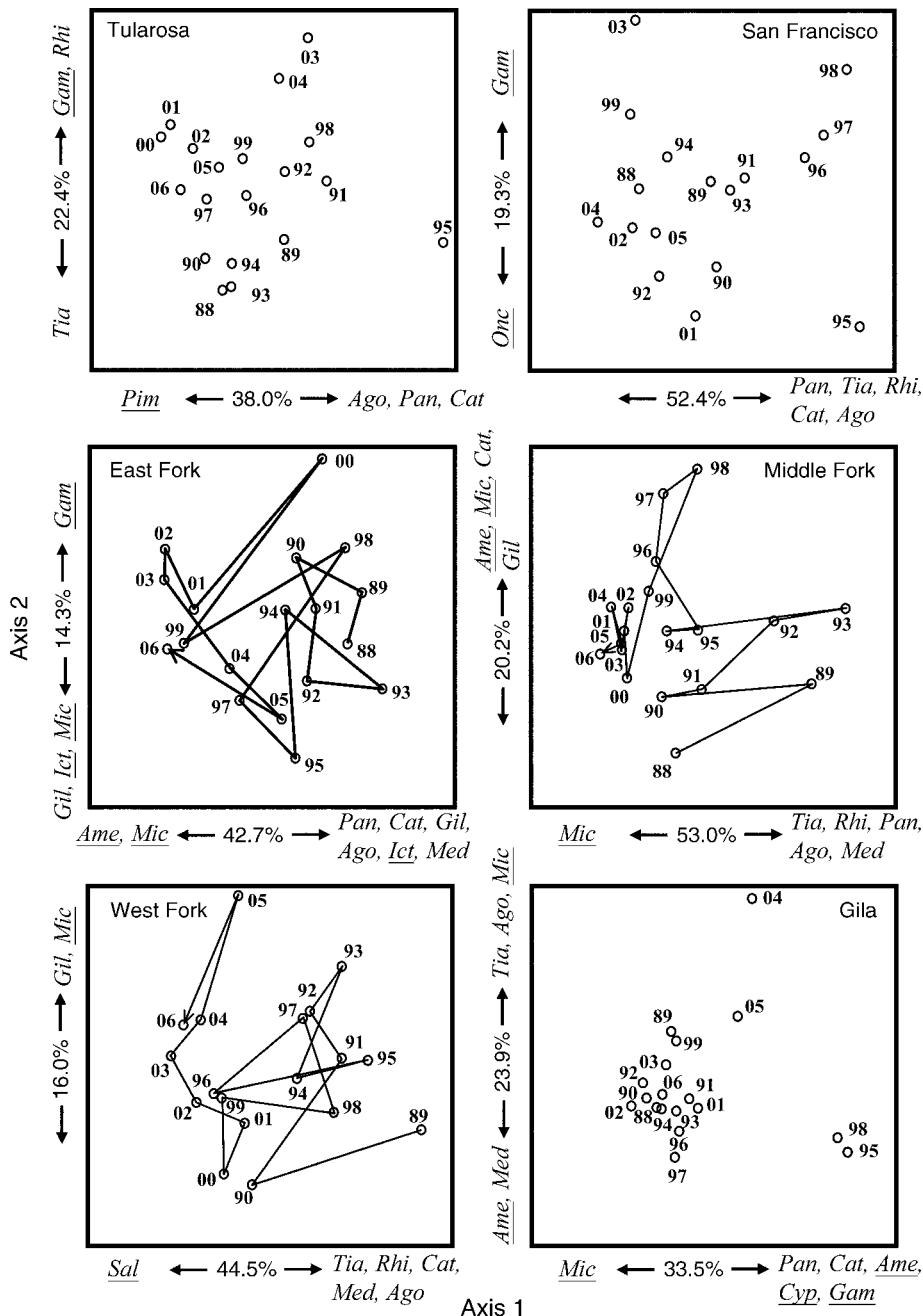


FIG. 4. Principal components analyses (PCA) of change over time in fish assemblages at six sites in the upper Gila River drainage, New Mexico, USA. Open circles represent annual samples and are labeled with the last two digits of the year. Sites having significant temporal change in assemblage structure, as indicated by Mantel tests, have lines connecting years. The percentage of variation in assemblage structure explained by PCA is given for each axis. Arrows and species codes on the axes represent those species that were strongly associated with PCA axis scores. Species codes are the first three letters of the respective genus (e.g., *Ago*, *Agosia chrysogaster*; *Ame*, *Ameiurus natalis*; and *Rhi*, *Rhinichthys osculus*). Underlined species codes indicate nonnative species.

DISCUSSION

At the onset of this study, our presumption was that a natural flow regime would maintain native fish assemblages, suppress abundance and deter spread of nonnative fishes, and that the native fish assemblages present in 1988 would persist, albeit with variation over

time. Across six sites that broadly represented the range of warmwater habitats present in the upper Gila River drainage and that were equally affected by regional climate patterns, the fish assemblage there changed markedly over the 19 years of our study. We found, as others have (e.g., Poff and Allan 1995, Bunn and

TABLE 6. Interpretation of PCA axes of hydrologic variables at San Francisco River at Reserve, San Francisco River at Glenwood, and Gila River near Gila USGS gauges, New Mexico.

Axis	Code	Definition (high values indicate)
San Francisco River at Reserve		
PCA1	AnnualQ	annual discharge
PCA2	PostspawnQ	low spawn discharge and high post-spawn discharge
PCA3	PrespawnQ	flood pre-spawn, low variable post-spawn discharge
PCA4	PrespawnQ	high pre-spawn discharge, low spawn and post-spawn discharge
PCA5	SpawnQ	low pre-spawn discharge, high spawn discharge
San Francisco River at Glenwood		
PCA1	AnnualQ	annual discharge
PCA2	PostspawnQ	high post-spawn and low pre-spawn discharge
PCA3	SpawnQVar	high and variable spawn discharge, large post-spawn flood
PCA4	SpawnQVar	high flood and variable spawn discharge
PCA5	SpawnQVar	low spawn and post-spawn discharge
Gila River near Gila		
PCA1	AnnualQ	annual discharge
PCA2	PostspawnQ	high post-spawn discharge and flood, low pre-spawn discharge
PCA3	PrespawnQ	high pre-spawn discharge and flood, low spawn discharge
PCA4	SpawnVar	variable spawn discharge
PCA5	PostspawnVar	variable post-spawn discharge

Arthington 2002), that flow regime was a primary factor shaping stream-fish assemblages. Specifically, density of native fishes was greatest in years with elevated discharge, whereas nonnative predator density was least in these years. We also found, as have others (e.g., Moyle et al. 2003, Pusey et al. 2006), that pressures exerted by nonnative fishes adversely affected native fish assemblage structure. By evaluating the response of native fishes to variability in flow regime and abundance of nonnatives, we were able to test predictions on the relative importance of these two influences in structuring fish assemblages (e.g., Bunn

and Arthington 2002). Among sites, there was a high degree of spatial and temporal variation in occurrence and abundance of nonnative fishes. In the upper Gila River drainage, the effect of nonnative predators appeared to be most pronounced during natural drought within upper reaches of the drainage (i.e., West Fork, Middle Fork, and East Fork sites). The negative association between nonnatives and native fishes indicated a complex relationship between naturally variable flows and nonnative species. In these instances, natural flow alone was not sufficient to conserve native fish assemblages.

TABLE 7. Variable loadings for principal components analysis (PCA) of hydrologic variables at three USGS gauging stations on San Francisco and Gila rivers that were hypothesized to influence autumn densities of native fishes.

Variable	San Francisco near Reserve					San Francisco at Glenwood				
	PCA1 (46.7%)	PCA2 (19.7%)	PCA3 (9.3%)	PCA4 (7.4%)	PCA5 (4.9%)	PCA1 (42.7%)	PCA2 (20.6%)	PCA3 (12.4%)	PCA4 (6.6%)	PCA5 (5.2%)
Pre-spawning										
Median discharge	0.294	-0.091	0.188	0.060	0.258	0.247	0.260	0.246	-0.118	-0.147
Maximum daily	0.246	0.200	0.304	0.215	0.254	0.213	0.298	0.264	-0.157	-0.194
High flood pulses	0.253	0.216	0.232	0.302	-0.160	0.257	0.219	0.141	-0.027	-0.180
Spawning										
Median discharge	0.302	0.013	0.010	-0.053	0.361	0.326	-0.057	0.001	0.176	0.076
Minimum daily	0.286	-0.126	0.042	0.024	0.409	0.306	-0.104	0.138	0.064	0.251
Maximum daily	0.293	-0.042	-0.126	0.244	0.200	0.230	0.050	0.236	0.460	-0.107
Baseflow index	-0.202	-0.007	0.270	0.349	0.460	-0.168	0.007	0.448	0.092	0.404
High flood pulses	0.281	0.126	-0.051	0.325	0.153	0.307	0.011	-0.157	0.047	0.095
Reversals	-0.165	0.155	-0.044	0.323	0.200	-0.102	-0.016	0.418	0.561	0.104
Post-spawning										
Median discharge	0.232	0.280	-0.241	0.073	-0.140	0.220	0.221	-0.162	-0.047	0.030
Minimum daily	0.232	0.175	0.298	0.312	-0.008	0.285	0.119	-0.080	0.039	0.274
Maximum daily	0.071	0.478	0.055	0.091	-0.127	0.005	0.382	0.272	0.279	-0.034
Baseflow index	0.099	0.252	0.426	0.395	0.085	-0.107	0.365	0.310	0.080	0.268
Low food pulses	0.238	-0.169	0.171	-0.026	0.195	0.251	-0.191	0.130	0.221	0.197
High flood pulses	-0.011	0.393	0.239	0.285	0.215	0.061	0.391	0.134	0.368	0.298
Reversals	-0.093	-0.155	0.508	0.228	-0.026	-0.224	-0.084	-0.009	0.201	0.584

Notes: The value in parentheses for each PC axis is the percentage of variance explained. Bold underlined values are significant negative and bold italic are significant positive loadings ($P \leq 0.05$).



PLATE 1. West Fork Gila River, New Mexico, July 2006. This reach supported a largely intact native fish fauna, and nonnative fishes were comparatively uncommon. Upstream of this location, the river was chiefly within the Gila National Forest Gila Wilderness. Photo credit: D. L. Propst.

In 1988, the proportional abundance of native and nonnative fishes was roughly equal at the East and Middle Fork sites (Fig. 3), but by 2006 native fishes were almost absent at Middle Fork. Decline of native fishes coincided with increased nonnative predator density

(mainly yellow bullhead and smallmouth bass) and the onset of a major drought in 1998. At West Fork, the proportional abundance of nonnatives was an order of magnitude lower than natives, and rainbow trout stocked in autumn and spring was the main nonnative predator through 1996; thereafter, it and other nonnative predators were always present, but typically represented by only a few individuals. It was unlikely that stocked trout caused the decline of the West Fork fish assemblage because they rarely consumed fish and quickly moved from stocking locations after release (D. L. Propst, unpublished data). Rather, changes in the native fish assemblage were more likely a consequence of both drought and wildfire-induced sediment-laden flows. From the late 1990s through 2003, a series of intense wildfires burned almost the entire West Fork Gila River watershed (J. A. Monzingo, personal communication), and frequent discharge pulses flushed large volumes of fine sediment and ash through the drainage. Neither the Middle Fork nor the East Fork site was subjected to wildfire-induced sediment flows.

TABLE 7. Extended.

Variable	Gila near Gila				
	PCA1 (44.3%)	PCA2 (20.3%)	PCA3 (9.5%)	PCA4 (6.6%)	PCA5 (5.4%)
Pre-spawning					
Median discharge	0.256	0.222	0.279	0.070	-0.108
Maximum daily	-0.193	0.291	0.267	-0.097	-0.270
High flood pulses	0.247	0.259	0.294	0.084	0.091
Spawning					
Median discharge	0.316	-0.033	-0.195	0.065	0.015
Minimum daily	0.314	-0.051	-0.100	-0.014	0.046
Maximum daily	0.269	0.088	0.351	-0.020	0.141
Baseflow index	0.269	0.013	0.182	0.293	0.077
High flood pulses	0.258	-0.057	0.268	0.101	0.396
Reversals	-0.098	0.075	-0.059	0.810	-0.128
Post-spawning					
Median discharge	0.232	0.280	0.241	0.073	-0.140
Minimum daily	0.232	0.175	0.298	0.312	-0.008
Maximum daily	0.071	0.478	0.055	0.091	-0.127
Baseflow index	0.099	0.252	0.426	0.395	0.085
Low food pulses	0.238	-0.169	0.171	-0.026	0.195
High flood pulses	-0.011	0.393	0.239	0.285	0.215
Reversals	-0.093	-0.155	0.508	0.228	-0.026

Over the course of this study, Tularosa and San Francisco had the most persistent native fish assemblages, but one native species declined at each site. Within the limited range of human disturbance in the upper Gila River drainage, both Tularosa and San Francisco sites were modified more than any forks site; each was downstream of human settlement, irrigated cropland, and in watersheds with somewhat greater human use (e.g., livestock grazing and roads). Neither, however,

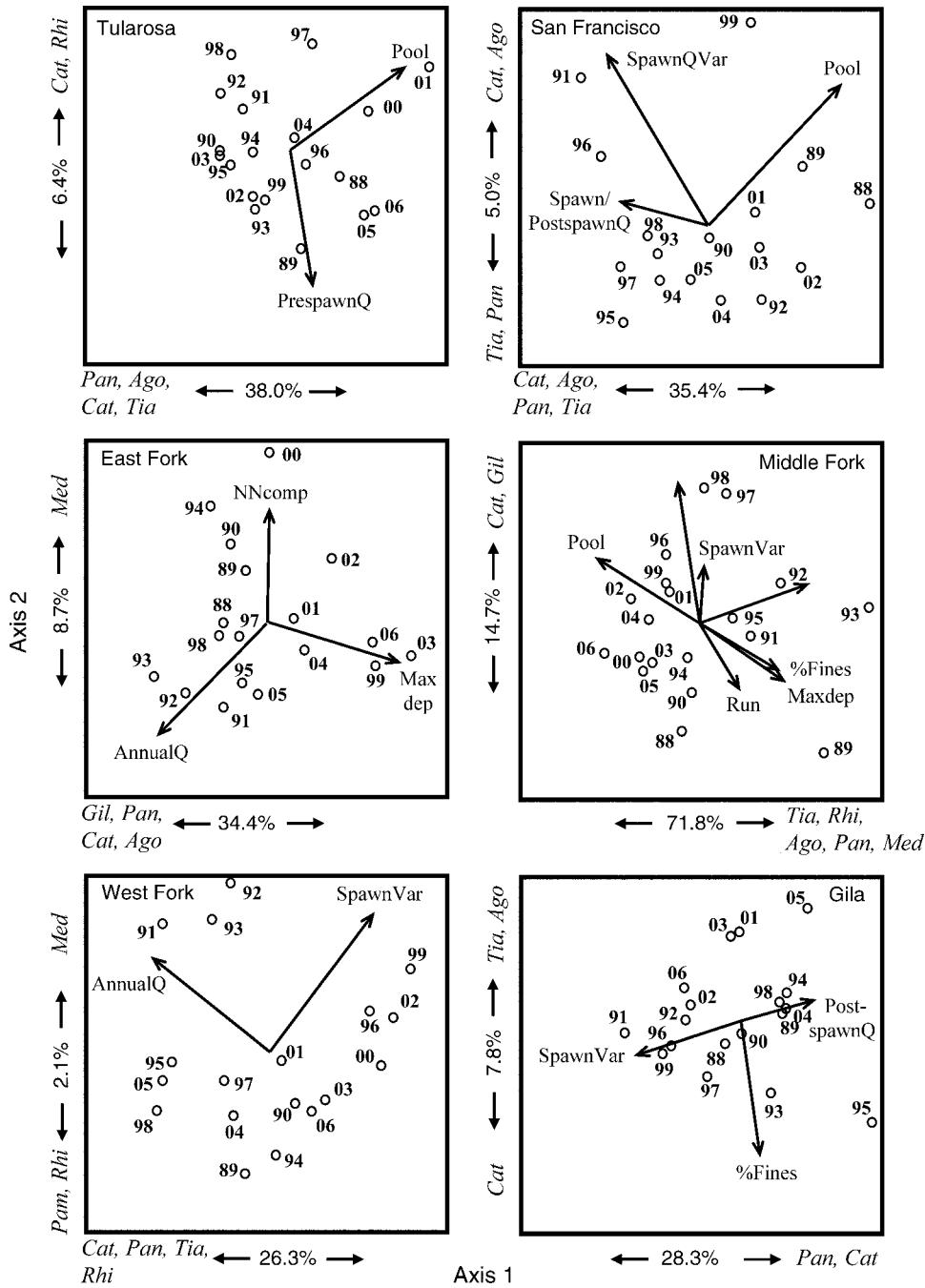


FIG. 5. Redundancy analyses (RDA) of drivers of assemblage change at six sites in the upper Gila River drainage, New Mexico, USA. Open circles represent annual samples and are labeled with the last two digits of the year. Vectors represent the strength and direction of association for variables that were included in a model predicting variation in assemblage structure across years. The percentage of variation in assemblage structure explained by RDA is given for each axis. Arrows and species codes on the axes represent those species that were strongly associated with RDA axis scores. Species codes are the first three letters of the respective genus (e.g., *Gil*, *Gila nigra*; *Pan*, *Pantosteus clarki*; and *Tia*, *Tiaroga cobitis*). Hydrologic drivers are defined in Table 6 and physical habitat and biological drivers are defined in the *Methods: Drivers of assemblage change*.

supported more than a few nonnative fishes and none in most years. Decline of loach minnow at Tularosa and longfin dace at San Francisco began within two years of drought onset and was associated with an increase in

pool habitat. While loach minnow declined at Tularosa, speckled dace increased. Fish assemblage dynamics at these two sites was likely within the range of natural variability of this system. However, the long-term

TABLE 8. Results for stepwise multiple regressions to predict densities of nonnative predators and competitors at the six long-term monitoring sites in the upper Gila River drainage, New Mexico.

Site	Years	<i>F</i>	<i>P</i>	<i>R</i> ²	Parameter	Estimate	<i>t</i>	<i>P</i>
Tularosa	19	ns						
San Francisco	17	41.4	<0.001	0.84	high prespawnQ – low spawnQ (PCA3)	0.612	4.31	0.001
					reversals – high postspawnQ (PCA5)	–0.374	–2.63	0.018
East Fork	18	16.8	<0.001	0.78	high prespawnQ – low spawnQ (PCA3)	0.806	6.25	<0.001
					maximum depth	0.491	3.88	0.002
					%Pool	0.395	3.11	0.008
Middle Fork	19	6.9	0.017	0.29	%Pool	0.538	6.93	0.017
West Fork	18	6.3	0.029	0.44	%Riffles	0.444	2.36	0.031
					%Fines	0.442	2.35	0.032
Gila	18	8.7	0.009	0.35	AnnualQ (PCA1)	–0.594	–2.95	0.009

Note: Years indicates the number of years that a site was monitored. Parameter estimates were standardized to facilitate comparisons.

resilience of these fish assemblages may be lessened because of continued presence, albeit low abundance, of nonnative fishes and impediments to movement by native fishes among associated reaches.

Despite being the most downstream, in a reach most affected by human activity, and being exposed to the greatest number of nonnative fishes, the native fish assemblage at Gila site did not change. All native fishes present in 1988 were found in 2006, no native fish declined or increased in abundance, and total native fish density was comparable across years. No nonnative species was regularly collected and none was ever represented by more than a few individuals. Drought had no evident influence on native fishes and did not result in an increase in nonnative fish abundance or diversity. Paucity of optimal habitat (mainly pools) for nonnative predators and comparative abundance of habitats (e.g., cobble riffles and shallow gravel runs) favored by native fishes, particularly small-bodied species, partially explains the persistence of the native fish assemblage. Other factors, such as thermal regime and turbidity, also might have mediated interactions between native and nonnative fishes.

Theoretical and empirical evidence suggests that native and nonnative species respond differently to a natural flow regime (Minckley and Meffe 1987, Moyle and Light 1996, Poff et al. 1997, Brouder 2001, Bunn and Arthington 2002, Propst and Gido 2004). Empirical evidence of a negative response of nonnative fishes to natural flows, however, is limited to a few examples (e.g., Meffe and Minckley 1987, Minckley and Meffe 1987), and these are rather specific to canyon-bound reaches where shelter from large volume floods is minimal. Although it is generally believed that establishment of nonnative species is facilitated by disturbance, particularly human-induced (e.g., Bunn and Arthington 2002), we found little evidence that disturbance influenced establishment and persistence of nonnative fishes in the upper Gila River drainage. In part, this may be because a disturbance threshold (*sensu* Groffman et al. 2006) was not crossed at any of our sites. Alternatively, streams of the upper Gila drainage may not experience

flow variation as extreme (particularly floods) as those of other streams in the region, such as Aravaipa Creek, where flow has a more demonstrative negative affect on nonnative fishes. Nonetheless, we did find that native and nonnative species generally responded differently to a natural flow regime. Whereas it was not evident that elevated discharge influenced the persistence of nonnative fishes, they seemed to be favored by low flows, perhaps in response to increased concentrations of native fish prey and simplification of habitats as water volume was diminished (e.g., Magoulick and Kobza 2003). In contrast, densities of natives tended to increase with elevated flows. It was not clear, however, if mixed native and nonnative fish assemblages can coexist over extended natural climate cycles of wet and dry periods. Under the right conditions (e.g., Middle Fork site), nonnative predators can, in the span of a few years, eliminate a native fish assemblage in an unmodified setting, particularly if this occurs when the native assemblage is naturally stressed, as during drought.

The differential responses of fishes to flow-induced disturbances were mediated in part by differences in life history strategies of native and nonnative fishes (e.g., Olden et al. 2006). For example, among native species at Middle Fork, the most marked declines were of small-bodied, short-lived (≤ 3 years) species, whereas long-lived (≥ 4 years), large-bodied native species persisted longer, but only as adults, and their numbers diminished with time. Because native Gila River drainage species typically spawn briefly during snowmelt or in association with storm-induced flows (John 1963, Minckley and Barber 1970, Minckley 1973, Bestgen and Propst 1989, Propst and Bestgen 1991), drought likely reduced recruitment success. Lowered recruitment at Middle Fork in concert with stable or increased abundances of nonnative predators resulted in the elimination of these species. The Gila site, in contrast, was not plagued by nonnative predators and short-lived native fishes did not have to simultaneously survive drought-induced recruitment reduction and nonnative predation. This downstream site might also have been more resistant to adverse effects of drought because of greater discharge

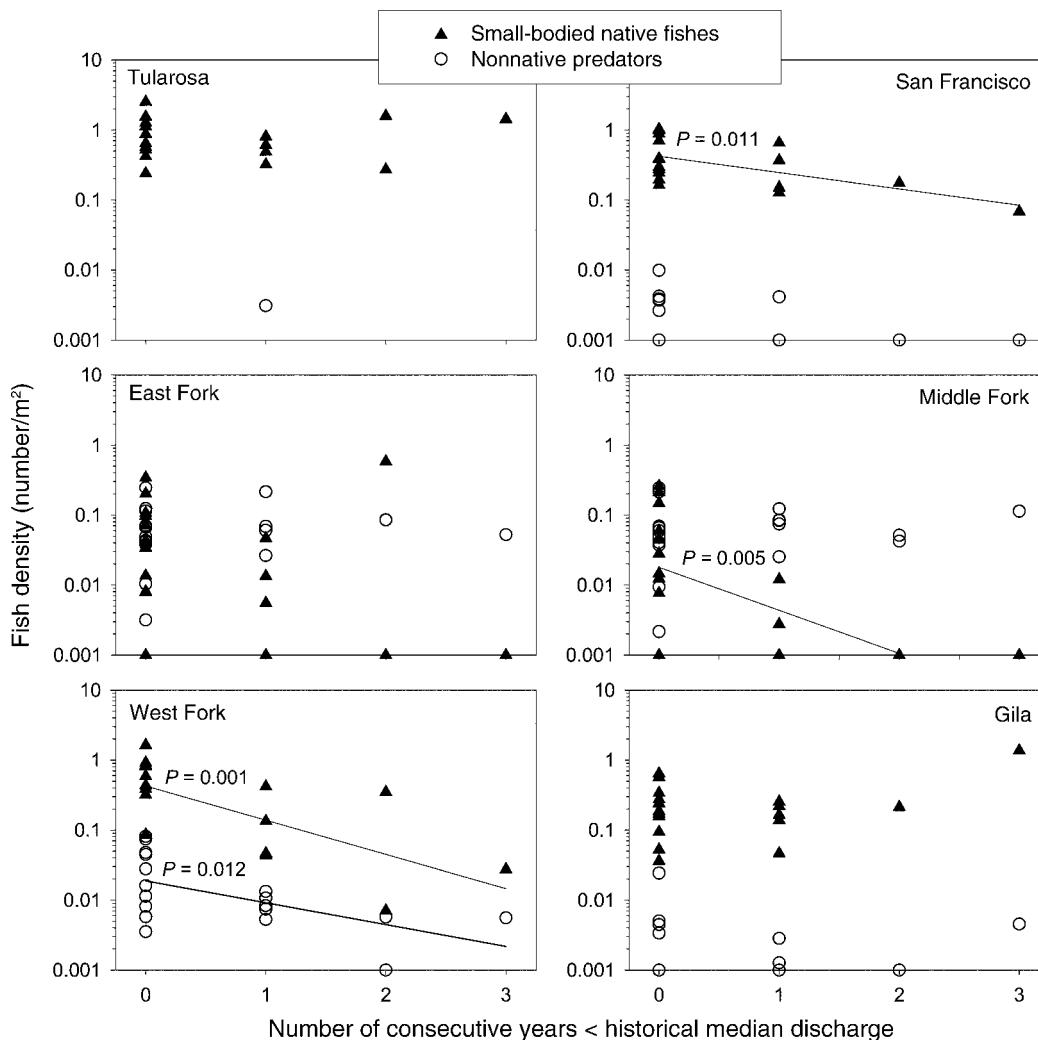


FIG. 6. Density of small-bodied native fishes and nonnative predators (log scale) at each upper Gila River drainage site, New Mexico, USA, contrasted with the number of consecutive years when median annual discharge was less than the period of record median discharge (1.737 m³/s). Regression lines (and P values) are provided only for significant correlations.

and thus a greater range of habitats (Magoulick and Kobza 2003), although few deep-water habitats were present. Consequently, the native fish assemblage of Gila persisted through several years of drought. Similar, life history-based explanations might be constructed to elucidate persistence of native fish assemblages at the San Francisco and Tularosa sites and collapse at the East Fork site.

The dramatic declines in native fish assemblages at the forks sites but persistence at others, and the discontinuous distribution of nonnatives in the upper Gila River drainage suggest the system is fragmented with limited movement of fishes among sites. Although a natural flow regime might help maintain connectivity within a river system (e.g., Bunn and Arthington 2002), naturally high flows may also enable movement of nonnatives among sites. The largely intact native fish assemblage of the San Francisco site was partially protected by an

irrigation diversion that prevented upstream movement of nonnative predators. While this barrier protected a vulnerable native fish assemblage, it is unclear what long-term effects this isolation will have on population viability and persistence. Nonnative infested reaches and water diversions isolated other native-dominated reaches and likely decrease the resilience of these populations if diminished or depopulated by drought (e.g., Gilliam and Fraser 2001, Fagan et al. 2005, Poff et al. 2007).

In the comparatively unmodified upper Gila River drainage, native fish assemblages persisted largely intact at sites lacking an established and abundant nonnative predator. Native fishes responded positively to elevated discharge associated with spring runoff and late-summer storms, but were less abundant during periods of drought. Nonetheless, in the absence of nonnative predators, native fish assemblages persisted through drought. While a natural flow regime was essential to

maintaining those physical attributes native fishes were adapted to, and general absence of human-induced disturbance have not been sufficient to preclude establishment of nonnative predators.

Conservation implications

Maintenance of connectivity within the remaining ranges of native fishes in the Gila River basin is arguably critical to ensuring their long-term persistence (Fagan et al. 2005, Rahel 2007). For example, loach minnow broadly persists over much of its historical range (Olden and Poff 2005), but at four of our six sites it was apparently extirpated in 10 years or less. Loss of connectivity among populations has reduced the likelihood that many will recover naturally, even if causes for elimination are removed. It is almost certain similar, but undocumented, losses have occurred throughout the species range, and its status is much more fragile than presumed. Other native Gila River drainage fishes have experienced similar declines. Whereas natural flows, particularly high flows, help maintain connectivity (Bunn and Arthington 2002), unpredictable and intermittent connections are likely insufficient for persistence of scattered populations. Irrigation diversion structures and nonnative predator-dominated reaches compromise connectivity, even where a natural flow regime is retained. However, connectivity, as Eby et al. (2003) suggested, also exposes native fish assemblages to invasion from nonnative infested habitats. Conserving native populations of fishes in the upper Gila River drainage will require mitigating human activities that block or impede movement of native fishes and reversing genetic and demographic consequences of isolation through population augmentation.

Although native fish assemblages may persist through drought, their resistance and resilience are compromised if nonnative predators are present. While retention of natural hydrologic regimes is crucial for persistence of native fish assemblages in arid-land streams, removal and preclusion of nonnative predators and competitors are equally important. The upper Gila River watershed is characterized currently by low and dispersed human activity, and this condition undoubtedly contributed to the persistence of native fish assemblages. If human population, and its attendant impacts such as water extraction, increases, this will likely increase the severity of drought conditions.

Additionally, if climate change imposes increasing aridity on the American Southwest, as projected (Seager et al. 2007), drought frequency and intensity will increase. Under these scenarios, our data suggest native fishes will be restricted to a diminishing number of locations with a consequent reduction in the probability of species survival. To some extent, these landscape level changes are irreversible, but the likelihood of species loss can be reduced by active management and protection of key native fishes strongholds to eliminate problem nonnatives and preclude their invasion or introduction,

particularly sport fishes, by resource management agencies. Such an approach, however, also requires engaged and informed management that diminishes or eliminates negative effects of isolation (e.g., loss of genetic diversity) and ensures maintenance of mixed age populations of sufficient numbers to persist through natural environmental variation.

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