

# Multidecadal responses of native and introduced fishes to natural and altered flow regimes in the American Southwest

Keith B. Gido, David L. Propst, Julian D. Olden, and Kevin R. Bestgen

**Abstract:** Both theory and empirical evidence identify flow regime as a primary factor driving the structure of riverine fish communities and spatial patterns of species invasions. We used long-term fish community monitoring data to evaluate hypothesized responses to interannual variability in flow attributes across seven rivers in the American Southwest. We asked the following three questions: (1) Can annual variation in species abundances be explained by attributes that represent flow seasonality, variability, and consistency? (2) Can species responses be predicted based on their origin (native versus nonnative) or life-history strategy? and (3) Are species responses to variation in specific flow attributes consistent across river systems with modified and natural flow regimes? We found that species responses to flow attributes were best predicted by origin, suggesting responses to flows are associated with adaptations to regional hydrologic variability. Additionally, most species responded negatively to increased flow variability, particularly in systems with an altered flow regime. Our findings demonstrate site- and taxa-specific responses to flows that can guide conservation of fishes in lotic systems of the American Southwest and elsewhere.

**Résumé :** Des considérations tant théoriques qu'empiriques indiquent que le régime d'écoulement constitue un des principaux facteurs déterminants de la structure des communautés halieutiques fluviales et de la répartition spatiale des espèces envahissantes. Nous avons utilisé des données de surveillance de communautés de poissons recueillies sur de longues périodes pour évaluer différentes hypothèses concernant les réactions à la variabilité interannuelle d'attributs de l'écoulement pour sept rivières du Sud-Ouest américain. Nous avons posé les trois questions suivantes : (1) Les variations annuelles de l'abondance des espèces peuvent-elles être expliquées par des attributs représentant la saisonnalité, la variabilité et l'uniformité de l'écoulement? (2) Les réactions d'une espèce peuvent-elles être prédites à la lumière de l'origine (indigène ou non indigène) ou du cycle biologique de l'espèce concernée? (3) Les réactions des espèces à la variation d'attributs donnés de l'écoulement sont-elles les mêmes pour des systèmes fluviaux présentant des régimes d'écoulement modifié et naturel? Nous avons constaté que le meilleur prédicteur des réactions des espèces aux attributs de l'écoulement était leur origine, ce qui laisse croire que les réactions à l'écoulement sont associées à des adaptations à la variabilité hydrologique régionale. En outre, la plupart des espèces réagissaient négativement à une variabilité accrue de l'écoulement, en particulier dans les systèmes à régime d'écoulement modifié. Nos résultats démontrent que les réactions au régime d'écoulement diffèrent selon l'emplacement et le taxon. Cette constatation qui peut orienter l'approche de conservation des poissons dans les systèmes lotiques du Sud-Ouest américain et d'ailleurs. [Traduit par la Rédaction]

## Introduction

Knowledge of factors influencing spatiotemporal fluctuations in animal and plant populations remains a fundamental challenge in ecology. Both natural and human-induced factors, such as regional climate and local habitat modifications, can be strong drivers of interannual variation in species abundances, but the magnitude and direction of these relationships depends on the autecology of species (Lima et al. 2002; Craine et al. 2010). Both experiments and observations across systems and species play important roles in untangling the context-dependency of population dynamics in complex ecological systems. Increasingly, long-term observational studies are providing important contributions to understanding patterns and drivers of community structure in settings where climate change, species invasions, and habitat alteration are additional structuring forces (Kratz et al. 2003; Fukami and Wardle 2005). In this paper, we use long-term flow records and fish monitoring data across seven river systems to show that (i) flow attributes influence annual variation in fish recruitment, (ii) species origin can generally predict interspecific

responses to annual variation in flow attributes, and (iii) the degree of hydrologic alteration influences intersite responses of fishes to flow attributes.

Natural and human-induced changes to flow regimes are major factors influencing abundance and recruitment of lotic organisms because they alter spawning habitat availability and quality, modify food resources, and constrain dispersal (Poff et al. 1997; Bunn and Arthington 2002; Gido and Propst 2012). Natural regimes that include high peak flows are beneficial to fishes in some systems because they provide connectivity to floodplain habitats, cleanse spawning habitats of fine sediments, and stimulate ecosystem productivity (Junk et al. 1989; Poff et al. 1997; King et al. 2009). However, the effect of flooding on biota is dependent on timing, magnitude, and duration of flows that happen on both ecological and evolutionary time scales (Lytle and Poff 2004; Naiman et al. 2008; Fausch et al. 2001). For example, Leigh et al. (2010) distinguished the positive effects of “maintenance” flows from the negative effects of “catastrophic” flooding on stream organisms. Lebón-Cerviá (2009) reported that recruitment of brown trout

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(*Salmo trutta*) exhibited a unimodal response to discharge because there was an optimal amount of rearing habitat at intermediate flows. Finally, Craven et al. (2010) found that recruitment was positively related to short-term high flows during spawning, but this effect was less for species that broadcast their eggs. These studies illustrate the combined importance of flow conditions (extrinsic drivers) and intrinsic characteristics (traits) of species in dictating responses to different dimensions of the multifaceted flow regime (Mims and Olden 2012).

Morphological, physiological, and behavioral traits of stream organisms are strongly influenced by flow regimes (Lytle and Poff 2004); consequently, functional composition of stream communities are often influenced by flow attributes such as magnitude, predictability, and intermittency (Poff and Allan 1995; Bunn and Arthington 2002; Tedesco et al. 2008; Craven et al. 2010). Recently, Mims and Olden (2012) conducted a national (United States) scale analysis of relationships between specific flow attributes and relative prevalence of fish species representing the three life-history strategy endpoints outlined by Winemiller and Rose (1992). They found that opportunistic strategists (species with young age at maturity and rapid turnover) were more common in streams with high flow variability than in streams with predictable seasonal flows; periodic strategists, with large age at maturity and high fecundity, were positively related to high flow seasonality and negatively related to flow variability; and, equilibrium strategists, with high parental investment in offspring, were negatively related to flow variability and positively related to predictability. These patterns suggest that flow attributes influence species abundance and community structure across streams according to life-history theory and highlight the potential consequences of flow regime alteration on riverine biodiversity.

Human modification of stream flow is expected to have different consequences for native versus nonnative fishes when they possess ecological traits that most likely evolved under different flow regimes. In other words, the natural flow paradigm predicts that native species are more likely to benefit from free-flowing (unaffected by human activities) conditions, whereas human-modified flows likely favor nonnative species (e.g., Minckley and Meffe 1987; Bunn and Arthington 2002; Propst and Gido 2004; Olden et al. 2006). General empirical support for this assertion is from Kiernan et al. (2012), who found restoration of natural flows and associated temperature regimes in a California stream favored native species and suppressed nonnatives. Specifically, they attributed these changes to improved habitat, cooler water temperature, and displacement of nonnative species. Gido and Propst (2012) also found that small-bodied nonnative species with opportunistic life-history strategies benefitted from unnaturally stable low flows during summer in the San Juan River, New Mexico and Utah, presumably because low flows were associated with stable spawning substrates and increased water temperature. This finding was in contrast to a positive response of native fishes in years with elevated spring discharge. Because flows released from impoundments managed for flood control or irrigation are relatively stable (e.g., lower peak flows, higher base flows, dampened fluctuations), those regimes are predicted to favor equilibrium strategists, which in regions such as the Colorado River Basin are primarily nonnative species (Olden et al. 2006). Indeed, Mims and Olden (2013) found that equilibrium strategists were favored over opportunistic strategists in regulated rivers across North America. Studies cited above suggest species nativity in the ecosystem (i.e., origin) and life-history traits should be strong predictors of how species respond to specific deviations from a system's natural flow attributes.

We used abundance data obtained from long-term studies of native and introduced stream fishes to test hypothesized responses to flow attributes across multiple sites in the American Southwest. We asked the following three overarching questions: (1) Is annual variation in fish abundance explained by flow regime

attributes describing seasonality, variability, and consistency? (2) Are long-term abundance patterns of fishes predictable according to species origin or life-history strategy? and (3) Are species responses to annual variation in flow attributes consistent across systems regardless of modified or natural flow regimes? We adapted predictions from Mims and Olden (2012) who hypothesized that species abundance should vary as a function of their life-history strategies and river flow regime attributes. We hypothesized similar relationships (Table 1) but instead examined response to temporal variation (i.e., species abundance over time) rather than spatial flow variation (i.e., species abundance over space). In addition, we considered predictions on how introduced species, that may or may not have evolved in similar climatic and hydrologic regimes, might respond differently than native fishes. We predicted that (i) large magnitude and long duration spring flows should benefit recruitment of periodic strategists and native species adapted to naturally high discharge during spring; (ii) equilibrium strategists and nonnative species would be positively associated with increased consistency of flows (as measured by the deviation from base flow) because they are putatively superior competitors for food and spawning sites, as well as effective predators during stable conditions; and (iii) opportunistic strategists would exhibit the most pronounced recovery, and overall neutral response, following years with highly variable flows (i.e., storm-induced flow spikes or high spring discharge) because of their rapid turnover rate and ability to spawn between flow high pulses. However, opportunistic strategists are expected to decline under consistent flows because they are inferior competitors or more susceptible to predation. Using general patterns identified across multiple rivers, we provide resource managers an additional, and potentially generalizable, perspective for anticipating responses of stream fish communities to alterations of natural flow regimes. Likewise, patterns we found should inform management strategies aimed at mitigating the harmful effects of modified flow regimes through the implementation of environmental flows (Poff et al. 2010) and large-scale flow experiments (Konrad et al. 2011).

## Materials and methods

### Study area

The spatial extent of our study included six river systems in the Colorado River Basin and one in the Guzmán Basin (Fig. 1). These rivers were selected because of the availability of long-term fish community monitoring and daily stream discharge data, and because flow regimes spanned a range of hydrologic modifications. The study systems also had similar taxonomic and functional composition of fishes to facilitate direct comparisons (Mims et al. 2010). Mean daily discharge ranged from  $0.5 \text{ m}^3 \cdot \text{s}^{-1}$  in the Mimbres River, New Mexico, to  $163.7 \text{ m}^3 \cdot \text{s}^{-1}$  in the Green River, Utah (Table 2). Flow records were >50 years for all systems except the Mimbres River, which had 31 years of data, a period of length sufficient to accurately categorize the required dimensions of the flow regime (Kennard et al. 2010). All systems generally experienced increased discharge in spring, but the San Juan and Green rivers had more predictable spring snowmelt in contrast to more southern rivers. All rivers also experienced variable, storm-driven flows during the summer monsoon season (July–August). The Green and San Juan rivers have mainstem impoundments upstream of fish monitoring sites, and flows were seasonally diminished by diversion and groundwater pumping on the San Pedro River.

### Flow regime attributes

We selected a subset of five attributes that characterized the flow regime from a larger set to simplify our analysis and eliminate redundancy (Table 1). Attributes were based on daily discharge records from the US Geological Survey (USGS) streamflow

**Table 1.** Five flow regime attributes that were tested for associations with abundance of native and nonnative fishes at long-term monitoring sites on six rivers in the Colorado and one in the Guzmán basins.

Flow regime dimension	Flow attribute	Benefits	Costs	Life-history strategy			Origin	
				Opportunistic	Periodic	Equilibrium	Native	Nonnative
Seasonality	Mean spring daily discharge (Mar–June); High pulse duration	Inundate off-channel habitats during spawning and early juvenile rearing; Creation and conditioning of spawning habitats	Displacement of eggs and larval fishes; Reduced temperature	0	+	-	+P	-P
Consistency	Base flow index	Increase consistency of habitat	Increase biotic interactions	-	0	+	-P	+P
Variability	Summer coefficient of variation; High pulse count	Pulsed input of allocthonous material	Instability of spawning substrates; Increase sedimentation	0	0	-	0	-P

**Note:** Potential mechanisms (costs and benefits) that might elicit a positive (+), negative (-), or neutral (0) response of fish populations are the basis for predicted responses (slope of the relationship with each flow index). Superscript p indicates predictions that received at least partial support from our analysis.

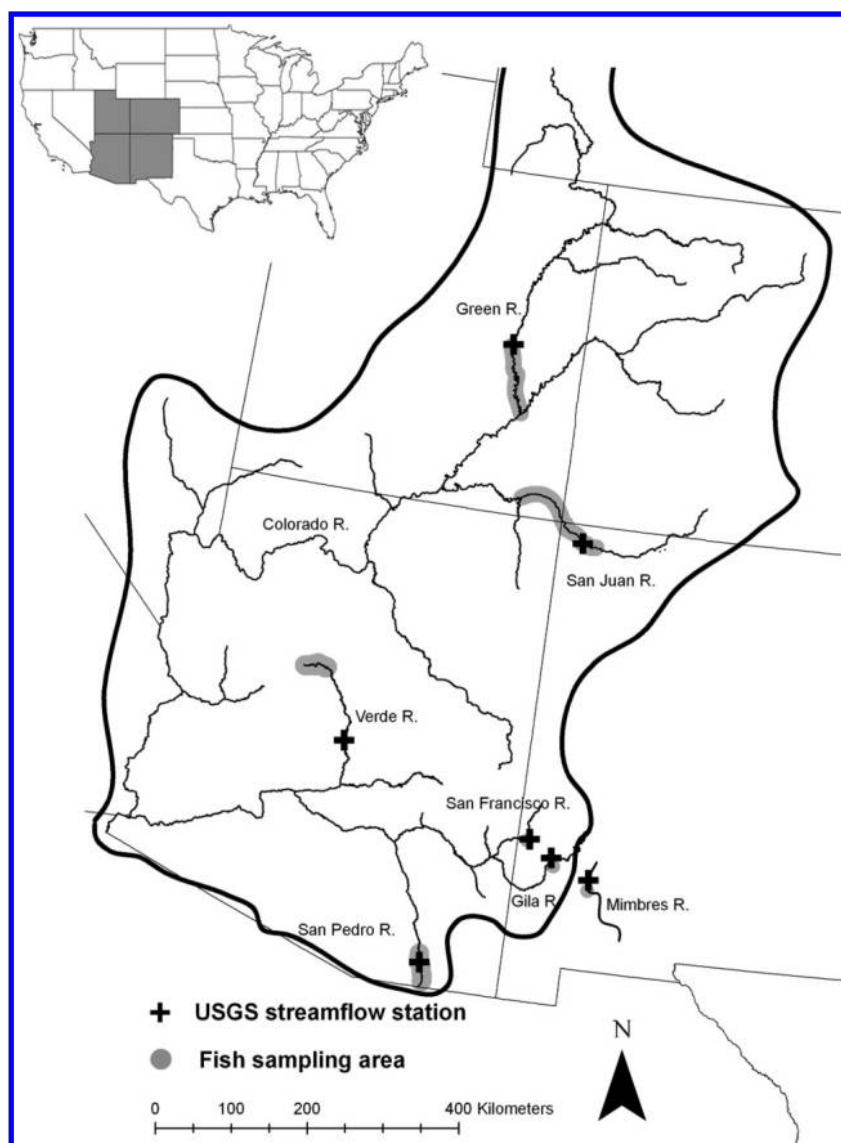
stations located in close proximity to fish sampling sites (Fig. 1). These attributes represented aspects of the flow regime that were predicted to influence fishes through basic demographic parameters of survival, fecundity, and onset and duration of spawning as evidenced by previous evaluations of flow – fish abundance relationships (Propst et al. 2008; Gido and Propst 2012). Chosen attributes characterized the flow regime of southwestern rivers driven by winter precipitation, spring snowmelt, and late-season monsoonal rainstorms by quantifying the magnitude of seasonally high spring flows, year-round consistency in discharge (deviation from baseflow), and variability in year-round and monsoonal flows.

Mean spring discharge considered annual variation in daily discharge measured at streamflow gauging stations from the beginning of March through June. This attribute indexed the magnitude of runoff associated with snowmelt and has been linked to the reproduction of several native fishes. Specifically, high spring discharge cleanses spawning substrates by mobilizing fine sediments and provides spawning cues for native fishes while reducing or delaying reproduction (likely via temperature suppression) of both native and nonnative fishes (Osmundson and Burnham 1999; Gido and Propst 2012). High pulse duration was calculated using the software Indices of Hydrologic Alteration (IHA; The Nature Conservancy 2006) based on the number of days during the year that discharge was greater than the 75th percentile of all flows during the period of record. Generally, longer high pulse duration relates to lower water temperature and increased access to off channel habitats, which in these systems was typically during spring runoff (Gido and Propst 2012). Base flow index also was calculated using IHA as the ratio of 7-day minimum flow (smallest values of mean discharge computed over any 7-consecutive days during the annual period) to the mean flow for the year. Larger values indicate more consistent flows (i.e., less deviation between low and high flows). Summer coefficient of variation (CV) was calculated from daily discharge for July through September, and it was selected because this period typically encompasses the monsoon season (July and August) when many age-0 native fishes are recruiting and some nonnative fishes spawn. High pulse count was calculated using IHA as the number of high flow pulse events (i.e., periods with discharge greater than the 75th percentile of all flows during the period of record) in the year. Consecutive days that are in the same type of pulse are counted as a single pulse event. Both summer flow variation and high pulse count were selected to index storm events that can result in heavy silt loads that cover coarse substrate as flows recede or, depending on timing (i.e., summer flow variation), can affect spawning success.

**Fish collections**

Long-term monitoring of fish communities within the seven study rivers ranged from 8 to 22 years. Sampling methods varied by river system, but in all cases site inclusion was based on species of interest, habitat characteristics, and monitoring objectives (see references in Table 2 for detailed methods). Samples were taken in autumn or spring in low-velocity, wadeable habitats, and thus abundance values largely reflected occurrence of juveniles of large-bodied fishes (>150 mm total length as adults) and all age classes of small-bodied fishes (<150 mm total length as adults; e.g., Gido and Propst 2012). In the San Juan River, seines were used to sample available habitats in an average of 27 secondary channels across a 138 river km reach each year. Two or more seine samples (3.2 mm mesh) were collected in late September from each of two backwaters (low or zero-velocity side channels of the main river) in 24 consecutive 8 km reaches of the lower Green River, Utah, or up to 96 samples per year depending on backwater habitat availability. A combination of seines and single-pass backpack electroshocking was used in the upper Gila, San Francisco, Verde, and Mimbres rivers. At these sites, fishes were sampled by

**Fig. 1.** Map of the study area, fish monitoring locations, and US Geological Survey streamflow gauges in the Colorado (boundary indicated) and Mimbres basins. Because some monitoring occurred across multiple sites, the entire reach sampled was shaded grey.



**Table 2.** Hydrologic record based on US Geological Survey daily discharge data from seven rivers with long-term fish monitoring programs.

River	Period of hydrologic record	Period of fish record	Mean daily discharge ( $\text{m}^3 \cdot \text{s}^{-1}$ )	Sampling season	Degree of hydrologic modification	No. of significant IHA	No. of significant EFC parameters	Sampling methods reference
Gila	1928–2010	1988–2010	4.4	Fall	Low	5	2	Propst et al. 2008
Green	1935–2010	1987–2009	163.7	Summer	High	18	10	K.R. Bestgen, personal communication
Mimbres	1979–2010	1990–2010	0.5	Fall	Low	1	0	Propst et al. 2008
San Francisco	1928–2010	1988–2010	2.5	Fall	Low	3	4	Propst et al. 2008
San Juan	1935–2010	1993–2010	57.0	Fall	High	18	4	Gido and Propst 2012
San Pedro	1913–2010	1989–2007	1.5	Spring	High	16	16	Stefferd and Stefferud 1998
Verde	1949–2000	1993–2000	16.2	Spring	Low	0	2	Rinne and Miller 2006

**Note:** Our classification of hydrologic alteration was based on long-term trends in 67 flow regime indices proposed by Mathews and Richter (2007). We report the number of significant trends for the 33 indicators of hydrologic alteration (IHA) and 34 environmental flow component (EFC).

mesohabitat within sites that ranged from 150 to 300 m in length. A single site was sampled on each the Gila and San Francisco rivers, two sites on the Mimbres River, and four sites were sampled on the Verde River. In the San Pedro River, fishes were sampled exclusively by electrofishing mesohabitats in an

approximately 250 m reach at each of four sites, and samples were obtained in April or early May when age-0 fishes were unlikely to be present or captured (Stefferd and Stefferud 1998). Thus, for the San Pedro River, we compared densities of fishes caught in spring to the previous year's flow regime attributes, assuming

over-winter mortality had a minimal influence on recruitment success.

Abundance estimates were the number of individuals collected per unit area sampled for all sites. We chose to characterize abundances using density because fishes at the majority of sites (San Juan, Gila, Mimbres, San Francisco, and Green rivers) were collected and quantified at the scale of mesohabitats (e.g., pool, riffle, backwaters). For the two sites where abundance was quantified at the scale of a study reach (San Pedro and Verde), we calculated densities based on a single reach area estimated at base flow. Estimates for San Pedro and Verde rivers likely underestimated true fish density because density estimates were based upon total area of sample site rather than just the area actually sampled, as was the case where sampling occurred by mesohabitats within each site. The consistency of methods within sites and relatively large numbers of individuals captured should accurately reveal relative changes in abundance over the time series. Moreover, because sampling occurred in periods of predictably low discharge and high water clarity (late spring in San Pedro or autumn at other sites), large numbers of individuals (>500) were often caught, indicating relatively high sampling efficiencies.

### Functional traits

We quantified fish abundance – flow relationships across river systems to assess differences in the magnitude and direction of these associations according to species origin and life-history strategy. Fish life-history strategies were evaluated according to the model of Winemiller and Rose (1992) that positions species along three primary life-history axes defining opportunistic, periodic, and equilibrium endpoints. The three axes of the model are (1)  $\ln(\text{fecundity})$ , defined as the number of eggs or offspring per female per spawning season; (2)  $\ln(\text{length at maturation})$ , defined as mean female length at maturation (mm); and (3)  $\ln(\text{egg size} + 1) + \ln(\text{parental care} + 1)$ , defined as the mean diameter of mature, fully yolked ovarian oocytes (mm) and an index of parental care following Winemiller (1989). Fish life-history traits were obtained from a comprehensive database for freshwater fishes of the United States synthesized from various literature, agency, and expert accounts (reported in Mims et al. 2010). Species were assigned to one of the three life-history strategies by calculating the Euclidean distance in trivariate life-history space between each species' position and the strategy endpoints and designating the species according to its proximity to the closest strategy (Olden and Kennard 2010). Strategy endpoints were defined as follows: opportunistic (minimum fecundity, minimum juvenile investment, and minimum maturation size), periodic (maximum fecundity, minimum juvenile investment, and maximum maturation size), and equilibrium (mean fecundity, maximum juvenile investment, and maximum maturation size), based on the entire fish fauna of the United States (Mims et al. 2010). This calculation was based on normalized trait values (i.e., standardized range between 0 and 1 for each trait) to ensure equal contributions of the three life-history parameters.

### Data analysis

To quantify flow attributes and evaluate the degree of hydrologic modification across the study sites, the IHA software was used to test for temporal trends in 67 flow regime attributes using linear regression (for detailed description of flow indices and regression analysis see The Nature Conservancy (2006) and Mathews and Richter (2007)). These indices included 33 indicators of hydrologic alteration and 34 environmental flow component variables. We classified the degree of hydrologic alteration based on the number of significant ( $P$  value < 0.05) trends in flow indices across the period of record for each streamflow station. We also evaluated annual variation in the five flow attributes identified as drivers of fish abundance within and across sites using principal components analysis (PCA) based on a correlation matrix of index

values measured over time. This ordination allowed us to simultaneously compare variability in flow attributes across sites and among years within sites.

Correlation analysis was used to quantify the association between species abundance at each site and each of the five flow attributes identified as drivers of fish abundance. We only included species that were present for >6 years during the time series; excluded species were usually in very low abundance when present. Because the number of years of data used in the analysis differed across sites and could bias cross-site comparisons, we used MetaWin ver. 2.0 (Rosenberg et al. 2000) to calculate an effect size based on Fisher's z-transformation of a product moment ( $r$ ) correlation of species density and each flow attribute as follows:

$$z = \frac{1}{2} \times \ln\left[\frac{1+r}{1-r}\right]$$

and the variance of  $z$  as

$$v_z = 1/(n - 3)$$

where  $n$  is the number of years sampled. Similar to correlation coefficients, positive effect sizes indicate a positive response to a flow attribute and negative values represent a negative response.

Two-way ANOVA was used to test if species responses (effect size) to each flow attribute differed by life-history class (i.e., opportunist, equilibrium, or periodic), site hydrologic modification (low or high; see below), or an interaction between the two. A separate ANOVA tested if responses differed by species origin (i.e., native or nonnative), hydrologic modification, or their interaction. Thus, a total of 10 ANOVAs (5 attributes  $\times$  2 functional classification schemes) were conducted. Because of the exploratory nature of our study and disparate nature of our data, we chose not to correct for multiple comparisons so that we could explore weaker ( $P > 0.10$ ), but potentially interesting, patterns of variation across treatment groups. To control for different taxonomic responses to flow, we only considered species or genera that occurred in both naturally flowing and hydrologically altered rivers (Table 3). Because some species (e.g., the genera *Catostomus* and *Gila*) were not present in both types of rivers, but are ecologically similar and have the same life-history classification, we pooled responses of congeners for this analysis. We believed this was justified based on previous studies that indicated species within these genera generally responded similarly to flow attributes (Propst et al. 2008; Gido and Propst 2012). All statistical analyses were conducted in R (R Development Core Team 2008).

### Results

Analysis of long-term trends in flow records indicated a high degree of hydrologic modification in three (Green, San Juan, and San Pedro rivers) of the seven river systems with long-term fish monitoring data. These systems showed significant temporal trends for 22–32 of the 67 flow attributes examined (Table 2) and were classified as having a high degree of hydrologic modification. All three experienced diminished maximum flows. While minimum flows in the San Juan and Green rivers increased, those in the San Pedro River declined: a consequence of different sources of hydrologic alteration. The other four rivers had significant trends in less than eight flow attributes and thus were classified as having a low degree of hydrologic modification.

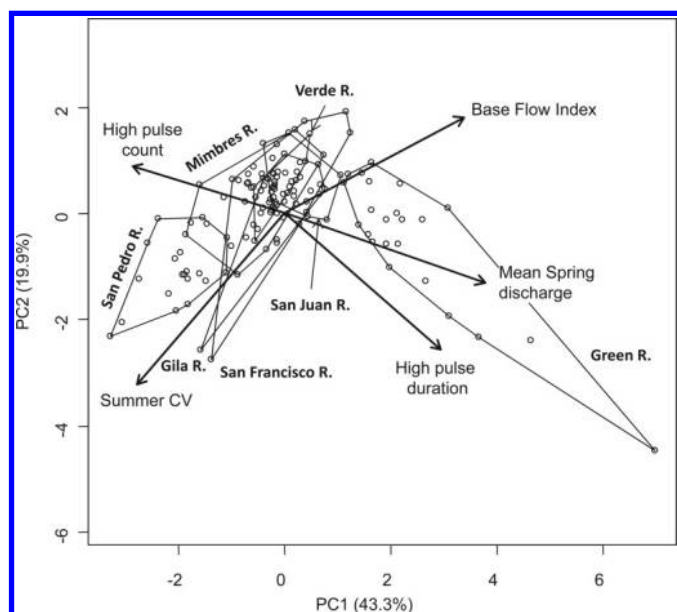
The first two axes of the PCA revealed patterns of annual variation among rivers in the five flow attributes (Fig. 2). The first axis explained 43% of the variation in flow attributes within and among sites and mostly represented a gradient of flow magnitude (i.e., mean spring discharge). The second axis explained 20% of the total variation in flow attributes and reflected gradients of flow

**Table 3.** Occurrence, life-history classification, and origin of fishes used to evaluate species responses to flow attributes.

Species	Common name	Life-history strategy	Origin	Altered			Natural			
				Green	San Juan	San Pedro	Gila	San Francisco	Verde	Mimbres
<i>Agosia chrysogaster</i>	Longfin dace	Opportunistic	Native			X	X	X	X	X
<i>Ameiurus melas</i>	Black bullhead	Equilibrium	Nonnative	X	X	X				
<i>Ameiurus natalis</i>	Yellow bullhead	Equilibrium	Nonnative		X		X		X	
<i>Catostomus clarkii</i>	Desert sucker	Equilibrium	Native			X	X	X	X	
<i>Catostomus discobolus</i>	Bluehead sucker	Equilibrium	Native	X	X					
<i>Catostomus insignis</i>	Sonora sucker	Equilibrium	Native				X	X	X	
<i>Catostomus latipinnis</i>	Flannelmouth sucker	Equilibrium	Native	X	X					
<i>Catostomus plebeius</i>	Rio Grande sucker	Equilibrium	Native							X
<i>Cyprinella lutrensis</i>	Red shiner	Opportunistic	Nonnative	X	X		X		X	
<i>Cyprinus carpio</i>	Common carp	Periodic	Nonnative	X	X				X	
<i>Fundulus sp.</i>	Plains killifish	Opportunistic	Nonnative		X					
<i>Gambusia affinis</i>	Western mosquitofish	Opportunistic	Nonnative	X	X	X	X	X		
<i>Gila nigrescens</i>	Chihuahua chub	Periodic	Native							X
<i>Gila robusta</i>	Roundtail chub	Periodic	Native	X					X	
<i>Ictalurus punctatus</i>	Channel catfish	Equilibrium	Nonnative	X	X					
<i>Lepomis cyanellus</i>	Green sunfish	Equilibrium	Nonnative	X	X	X			X	
<i>Meda fulgida</i>	Spikedace	Opportunistic	Native				X			
<i>Micropterus dolomieu</i>	Smallmouth bass	Equilibrium	Nonnative				X		X	
<i>Micropterus salmoides</i>	Largemouth bass	Equilibrium	Nonnative		X					
<i>Notropis stramineus</i>	Sand shiner	Opportunistic	Nonnative	X						
<i>Oncorhynchus mykiss</i>	Rainbow trout	Equilibrium	Nonnative							X
<i>Pimephales promelas</i>	Fathead minnow	Opportunistic	Nonnative	X	X	X		X		
<i>Ptychocheilus lucius</i>	Colorado pikeminnow	Periodic	Native	X	X					
<i>Rhinichthys osculus</i>	Speckled dace	Equilibrium	Native	X	X			X	X	
<i>Tiaroga cobitis</i>	Loach minnow	Opportunistic	Native				X	X		

Note: Species within the same genus were combined for across-system analysis.

**Fig. 2.** Comparison of annual flow regimes across the seven study systems according to a principal component analysis of the five core flow attributes. Polygons encompass data from multiple years within each site and arrows indicate variable loadings.



variability (summer CV), primarily within sites. There was high overlap in flow attributes among most rivers, except for the Green and San Pedro rivers. The Green River experienced the greatest annual variation in mean spring discharge, whereas the San Pedro, Gila, and San Francisco rivers experienced some years with highly variable summer flows.

Twenty-five species, including 13 of nonnative origin, were included in our analyses (Table 3). Eight species were classified as opportunistic, 12 as equilibrium, and 5 as periodic strategists. Many species responded strongly to annual variation in flow attributes, but responses only varied notably between species with different origin ( $P$  values  $< 0.09$ ) and sites with different levels of flow alteration ( $P$  values  $< 0.03$ ; Table 4). Life-history classification was a relatively weak predictor of species responses according to the five flow attributes ( $P$  values  $> 0.35$ ).

Our prediction that large magnitude and long duration spring flows would enhance recruitment of native species was partially supported in that their densities were generally higher in years with higher mean spring flows (Fig. 3A). Conversely, densities of nonnative species were generally lower in those years. However, this pattern was only marginally significant ( $P$  value = 0.09) and was more apparent in systems with natural than altered flow regimes. With the exception of *Gila* spp. in systems with altered flow regimes, mean responses of native fishes to mean spring flows were all positive, with the strongest responses from native speckled dace (*Rhinichthys osculus*) and sucker species (*Catostomus* spp). Contrary to our prediction, there was little statistical evidence that native fishes respond positively to extended duration high flows (not shown).

Support of our prediction that densities of nonnative species would be lower in years with more variable flows (i.e., high summer discharge CV and high pulse count) was evident in systems with altered flows (Figs. 3B and 3C). Although the interaction between species origin and hydrologic modification was not significant ( $P$  value = 0.124), several species exhibited opposing responses in altered systems as opposed to those with natural flows. Nonnative western mosquitofish (*Gambusia affinis*), red shiner (*Cyprinella lutrensis*), fathead minnow (*Pimephales promelas*), and common carp (*Cyprinus carpio*) generally declined with increasing variability in summer flows in altered systems, but their densities

were positively associated with variable summer flows in naturally flowing systems (Fig. 3B). Contrary to our prediction that densities of native species would not be associated with variability in flows, native species generally responded negatively to summer discharge CV (Fig. 3B). For the other index of variability (high pulse count), the mean response of native species switched from slightly positive or neutral in systems with natural flow regimes to negative in altered systems (Fig. 3C).

Finally, data from naturally flowing systems supported the prediction that nonnative species densities would be higher in years with a higher base flow index (i.e., more consistent flows) and native fishes densities would be lower (Fig. 3D). However, taxa exhibited a variable response to this index in flow-altered systems, as indicated by a significant interaction between hydrologic modification and species origin (Table 4).

## Discussion

Our study provided evidence that native and nonnative species respond differently to annual variation in flow regime attributes, and that these responses differ for fish in free-flowing versus regulated river systems in potentially complex ways. These findings illustrate that forecasting fish abundance – flow relationships in arid and semi-arid rivers will benefit from detailed information on the degree and mode of hydrologic alteration as well as community composition. Some of our predictions based on current theory or empirical data were supported, but others were not (Table 1). For example, native fishes generally responded positively to high mean spring discharge in both hydrologically altered and natural systems, which was consistent with our prediction. However, we also expected a negative response of nonnative fishes, but their responses were variable (Fig. 3A). In the American Southwest, many native fishes spawn on the descending limb of the hydrograph in late spring when water temperature is relatively cool (Gido and Propst 1999; Brouder 2001; Kiernan et al. 2012). This strategy may benefit recruitment during years with high spring flow by allowing larvae and juveniles access to off-channel habitats, increased abundance of clean spawning substrates and backwaters, or decreased risk of predation (Grams et al. 2010; Gido and Propst 2012). The success of nonnative fishes, however, is less likely tied to the occurrence of predictable spring floods because many of these species originate from Great Plains streams where elevated spring discharge is less certain (e.g., Dodds et al. 2004). Interestingly, the one nonnative species that responded positively to elevated spring discharge was smallmouth bass (*Micropterus dolomieu*), which spawns during spring (Dauwalter and Fisher 2007) and in cooler water than most other nonnative species considered in this study. Alternatively, densities might reflect a greater probability of migration into streams from nearby impoundments during high flows (e.g., Martinez et al. 2001).

Density of most taxa generally declined in years with more variable flows (high summer discharge CV or high pulse count) in systems with altered flow regimes, but responses were more varied in less altered systems. These results were in accord with our predictions that reduced stability and increased frequency of spates would have a negative effect on nonnative fishes. There are a variety of mechanistic pathways in which variable flows might limit recruitment of stream fishes (e.g., Bestgen et al. 2006), including the disruption of spawning and reduced food availability. This is particularly applicable for summer-spawning native and nonnative fishes that might be interrupted by monsoonal storm-induced flows that introduce large sediment loads derived from tributary watersheds (Gido and Propst 2012). Inorganic sediments can have substantial impacts on resource availability in streams by smothering and scouring of organisms (Waters 1995). Additionally, increased storm frequency and sediment deposition might diminish survival of native species

**Table 4.** *P* values from analysis of variance (ANOVA) testing for differences in mean response of fishes from different classifications to five flow attributes, from sites with altered and natural flow regimes, and the interactions among these factors.

	Flow alteration	Origin	Origin × flow alteration	LH strategy	LH × flow alteration
Mean spring	0.4125	<b>0.092</b>	0.692	0.898	0.998
Summer coefficient of variation	<b>0.033</b>	0.257	0.124	0.385	0.539
High pulse count	<b>0.029</b>	0.874	0.778	0.864	0.447
Base flow index	0.451	0.212	<b>0.012</b>	0.775	0.354
High pulse duration	0.985	0.670	0.816	0.419	0.893

**Note:** Species were classified by origin (native or nonnative) and life-history strategy (LH) as opportunistic, periodic, and equilibrium strategists. Bold values indicate  $P < 0.10$ .

juveniles that hatched prior to the monsoons by reducing prey or habitat availability, (e.g., Bestgen et al. 2006).

Declines in density of both native and nonnative fishes, in response to more variable flows, was more common in hydrologically altered than in naturally flowing systems. Overall, flows were less variable in the regulated Green and San Juan rivers and most variable in the San Pedro River, which suffers from massive groundwater extraction (Fig. 2). One explanation for the consistency in fish responses in hydrologically altered systems may involve the effect of flow alteration on channel morphology, in that both dams and groundwater pumping can cause channel narrowing and incising, thereby reducing connectivity to floodplains (Petts 1984; Ward and Stanford 1989; Bowen et al. 2003). Thus, it is possible that the negative effects of monsoonal driven flow spikes in flow-altered systems are poorly buffered because of diminished access to off-channel habitats. Of particular concern in altered systems, especially from a conservation perspective, is the negative response of native fishes to increased flow variability. It is likely that timing of flow spikes coupled with altered channel morphology in modified systems results in a generally negative impact on recruitment of native fishes, despite their presumed adaptations to naturally variable flow regimes.

Increased densities of nonnative species in years with more consistent flows (i.e., high base flow index) in naturally flowing systems matched our predictions. Moreover, years with high base flow index were generally years with low mean annual discharge (i.e., reduced spring flows). This result was in accordance with previous research in the Gila River that reported increases in nonnative fishes in low flow years (Propst et al. 2008; Stefferud et al. 2011). Similarly, Eby et al. (2003) suggested that decreased flow variability in Aravaipa Creek, a tributary of the San Pedro, resulted in an increase in nonnative fishes. Thus, drought and long-term reductions in stream flow variability likely play critical roles in the persistence of nonnative fishes in systems with naturally variable flow regimes. Of the three systems with flow alteration, the two below impoundments (Green and San Juan rivers) had the highest base flow index and the San Pedro River, without a flow-regulating dam, had the lowest (Fig. 2). The variability in the type of flow alteration (e.g., impoundment versus water withdrawal) across our hydrologically altered systems might explain the differing response of fishes to annual variation in flow consistency.

Flow regimes that vary across broad regions or along a gradient of hydrologic modification act as filters of species occurrence and abundance that can be predicted based on the Winemiller and Rose (1992) trilateral model of life history (Mims and Olden 2012, 2013). However, our analysis did not reveal a consistent response of fishes with similar life histories to interannual variation in different flow attributes. The discrepancy in results might be attributed to the greater variation in key aspects of flow regimes (variability, predictability, and seasonality) across regions than within river systems across years. Even within the limited regional extent of our study, there was as much variation in flow attributes among river systems as within systems (Fig. 1). Thus, species with different life-history strategies, once established,

might not respond consistently to more subtle differences in flows across years. It is also possible that differences in other ecological traits might override interannual variation in abundance attributed to trilateral life-history traits (fecundity, size and maturity, and parental investment). For example, because flow magnitude is tightly linked to temperature (e.g., Gido and Propst 2012), a species' thermal preference might predict response to flow attributes such as mean spring or summer discharge. Because species origin was somewhat predictive of response to interannual flow variation (also supported at larger spatial scales by Mims and Olden 2013), more detailed evaluation of traits linking responses of native and nonnative fishes to specific flow and temperature attributes will help refine predictions of species responses to variable flow regimes and ultimately inform strategies for environmental flows and thermal management below dams (Olden and Naiman 2010; Konrad et al. 2011).

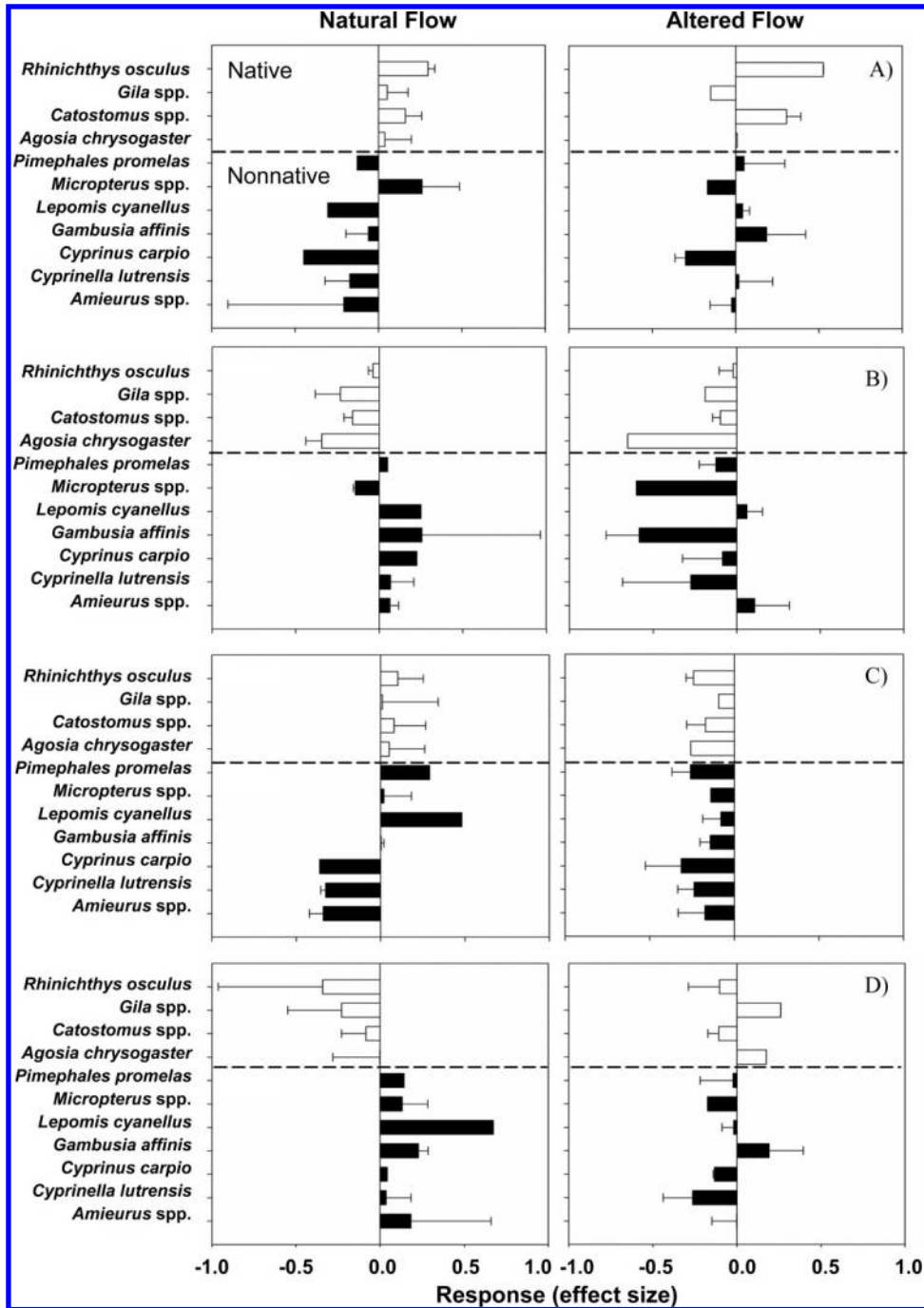
Management implications of our study are considerable, in that we demonstrated the potential for identifying critical aspects of the flow regime that are beneficial to native fishes and might disadvantage nonnative fishes. For example, increasing flow variability in regulated systems via dam releases might be a feasible approach to reduce abundance of nonnative fishes by disrupting spawning success (e.g., Korman et al. 2011). However, the general negative response of native taxa to increased flow variability observed in this analysis suggests careful consideration of the species of concern and the timing of such flow manipulations is essential for this approach to yield desired results. Our findings also might help direct decisions in streams with minimally altered flow regimes. For example, increased nonnative recruitment in stable years (i.e., high base flow index) might warrant mitigation efforts, such as mechanical removal, during those years to limit their negative impacts on native fishes.

We also showed that maintenance of high spring discharge (i.e., snowmelt driven) in naturally flowing and altered systems is beneficial to native fishes. This finding provided empirical support of predictions of the natural flow paradigm (Poff et al. 1997) and further justified prescriptions for more natural flows in western streams in general (Stanford et al. 1996; Kiernan et al. 2012). The influence of flow variability on native fish abundance was less clear in systems with modified flow regimes. Previous work on the San Juan River has shown that prolonged duration of low flows during summer caused an increase in abundance of small-bodied nonnative fishes (Propst and Gido 2004; Gido and Propst 2012). However, across these seven systems, increased variability in flows (summer CV or high pulse count) was generally associated with declines in abundance of both native and nonnative fishes in altered systems. As such, some combination of high spring flows and pulsed flows timed to disrupt spawning of nonnative fishes in summer might benefit native and suppress nonnative fishes.

This regional study demonstrated the challenges in defining the environmental flows that are necessary to provide requisite conditions for enhancement of native fishes in altered systems, while highlighting the importance of maintaining natural flows in less altered systems. Within the constraints of flow manipulation that



**Fig. 3.** Bar graphs representing mean and standard error of response (measured as an effect size) of species or genera to (A) mean spring discharge, (B) summer coefficient of variation (CV) in discharge, (C) high pulse count, and (D) baseflow index across seven river systems in the Colorado and Guzmán basins. Taxa are sorted by origin (native taxa white bars, nonnative taxa black bars). Plots in the left column are for systems with more natural flow regime, and systems in the right-hand column have an altered flow regime.



might occur within hydrologically altered systems, managers need to consider the origin of species and the specific flow attributes that can be manipulated. Reconciling the diversity of species responses to different facets of the flow regime, only a fraction of which can be manipulated via modified dam operation, is a conservation challenge that will continue into the future (Konrad et al. 2011). Ultimately, conservation of native fishes in altered and unaltered systems will require multiple and simultaneously implemented strategies that cohesively incorporate species autecology, physical characteristics of the system being managed, and capabilities of entities responsible for management.

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