

Spatially variable response of native fish assemblages to discharge, predators and habitat characteristics in an arid-land river

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SUMMARY

1. Fish assemblages and habitats were sampled annually at fixed sites in three tributaries of the Gila River catchment over a 21-year span that included prolonged low- and high-flow periods. Model selection was used to evaluate responses of seven native fishes with variable ecological traits (four small-bodied cyprinids, one large-bodied cyprinid, and two large-bodied catostomids) to mean annual discharge and predacious non-native fishes across the three sites. We also compared habitat use and overlap of native and non-native fishes to identify potential for negative interactions among species.

2. Assemblage structure (species abundance and richness) and recruitment of native species was strongly and primarily affected by mean annual discharge and secondarily by location and densities of non-native predators (mainly the centrarchid *Micropterus dolomieu*).

3. Densities of age-0 catostomids and small-bodied cyprinids were positively associated with discharge, and this pattern was strongest in the tributary with the lowest densities of non-native predators. Absence or extreme low abundance of natives during low-flow years was most pronounced at the sites where non-native predators were comparatively common. Densities of adults of large-bodied native species also varied by site, but often were positively associated with densities of non-native predators.

4. Spatially variable responses of native fish assemblages indicated that the persistence of native fishes could be jeopardized if key habitats were lost or flow regimes unnaturally altered, particularly during low-flow conditions when recruitment of native fishes is low and predation by non-natives is high. Large-bodied species may be less vulnerable to multiple years of poor conditions because adults are able to avoid predation by non-natives and thus can rely on occasional high discharge years for successful recruitment.

5. As in other arid-land streams, native fish assemblages of the Gila River Basin continue to decline. Our results indicate that conservation requires specific knowledge and consideration of physical influences as well as life-history attributes of native and non-native fishes.

Keywords: Gila River USA, hydrological regime, life-history traits, long-term research, species persistence

Introduction

Water resource exploitation, stream habitat modification and introductions of non-native organisms have been linked to marked changes in native stream fish

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assemblages worldwide during the past century (Miller, Williams & Williams, 1989; Contreras-Balderas *et al.*, 2002; Olden & Poff, 2005; Dudgeon *et al.*, 2006). Our understanding of the relative importance of individual stressors and how they relate to natural variability indicate potentially complex interactions among these three categories of disturbance, which can be additive, synergistic or indirect in their impact. Additionally, the variability of the environment must be measured for sufficiently long to determine whether the stressor is chronic or short-term (Matthews, 1998). Multiyear periods of above- and below-mean discharges are a normal part of arid-land river systems. For example, Molles & Dahm (1990) demonstrated that the four El Niño events that occurred between 1928 and 1986 coincided with the four highest spring discharge years in the Gila River. Since El Niño/La Niña-Southern Oscillation (ENSO) events vary in their frequency and intensity, understanding the biological response requires long-term monitoring over one or more wet and dry cycles (Ottersen *et al.*, 2001). Generally, little is known of the particular mechanisms by which climatic events directly or indirectly affect fish assemblages and the ways these events alter the relative effects individual species have on assemblages (Lake, 2003; Matthews & Marsh-Matthews, 2003).

Correlations between flow regimes, non-native fishes and the persistence of native fishes have been relatively well documented (e.g. Pusey *et al.*, 1989; Marchetti & Moyle, 2001; Hermoso *et al.*, in press). Many of these studies contrast the relative importance of modified environmental conditions (e.g. flow) and invasive species as drivers of change in native fish assemblages (e.g. Hermoso *et al.*, in press), and it has been postulated that natural flows facilitate the coexistence of native and non-native fishes (Bunn & Arthington, 2002). Indeed, Minckley & Meffe (1987) demonstrated that individual floods eliminated or significantly reduced non-native species in constrained reaches of the Gila River basin, whereas native species persisted. They concluded that non-native fishes were not evolutionarily adapted to sudden and violent floods and had not developed behavioural mechanisms to allow them to maintain their position in the channel during floods. Eby, Fagan & Minckley (2003) found that changes in composition of a native assemblage were not a result of short-term environmental extremes, but instead were because of

chronic changes in baseflow and the presence of a few non-native species. Previously, we determined that native and non-native fishes responded in opposite directions to a naturally varying flow regime (Propst, Gido & Stefferud, 2008); the interactions between non-native predators and different species and size classes of native fishes, however, were not specifically evaluated. Given strong size-dependent processes (Harvey, 1987; Dudley & Matter, 2000; Franssen, Gido & Propst, 2007), it is likely that populations of species that are large-bodied [adults greater than 150 mm total length (TL)] will respond differently to disturbance than populations of small-bodied fishes (adults less than 100 mm TL).

In 1989, we selected three sites on tributaries of the Gila River that broadly represented the range of environmental conditions available for warmwater fish assemblages in the region. The purpose was to document changes in conservation status of native fishes and to characterize the factors causing population fluctuations. Here, we use this 21-year dataset to evaluate associations among discharge, stream habitat and fish densities at the three sites. Each tributary experienced similar patterns of annual discharge, but varied in physical habitats and abundances of non-native predators. Our primary objectives were to evaluate the relative importance of annual variation in discharge and non-native predator abundance in regulating densities of different size classes and species of native fishes. We hypothesized that (i) longevity would mediate the response of native fishes to hydrological variation, (ii) body size and habitat use by native fishes would influence the impact of non-native predators and (iii) the relative influence of hydrology and non-natives on native fishes would vary across sites.

Methods

Study area

Fish and habitat sampling occurred at fixed sites located on three tributaries (East, Middle and West forks) to the Gila River that converge near Gila Hot Springs, New Mexico, USA (Fig. 1). We established fixed study sites (each ca. 225 m long) in the East Fork (elevation 1876 m) approximately 36 km above its confluence with the Gila River, the Middle Fork (1733 m) 0.7 km upstream of West Fork confluence, and West Fork (1737 m) about 10.5 km upstream of its

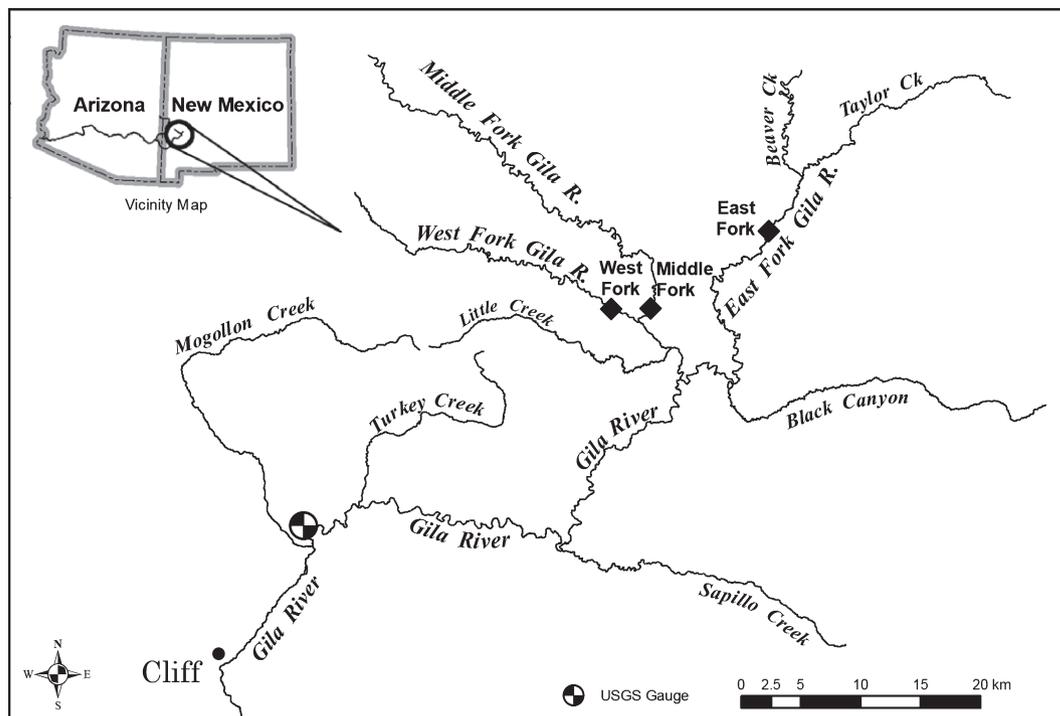


Fig. 1 Upper Gila River drainage in southwest New Mexico, USA. Locations of study sites are indicated by black diamonds and USGS stream gauging station (Gila near Gila, 94305000) denoted with surveyor's symbol.

confluence with East Fork. All sites had low-impact local land use comprising dispersed livestock grazing near the East Fork site and light angling and recreational use near the other two sites. No site was affected by impoundments or water diversions. Proportions of primary mesohabitats (pools, glides, runs and riffles) at the sites were generally similar, the most notable difference being number of large pools >1 m deep (West Fork had one or two, Middle Fork three and East Fork one).

Precipitation was generated mainly by cyclonic weather patterns during summer and slow-moving winter frontal systems. Floods can occur at any time of the year, but discharge usually peaked in March and declined to a minimum during June and July. Mean annual discharge data (based on the water year, 1 October to 30 September) were obtained from the nearest U.S. Geological Survey gauging station approximately 70 km downstream of the West and Middle forks sites and 100 km from the East Fork site (<http://waterdata.usgs.gov/nwis/sw; Site 94305000>). We included only mean annual discharge in our analysis because this was strongly related to other aspects of the flow regime [e.g. discharge variability, timing of flows, numbers of spates; calculated using

Indicators of Hydrologic Alteration, version 7 software (Richter *et al.*, 1996)]. Here, we define dry or wet periods as three or more consecutive years with annual mean daily discharge less or more, respectively, than mean daily discharge. Although variable discharge events may have occurred among the three tributaries, there was a strong association ($r^2 = 0.84$) between annual mean discharge at the Gila River gage and one on a nearby tributary (San Francisco River), suggesting consistent regional patterns.

Over the course of our study, mean daily discharge was $4.89 \text{ m}^3 \text{ s}^{-1}$, but annual mean daily discharge cycled from a wet period (1989–1998: $6.03 \text{ m}^3 \text{ s}^{-1}$) through a drought (1999–2004: $2.56 \text{ m}^3 \text{ s}^{-1}$) and back to near long-term mean (2005–2009: $5.36 \text{ m}^3 \text{ s}^{-1}$) (Fig. 2). Between 1989 and 1998, floods exceeding $28.32 \text{ m}^3 \text{ s}^{-1}$ occurred in 6 of 8 years, twice between 1999 and 2004, and 4 of 5 years between 2005 and 2009. The greatest mean daily discharge ($438.9 \text{ m}^3 \text{ s}^{-1}$) during the study occurred in February 2005.

Sampling and data

From 1989 through 2009, all sites were sampled annually during October–early November, a period

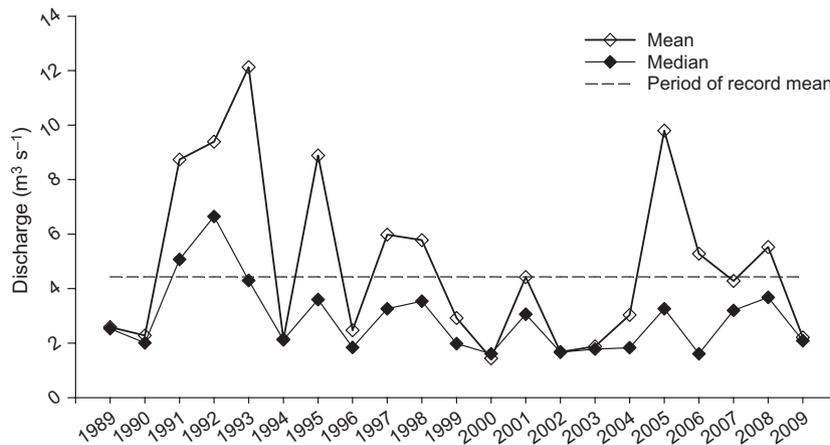


Fig. 2 Annual (1 October–30 September) Gila River mean and median daily discharge at USGS Gila near Gila gauge (09430500), New Mexico, USA. Horizontal dashed line = period of record (1 December 1927–30 September 2009) mean daily discharge.

that facilitated field identification of age-0 individuals and avoided stress that might occur during spring (spawning) or summer (elevated water temperature). A combination of backpack electrofishing and seining (3.0×1.2 m, 3.2-mm mesh) was performed to reduce biases associated with a single sampling gear (Rabeni *et al.*, 2009). Electrofishing was used to sample pools and runs and glides next to streambanks, seining was used to sample mid-channel runs and glides and shocking into a seine was used in riffles. We sampled all mesohabitats sequentially beginning at the lower end of the site, making a single pass through each mesohabitat. Mesohabitats were visually defined by their lateral position in the channel, surface water velocity, flow pattern (e.g. laminar, circular or turbulent), depth and cover. All fish captured in a mesohabitat were identified and enumerated, and those 75 mm or larger were measured for TL (± 1 mm). Native fishes were returned to the site of capture, except occasional specimens deposited at the Museum of Southwestern Biology, University of New Mexico. All non-native specimens were retained. Following fish collection, mesohabitat length (± 0.1 m) and several measurements of width (± 0.1 m), depth (± 0.01 m), and water velocity (cm s^{-1}) were recorded for each mesohabitat, which were grouped into four types based on water velocity (v) and depth (d): slow-deep pools ($v \leq 0.25 \text{ m s}^{-1}$, $d \geq 0.30$ m), slow-shallow glides ($v = 0.15\text{--}0.30 \text{ m s}^{-1}$, $d \leq 0.35$ m), moderate velocity and depth runs ($v = 0.25\text{--}0.50 \text{ m s}^{-1}$, $d = 0.25\text{--}0.50$ m), and rapid-shallow riffles ($v \geq 0.40 \text{ m s}^{-1}$, $d \leq 0.30$ m). Notes on surface substrate materials were taken. Water temperature ($^{\circ}\text{C}$) was determined between 11:00 and 15:00 hours at each site.

Life-history attributes of each native species and key non-native predators were compiled from published literature and data collected as part of our long-term monitoring (Table 1). Life-history data were used to evaluate hypotheses about how species with different ecological traits would respond to annual variation in discharge and non-native predators. We used fish density (number of fish m^{-2} sampled) as our abundance metric. For analyses, we classified fishes as small-bodied native species (<100 mm TL as adults), large-bodied native species (>150 mm TL as adults) and large-bodied non-native predators. Based on length-frequency and species reproductive ecology, we grouped large-bodied fishes into size classes that corresponded with age groups [i.e. young-of-year, juvenile (immature) and adult (mature)].

Analyses

Linear regression models were used to evaluate associations among densities of native species (including age groups of large-bodied native fishes), mean annual discharge, densities of juvenile and adult non-native predators and location. We did not consider all possible models, and only included site as an interaction with other terms. For juvenile and adult large-bodied taxa, we included time-lagged mean annual discharge of $1(Q_{t-1})$ or $2(Q_{t-2})$ years, respectively. Coefficients of determination (R^2) were used to evaluate the predictive capacity of the global model, and Akaike's information criterion (AIC) was used to select the best approximating model by comparing each of the candidate models simulta-

neously (Burnham & Anderson, 2002; Johnson & Omland, 2004). The AIC scores were adjusted for bias because of small sample size (AIC_c), and Akaike weights (w_i) were calculated for each candidate model. Thus, the model with the lowest AIC_c and the highest w_i was considered the best.

To evaluate potential habitat overlap between native and non-native fishes, habitat use was calculated as the proportion of individuals of a species or species age group collected in a mesohabitat at a site in a year. Because of the lack of independence of habitat use across years (i.e. habitat availability remained relatively stable), we did not statistically test for difference in proportional occurrence across habitats for each species. Rather, we assumed that used habitats [i.e. contained some attribute(s) that benefited that species] were those in which 20% or more (an arbitrary, and probably conservative value) of individuals of that species (or life stage) occurred. Habitats in which <20% of individuals of a species occurred were assumed to be suboptimal for that species.

Results

Response of native fishes to drivers

Assemblage changes. At the outset of the study in 1989, seven native fishes occurred at each site, except that *Rhinichthys osculus* was absent from East Fork. The majority of non-native fishes were *Ameiurus natalis*, *Salmo trutta* or *Micropterus dolomieu*, but their abundances and frequencies of occurrence varied across sites (Table 2). Densities of native fish were about four times greater during the pre-drought period (1989–1998) than during or after the drought at West Fork (Fig. 3), but non-native fishes were always uncommon, including the most frequently collected non-native, *S. trutta*. At Middle Fork, lowest native fish density occurred during the drought and coincided with greatest non-native predator density. At East Fork, native fish density was greatest during pre-drought years and least in the post-drought period, and non-native predator density was greatest during the drought but remained high thereafter. All sites lost native species, but only one native [*Oncorhynchus gilae* (Miller) at West Fork] and one non-native species (*Lepomis cyanellus* at East Fork) were added.

The overall strengths of regression models testing the response of native fish densities to discharge, non-natives and location were variable across species and size classes (Global model R^2 ranged from 0.00 – 0.72) (Table 3). Models with poor fit (Global model $R^2 < 0.15$) occurred for two small-bodied species, *Agosia chrysogaster* and *Tiaroga cobitis*, as well as for young and juvenile *Gila nigra* and juvenile *Catostomus insignis*, both large-bodied species. For models of small-bodied species that had moderate to good fit with the data (Global model $R^2 > 0.15$), the best approximating models for both *Meda fulgida* and *R. osculus* included mean annual discharge and site. These were primarily driven by higher densities and a more pronounced density \times discharge relationship for these species at West Fork (Fig. 4). For models of large-bodied species with reasonable fit to the data (Global model $R^2 > 0.15$), the importance of independent variables varied with age class. The strongest models (highest Global R^2) were for adults and all included sites in the best approximating models. These were generally because of higher densities of adults at East Fork and lowest densities at West Fork (Fig. 5). Mean annual discharge (or time lag of Q) and non-native predator densities were included in some models for large-bodied species, but not as consistently as site. For young-of-year catostomids, best approximating models included either discharge and site or discharge and non-native predator densities. There was a clear positive association between discharge and density of young catostomids, with some of the variability in this relationship explained either by characteristics of the site or by variable densities of non-native predators across sites.

Habitat. Proportion of mesohabitat types (pool, glide, run and riffle) at each site remained fairly constant from 1989 through 2009, and differences in proportion among sites were comparatively small. A pulse of fine sediment covered riffle substrates at West Fork during the late 1990s to mid-2000s. At Middle Fork, depositions of fine sediment beginning in the early 2000s covered riffle substrates and in 2007–2009 isolated and then filled two of the three pools there. Since 1989, mid-day water temperature averaged 14.8 °C at West Fork, 18.7 °C at East Fork and 19.0 °C at Middle Fork. During 2008–2009, thermographs recorded water temperatures consistently 2–3 °C higher at Middle

Table 2 Mean density (number fish m⁻² ± 1 SE) and frequency of occurrence of fishes at Gila River East, Middle and West forks sites, New Mexico, USA, 1989–2009

Species	East Fork		Middle Fork		West Fork	
	Mean density ± 1 SE	Freq. occur.	Mean density ± 1 SE	Freq. occur.	Mean density ± 1 SE	Freq. occur.
Native fishes						
<i>Agosia chrysogaster</i>	0.064 ± 0.029	12/20	0.018 ± 0.006	10/21	0.070 ± 0.017	19/21
<i>Gila nigra</i> young	0.004 ± 0.002	5/20	0.008 ± 0.006	6/21	0.002 ± 0.001	5/21
<i>G. nigra</i> juvenile	0.010 ± 0.005	8/20	0.004 ± 0.002	8/21	0.003 ± 0.002	10/21
<i>G. nigra</i> adult	0.027 ± 0.007	17/20	0.009 ± 0.002	17/21	0.005 ± 0.002	11/21
<i>Meda fulgida</i>	0.009 ± 0.005	5/20	0.003 ± 0.001	6/21	0.081 ± 0.017	19/21
<i>Rhinichthys osculus</i>	0.001 ± 0.001	2/20	0.011 ± 0.005	9/21	0.234 ± 0.054	21/21
<i>Tiaroga cobitis</i>	0.002 ± 0.001	5/20	0.010 ± 0.004	10/21	0.012 ± 0.004	10/21
<i>Catostomus insignis</i> young	0.073 ± 0.017	15/20	0.027 ± 0.009	16/21	0.159 ± 0.049	21/21
<i>C. insignis</i> juvenile	0.026 ± 0.007	14/20	0.008 ± 0.004	15/21	0.016 ± 0.003	17/21
<i>C. insignis</i> adult	0.103 ± 0.051	20/20	0.043 ± 0.009	20/21	0.032 ± 0.006	21/21
<i>Pantosteus clarkii</i> young	0.048 ± 0.012	15/20	0.020 ± 0.007	13/21	0.103 ± 0.025	20/21
<i>P. clarkii</i> juvenile	0.022 ± 0.007	11/20	0.001 ± 0.001	5/21	0.011 ± 0.002	16/21
<i>P. clarkii</i> adult	0.074 ± 0.016	20/20	0.003 ± 0.001	12/21	0.014 ± 0.003	16/21
Non-native fishes						
<i>Cyprinella lutrensis</i> (Girard)				1/21		
<i>Pimephales promelas</i> Rafinesque		3/20		2/21		
<i>Ameiurus natalis</i> (Rafinesque) young	0.007 ± 0.003	8/20	0.047 ± 0.010	21/21		3/21
<i>A. natalis</i> juvenile		2/20	0.006 ± 0.002	16/21		2/21
<i>A. natalis</i> adult		3/20	0.026 ± 0.007	20/21		1/21
<i>Ictalurus punctatus</i> (Rafinesque)		1/20				
<i>Ictalurus</i> sp.	0.007 ± 0.002	11/20				
<i>Oncorhynchus mykiss</i> young						2/21
<i>O. mykiss</i> juvenile					0.004 ± 0.002	7/21
<i>O. mykiss</i> adult					0.006 ± 0.002	11/21
<i>Salmo trutta</i> young						1/21
<i>S. trutta</i> juvenile				1/21	0.003 ± 0.001	12/21
<i>S. trutta</i> adult					0.006 ± 0.002	15/21
<i>Gambusia affinis</i> (Baird and Girard)	0.099 ± 0.030	16/20	0.020 ± 0.008	11/21		
<i>Lepomis cyanellus</i> Rafinesque		5/20		4/21		
<i>Micropterus dolomieu</i> young	0.003 ± 0.002	5/20	0.026 ± 0.005	21/21		6/21
<i>M. dolomieu</i> juvenile	0.006 ± 0.002	11/20				5/21
<i>M. dolomieu</i> adult	0.030 ± 0.008	16/20	0.017 ± 0.004	20/21		
<i>Micropterus salmoides</i> Lacepède		3/20				

Mean density (±1 SE) not calculated for infrequently collected non-native species. Frequencies for *I. punctatus*, *I. sp.*, *L. cyanellus* and *M. salmoides* include young, juvenile and adult individuals.

Fork than at West Fork (unpubl. data), and during late summer 5–7 °C higher (no data available for East Fork).

All age groups of *M. dolomieu* and *A. natalis* were most common in deep slow-velocity habitats (Table 4) and their presence generally declined in mesohabitats as water became shallower and more rapid. Proportional habitat use by small-bodied, opportunistic strategists varied by species. The majority of *T. cobitis* and *R. osculus* occupied riffle habitats. *Agosia chrysogaster* was evenly distributed across habitats, and *Meda*

fulgida was in all habitats except riffles. Thus, only *A. chrysogaster* and *Meda fulgida* substantially overlapped with non-native predators. In general, periodic strategists primarily occurred in slow and deep habitats, overlapping with non-native predators, but the degree of this association varied with age class. There was a consistent pattern of homogenous distribution across habitats in young and juveniles of *G. nigra* and *C. insignis*, with increasing specificity in adults. Young and juvenile *Pantosteus clarkii* often occupied rapid velocity habitats.

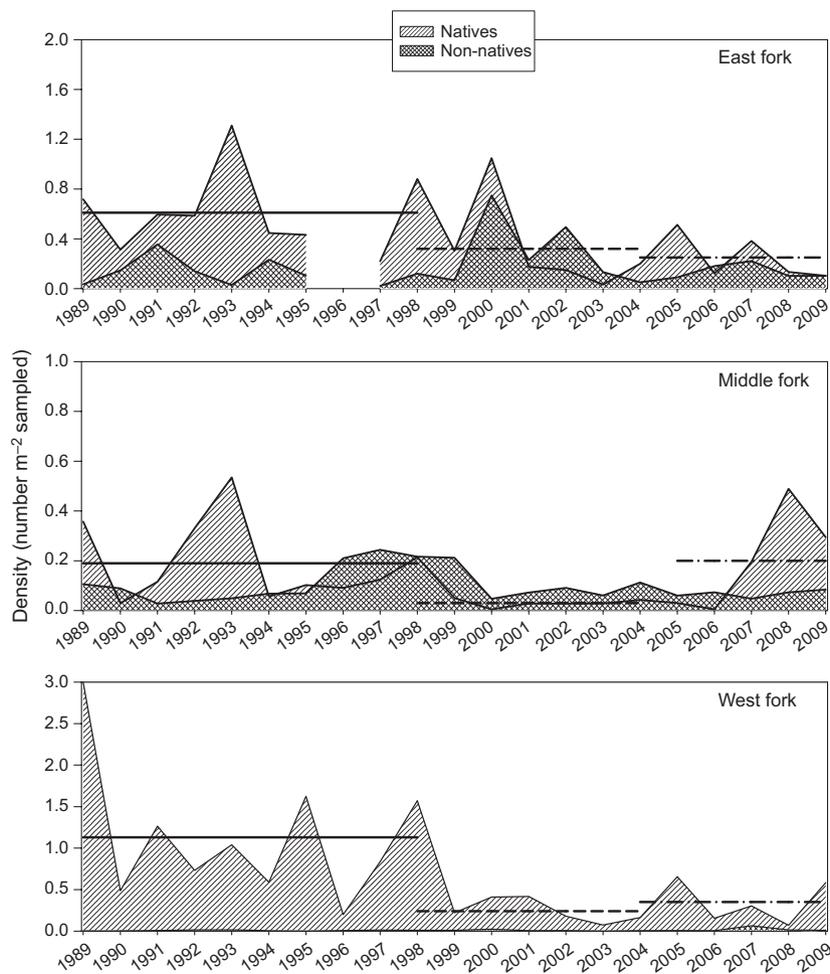


Fig. 3 Density (number m^{-2} area sampled) of native and nonnative fishes at Gila River East, Middle, and West forks sites, New Mexico USA. Solid horizontal = mean native fish density 1989–1998 (wet), dashed horizontal = native fish density 1999–2004 (dry); and dash-dot horizontal = native fish density 2005–2009 (average). Note different y-axis scales.

Discussion

Using a 21-year dataset, we were able to coarsely identify potentially complex effects of discharge, non-native predators and habitat use on success of native fishes in the Gila River. However, precisely parsing the relative influence of factors was considerably more complex and nuanced than we anticipated and characterising causes of observed changes was less straightforward than expected. Nonetheless, several patterns were evident.

Mean annual discharge was a primary driver affecting density of native fishes. Broadly, and consistent with other research (Propst & Gido, 2004; King, Tonkin & Mahoney, 2009; Tan *et al.*, 2010), native fish densities were highest at all sites in years with above average discharge. However, other aspects of flow regime such as timing (Bednarski, Miller & Scarnecchia, 2008) and stability of flows (Freeman *et al.*, 2001;

Peterson & Jennings, 2007) are also known to favour recruitment of stream fishes. Because these variables were highly correlated with mean annual discharge, we were unable to segregate the relative influence of each factor. Both site and non-native predators were included in many of the top candidate regression models. It was difficult, however, to tease apart quantitatively the relative importance of physical features of sites and non-native predators.

Among large-bodied species, habitat use varied by species and age group. Smaller individuals were found over a greater range of habitats than larger individuals (native and non-native), and a large majority of native and non-native adults occupied pool habitats. Our habitat-use data suggested that negative interactions between native and non-native fishes were more likely between small native and large non-native individuals. At East and Middle forks where large non-native predators were compar-

Table 3 Akaike's information criteria model scores (ΔAIC_c) and the relative likelihood of each model (w_j) to characterise response of native fishes density to annual mean discharge, tributary location (site) and density of non-native predators

		Species																									
		<i>Agosia chry-</i>		<i>Meda fulgida</i>		<i>Rhinichthys osculatus</i>		<i>Tiaroga cobitis</i>		<i>Gila nigra</i>		<i>G. nigra</i>		<i>Catostomus insignis</i>		<i>C. insignis</i>		<i>C. insignis</i>		<i>Pantosteus clarkii</i>		<i>P. clarkii</i>					
		<i>sogaster</i>	<i>fulgida</i>	<i>osculatus</i>	<i>cobitis</i>	<i>nigra</i>	<i>nigra</i>	<i>nigra</i>	<i>nigra</i>	<i>nigra</i>	<i>nigra</i>	<i>nigra</i>	<i>nigra</i>	<i>nigra</i>	<i>nigra</i>	<i>nigra</i>	<i>nigra</i>	<i>nigra</i>	<i>nigra</i>	<i>nigra</i>	<i>nigra</i>	<i>nigra</i>	<i>nigra</i>				
Model	k	Δ_j	w_j	Δ_j	w_j	Δ_j	w_j	Δ_j	w_j	Δ_j	w_j	Δ_j	w_j	Δ_j	w_j	Δ_j	w_j	Δ_j	w_j	Δ_j	w_j	Δ_j	w_j				
Null	2	12.96	0.00	30.36	0.00	75.02	0.00	8.50	0.01	2.21	0.18	8.68	0.01	32.60	0.00	11.87	0.00	0.99	0.14	37.08	0.00	19.29	0.00	18.77	0.00	56.72	0.00
Q	3	11.23	0.00	32.25	0.00	75.82	0.00	1.41	0.28	0.00	0.53	0.00	0.67	24.13	0.00	7.65	0.01	2.75	0.06	36.43	0.00	8.14	0.01	17.75	0.00	58.12	0.00
NN	3	0.28	0.45	12.85	0.00	56.55	0.00	7.53	0.01	2.74	0.14	7.74	0.01	27.73	0.00	3.05	0.09	0.00	0.22	24.46	0.00	11.46	0.00	6.55	0.03	56.57	0.00
Q × NN	5	0.00	0.52	16.95	0.00	59.06	0.00	3.19	0.12	2.87	0.13	2.20	0.22	20.32	0.00	0.24	0.37	4.17	0.03	25.24	0.00	0.00	0.58	7.82	0.02	60.57	0.00
Q × site	7	7.97	0.01	0.00	0.80	0.00	0.94	0.00	0.57	6.43	0.02	6.53	0.03	0.00	0.81	0.00	0.42	1.00	0.14	6.46	0.03	0.73	0.40	10.54	0.00	9.22	0.01
NN × site	7	6.44	0.02	2.81	0.20	5.85	0.05	9.65	0.00	9.12	0.01	14.95	0.00	12.21	0.00	2.71	0.11	1.98	0.08	0.00	0.71	12.06	0.00	0.00	0.82	9.20	0.01
Q × NN × site	13	18.68	0.00	10.42	0.00	8.73	0.01	15.06	0.00	19.03	0.00	14.57	0.00	2.89	0.19	11.30	0.00	12.70	0.00	1.99	0.26	10.75	0.00	6.55	0.03	24.82	0.00
Q _{k-1}	3									6.54	0.03							1.07	0.13					16.79	0.00		
Q _{k-1} × NN	5									6.45	0.03							1.63	0.10					5.15	0.06		
Q _{k-1} × site	7									15.44	0.00							1.66	0.10					9.52	0.01		
Q _{k-1} × NN × site	13									23.14	0.00							8.16	0.00					6.51	0.03		
Q _{k-2}	3													30.91	0.00					38.04	0.00					56.35	0.00
Q _{k-2} × NN	5													28.56	0.00					27.07	0.00					58.15	0.00
Q _{k-2} × site	7													11.57	0.00					11.29	0.00					0.00	0.98
Q _{k-2} × NN × site	13													19.28	0.00					12.10	0.00					12.41	0.00
Global model		0.148		0.424		0.722		0.140		0.000		0.030		0.374		0.236		0.136		0.454		0.325		0.365		0.621	
adjusted R ²																											
Significance	Q	0.055		<0.01		<0.01		0.064		0.480		0.33		<0.01		0.01		0.06		<0.01		<0.01		<0.01		<0.01	
Sum of variable weights	Q _{k-1}	0.53		0.8		0.95		0.97		0.68		0.93		1.00		0.80		0.06		0.22		0.29		1.00		0.05	
	Q _{k-2}	-		-		-		-		-		0.05		-		-		-		0.33		-		-		0.10	
	NN	0.99		0.2		0.06		0.13		0.27		0.26		0.19		0.57		-		0.44		0.97		0.59		0.99	
	Site	0.03		1.00		1.00		0.58		0.03		0.03		1.00		0.53		0.53		0.32		1.00		0.41		0.89	
Evidence ratio		1.16		4.00		18.8		2.04		3.03		3.05		4.26		1.14		1.14		1.64		2.71		1.45		13.7	

'Best' ($\Delta AIC_c \leq 2.00$ and $w_j \geq 0.10$) models shaded. Because of potential serial correlation (i.e. lack of independence of data within the time series), significance tests of models may be biased. Q, discharge; NN, non-native predators; k, number of estimable parameters in an approximating model.

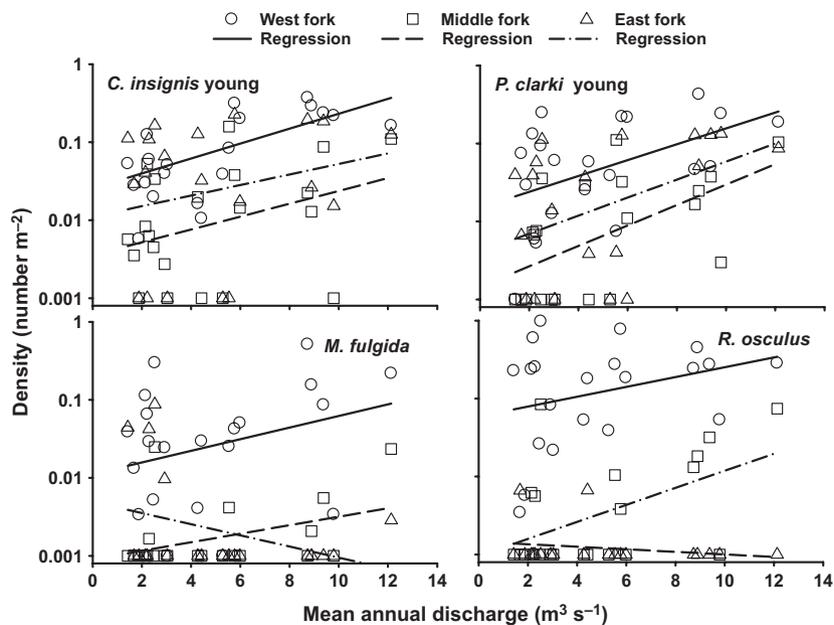


Fig. 4 Relationship between density (number m^{-2} area sampled) and mean annual discharge for species and size classes of native fishes that were identified to have a relationship with discharge in multiple regression models. Least-squares regression lines are fitted to data from each of the three tributaries to illustrate spatial variation in the relationships between density and discharge.

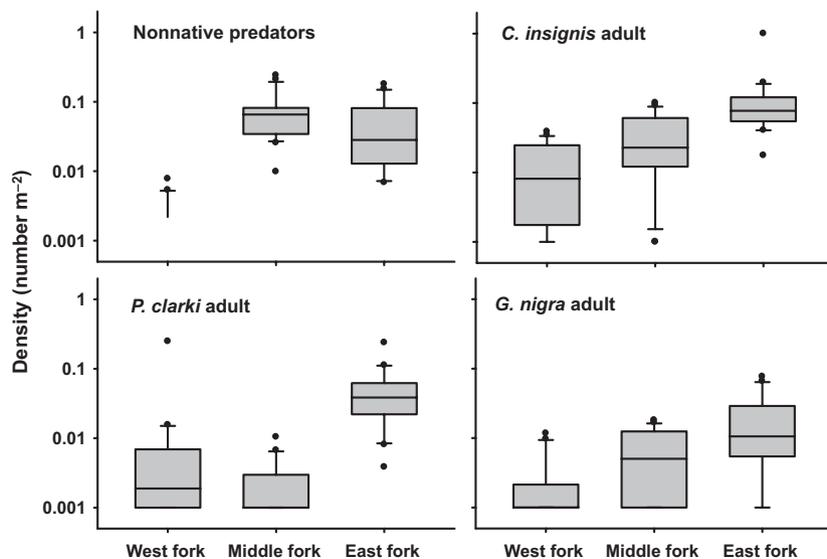


Fig. 5 Boxplots illustrating differences in density of nonnative predators and adults of large-bodied native fishes. Boxes represent 25th and 75th percentiles, whiskers represent 10th and 90th percentiles and median is line within each box.

atively common, small native fishes were uncommon or absent. But at West Fork, where large non-native predators were rare, most small-bodied, and young of all large-bodied native fishes persisted. There was a strong, albeit equivocal, indication that cohabitation of mesohabitats by native and non-native fishes resulted in the decline of small native fishes when densities of non-native predators increased. This interpretation is consistent with Schlosser (1987) who found that juvenile catostomid species occurring in habitats with

adult *M. dolomieu* were susceptible to predation, even in the presence of shallow water refuges.

Among non-native predators inhabiting our sites, it appeared that *M. dolomieu* had the strongest influence on native fishes. The native fish assemblage changed least at West Fork, where *M. dolomieu* rarely occurred and then in low numbers (three or fewer individuals per occurrence). The most marked decline of native fishes occurred at Middle Fork, where *M. dolomieu* was always present and sometimes comparatively

Table 4 Proportion of individuals (± 1 SE) found in mesohabitats at Gila River East, Middle and West forks sites, New Mexico (USA) 1989–2009

Species	Habitat			
	Pool	Glide	Run	Riffle
<i>Agosia chrysogaster</i>	0.30 \pm 0.05	0.22 \pm 0.05	0.26 \pm 0.05	0.22 \pm 0.04
<i>Meda fulgida</i>	0.20 \pm 0.06	0.24 \pm 0.07	0.40 \pm 0.07	0.16 \pm 0.06
<i>Rhinichthys osculus</i>	0.07 \pm 0.02	0.13 \pm 0.04	0.15 \pm 0.04	0.65 \pm 0.05
<i>Tiaroga cobitis</i>	<0.01	0.01 \pm 0.01	0.03 \pm 0.02	0.95 \pm 0.02
<i>Gila nigra</i> young	0.53 \pm 0.09	0.27 \pm 0.10	0.12 \pm 0.16	0.08 \pm 0.04
<i>G. nigra</i> juveniles	0.92 \pm 0.03	0.02 \pm 0.02	0.03 \pm 0.02	0.02 \pm 0.01
<i>G. nigra</i> adults	0.93 \pm 0.03	0.03 \pm 0.02	0.01 \pm 0.01	0.03 \pm 0.02
<i>Catostomus insignis</i> young	0.46 \pm 0.05	0.34 \pm 0.05	0.13 \pm 0.03	0.07 \pm 0.02
<i>C. insignis</i> juveniles	0.69 \pm 0.05	0.22 \pm 0.05	0.05 \pm 0.02	0.05 \pm 0.02
<i>C. insignis</i> adults	0.88 \pm 0.03	0.07 \pm 0.02	0.02 \pm 0.01	0.03 \pm 0.01
<i>Pantosteus clarkii</i> young	0.19 \pm 0.04	0.14 \pm 0.03	0.18 \pm 0.04	0.49 \pm 0.05
<i>P. clarkii</i> juveniles	0.32 \pm 0.06	0.06 \pm 0.01	0.07 \pm 0.03	0.55 \pm 0.07
<i>P. clarkii</i> adults	0.73 \pm 0.06	0.07 \pm 0.03	0.03 \pm 0.01	0.18 \pm 0.05
Age 1+ non-native predators	0.75 \pm 0.04	0.10 \pm 0.03	0.02 \pm 0.01	0.13 \pm 0.03
<i>Ameiurus natalis</i> (MF)	0.90	0.04	0.02	0.04
<i>Micropterus dolomieu</i> (MF & EF)	0.85	0.08	0.02	0.04
<i>Salmo trutta</i> (WF)	0.65	0.04	0.02	0.28

Shaded cells indicate occurrence of 0.20 or more of individuals in a particular mesohabitat. Non-native predator proportions only from sites where each species regularly occurred.

common. At East Fork, densities of native fishes declined during the second half of the study when density of *M. dolomieu* increased. The strong piscivory of *M. dolomieu* and its early ontogenetic onset (Johnson *et al.*, 2008; Archdeacon & Davenport, 2010) are indicative of the substantial impact it probably had on native species abundance, particularly individuals smaller than 100 mm TL at Middle Fork and East Fork.

The availability and use of mesohabitats also probably affected assemblage composition and species population structure. For example, non-native predators, which were seldom found in riffles, did not appear to influence densities of the riffle-dwelling *R. osculus*. However, riffles were adversely affected by diminished flows, and possibly deposition of fine sediment, and all small-bodied and young of large-bodied native fishes responded positively to increased flows, which presumably removed fine sediments from riffles. In contrast, strong candidate models for young *C. insignis* and juvenile *P. clarkii* included non-native predators, probably reflecting their use of pools that were also occupied by non-native predators. The persistent occurrence of *M. dolomieu* at Middle Fork may have been partly related to the presence of two or three large deep pools that provided habitat suitable

for non-native fishes. These pools provided refuge during a period of diminished flows that was limited at the other two sites. Following loss of two large pools after 2007, density of *M. dolomieu* decreased dramatically and density of native fishes, particularly small-bodied individuals, increased.

In addition to flow regime and presence of non-native species, differences in water quality and processing of fine sediment among the sites might have influenced the dynamics of native fish assemblages. Cooler water temperatures at West Fork were probably a primary factor limiting abundance of specific non-native predators, and native fish assemblage changes were thus driven predominantly by discharge and temperature. Higher water temperatures at Middle and East forks were probably more favourable for warmwater non-native predators, but were not high enough to limit native fishes (Carveth, Widmer & Bonar, 2006). It is also possible that elevated temperatures, particularly during drought, limited recruitment of native fishes. However, each native species present at these two sites, except *R. osculus*, was abundant and recruited successfully at sites downstream where temperatures averaged at least 1 °C higher than in these tributaries (Propst *et al.*, 2008). Therefore, we favour the hypothesis that

predation by non-natives, rather than warmer temperatures, was limiting recruitment of native fishes during low-flow years at Middle and East forks.

The large and deep pools at Middle Fork provided habitat suitable for non-native fishes and thus may have provided refuge during a period of diminished flows for non-natives that was not present, or at least in lower supply, at the other two sites. Pulses of sediment that covered the substrate and filled pools at the West and Middle forks during the drought probably impaired spawning substrates for *R. osculus* and *T. cobitis* and may have reduced food supplies for all fishes (Pilger, Gido & Propst, 2010). These factors, either singly or in combination, might have contributed to establishment and comparatively high densities of non-native fishes at Middle and East forks.

Our results highlight the linkage between natural flows and population dynamics of native species, and indicate how the presence of non-native species might exacerbate the effects of long-term drought conditions. For example, the elimination of *T. cobitis* from Middle Fork was coincident with comparatively high densities of non-native predators, especially *M. dolomieu*. In this instance, a conservation strategy for *T. cobitis* might have stressed elimination or control of a non-native predator. However, because *T. cobitis* occupies habitat not used by *M. dolomieu*, it is more likely drought and loss of riffle habitat was the ultimate reason for elimination of *T. cobitis* from Middle Fork. Here, an emphasis on non-native control would have directed resources to a likely problem but might not have yielded a long-term solution for *T. cobitis*.

Our study also demonstrated the necessity of obtaining data over extended periods of time. Had the study ended in 1998 we might have concluded that in an otherwise unmodified riverscape, native fishes could coexist with non-native predators that were present in low to moderate numbers. A different interpretation of the data might have resulted had the study occurred during the drought of 1999–2004. Data from these years strongly implicated non-native predators in decline of native fishes, particularly at a site having a moderately high proportion of habitat favoured by non-native predators. Only the full extent of our study indicated the regulatory roles of both flows and non-native predators in this system.

Conservation considerations

Native fish assemblages in arid lands have been and continue to be impacted by human-caused physical and biological alterations (Rinne *et al.*, 1996; Unmack & Fagan, 2004; Fagan, Kennedy & Unmack, 2005; Dudgeon *et al.*, 2006). If global warming alters precipitation patterns and droughts become increasingly severe in the American Southwest as climate models and paleoclimatic studies suggest (e.g. Seager *et al.*, 2007; Woodhouse *et al.*, 2010; respectively) and projected increases in human demands (Sabo *et al.*, 2010) are made upon water resources, aquatic habitats will diminish in extent and quality and become increasingly fragmented. Two strategies for conservation of arid-land fish assemblages have been applied broadly. One emphasises the importance of natural flow regime (e.g. Poff *et al.*, 1997; Bunn & Arthington, 2002), either its mimicry (e.g. Propst & Gido, 2004) or its restoration (e.g. King *et al.*, 2009). The second focuses on removal or control of non-native species (e.g. Tyus & Saunders, 2000; Minckley *et al.*, 2003; Clarkson *et al.*, 2005). Our results illustrate the interaction of these factors across three tributaries and over two decades. We conclude that conservation of arid-land native fish assemblages in most, perhaps all, instances will necessitate integration of natural flow and non-native control (e.g. Marks *et al.*, 2009), and will require attention to local conditions and resident species.

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