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SRP16564

Transactions of the American Fisheries Society
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/utaf20

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Available online: 14 May 2012

To cite this article: Keith B. Gido & David L. Propst (2012): Long-Term Dynamics of Native and Nonnative Fishes in the San Juan River, New Mexico and Utah, under a Partially Managed Flow Regime, Transactions of the American Fisheries Society, 141:3, 645-659

To link to this article: http://dx.doi.org/10.1080/00028487.2012.683471

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SRP16565

*Transactions of the American Fisheries Society* 141:645–659, 2012
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ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1080/00028487.2012.683471

ARTICLE

# Long-Term Dynamics of Native and Nonnative Fishes in the San Juan River, New Mexico and Utah, under a Partially Managed Flow Regime

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***Abstract***

**Nonnative fishes and flow alteration are primary threats to native fish persistence in lotic systems. We used several flow regime attributes and fish sampling data obtained from the San Juan River, New Mexico and Utah, during 1993–2010 to evaluate the potential use of flow manipulations to increase recruitment of native fishes that must cope with nonnative species. During this period, discharge in the river was partially manipulated by reservoir releases that augmented naturally high spring flows in this snowmelt-driven system. An information theoretic approach was used to rank candidate models that predicted species densities based upon selected combinations of flow attributes and abundances of nonnative species. Autumn density of age-0 fishes in secondary channels was the main response variable. The main predictor variables included flow attributes associated with interannual variation in daily discharge and water temperature; densities of nonnative competitors; and catch rates of a numerically dominant nonnative predator (the channel catfish *Ictalurus punctatus*). Top-ranked models for native species included positive associations with small-bodied nonnative fishes and negative associations with the abundance of channel catfish adults. Densities of native speckled dace *Rhinichthys osculus* and flannelmouth suckers *Catostomus latipinnis* increased with mean spring discharge, but the density of native bluehead suckers *C. discobolus* did not. With the exception of juvenile channel catfish, the top candidate models predicting densities of nonnative fishes all included the duration of low summer flows. These results confirmed findings from a previous study that demonstrated different responses of native and nonnative fishes to seasonal flows; the present study also revealed that densities of all fishes were generally lower in years with greater abundance of adult channel catfish. Regression analysis indicated that seasonal flow manipulations and suppression of nonnative predator populations could be effective management tools to restore and maintain the native fish community.**

Manipulating flows in regulated rivers is at least conceptually an important conservation tool (Poff et al. 1997), but implementation of effective flow management requires a data-driven understanding of how stream organisms respond to manageable attributes of flow regimes. The most comprehensive framework for prescribing environmental flows is to mimic a natural flow regime or attributes of that flow regime that restore natural stream ecosystem processes (Poff et al. 1997, 2010; Bunn and Arthington 2002). Specifically, the timing, frequency, duration, magnitude, and rate of change are thought to influence stream organisms because of evolutionary, behavioral, and morphological adaptations structured by these flow attributes (Lytle and Poff 2004). Although there are excellent examples of how fishes respond to flow manipulations (Murchie et al. 2008), understanding how entire communities respond to specific attributes of flow regimes (either natural or manipulated) over

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Received March 2, 2011; accepted November 20, 2011

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extended time scales is limited by the paucity of long-term data sets that account for climatic cycles, complex population dynamics, and confounding effects of nonnative species (Piffady et al. 2010).

Quantifying the influence of flows on the reproductive success of fishes is essential to properly managing fish populations in regulated rivers (Humphries et al. 1999; Marchetti and Moyle 2001; Balcombe et al. 2006; King et al. 2009). Indeed, recruitment often benefits from restoration of natural flow events, such as flow spikes (King et al. 2009) and floodplain inundation (Rolls and Wilson 2010). Moreover, recruitment of many species is positively associated with increased discharge in systems driven by spring snowmelt (Brouder 2001; Propst and Gido 2004; Propst et al. 2008; Piffady et al. 2010) and rainfall (Craven et al. 2010). Thus, maintenance of flow quantity (e.g., magnitude, duration, and frequency), particularly during the spawning season, is a strategy that is probably beneficial to native fishes. The relative importance of other aspects of flow regimes (e.g., timing and rate of change, minimum flow, and low-flow duration) for recruitment of fishes is less known. Given the constraints on managing flows (e.g., maximum allowable releases from reservoirs), identifying additional attributes of flow regimes that can be manipulated to elicit desired biological responses is of central importance to conservation of native fish communities.

Nonnative species can disrupt relationships between native species and flows and obscure the ecosystem response to flow management (Tyus and Saunders 2000; Bunn and Arthington 2002). It is possible that managing for natural flows eliminates or controls populations of nonnative organisms (Poff et al. 1997; Marchetti and Moyle 2001; Bunn and Arthington 2002; Propst and Gido 2004). However, if nonnative fishes have adaptations that allow a positive response to natural flows, other methods of control may be a necessary complement to flow manipulations that enhance native species. Thus, the ability to simultaneously control invasive species while benefiting native fishes is dependent on ecological traits of the species targeted for management. In river systems in the western USA, ecological traits of native and nonnative fishes and their response to variable flow regimes can often be quite different (Olden et al. 2006). In general, predictable spring discharge events in snowmelt-driven systems either prompt spawning or covary with factors (e.g., photoperiod and temperature) that are potential spawning cues for native fishes (Tyus and Karp 1990). In contrast, spawning of most nonnative species occurs during summer base flows and their spawning is typically intermittent through the spawning season (Gido and Propst 1999; Herrington and DeVries 2008).

Identifying a mechanistic relationship between flow attributes and species responses is a critical step in the process of extrapolating observational data to rigorous management decisions. Based on previous research in the San Juan River (New Mexico and Utah; Gido et al. 1997; Propst and Gido 2004) and a review of literature on fish responses to flows in snowmelt-driven systems, we developed a conceptual framework that describes the potential pathways by which aspects of a flow regime can influence stages of recruitment for common native and nonnative fishes (Figure 1). In general, flows can influence fish directly through energetic costs or indirectly by modifying habitat, resource availability, or interactions with other species. In snowmelt-driven systems, such as the San Juan River, there is a predictable increase in discharge during spring (March–June), followed by summer (July–September) low flows (often disrupted by late-summer monsoonal rains) and then winter minimum flows. Stable and cold temperatures presumably limit biotic interactions in winter (November–February); thus, we did not consider biotic interactions during these months as important drivers of recruitment. The timing, magnitude, and duration of spring runoff influence recruitment by altering spawning chronology, body condition, and physiology, as well as influencing habitat quantity and quality (Bestgen et al. 2006). Because flows are inextricably linked to temperature (e.g., mean spring water temperature decreases linearly with mean annual spring discharge in the San Juan River; $r = 0.90$, $\mathrm{df} = 17$, $P < 0.001$), these combined factors probably influence the onset of spawning. Whereas high flows (flow magnitude) might displace small fishes (Harvey 1991), invertebrates, and algae, most fish species and size-classes are resistant to these events (Franssen et al. 2006). Concurrently, elevated flows mobilize substrates and connect off-channel habitats (Stanford et al. 1996), thereby increasing the availability of basal resources and potential rearing habitats. Biotic interactions are likely to be minimal during spring high flows because of increased dispersion of fishes. Native fishes in the San Juan River generally reproduce during elevated spring flows; thus, hatching success and larval survival may also depend on timing, magnitude, and duration of spring flows. Assuming adequate hatching success, recruitment is most likely limited by conditions during summer that influence survivorship and growth. Biotic interactions (i.e., between native and nonnative fishes) are likely to peak during summer low-flow periods because fishes are concentrated in diminished habitats. Unfortunately, little evidence is available on predator–prey relationships or resource limitations in these contracted environments. For most nonnative species in the San Juan River, reproduction occurs during the summer low-flow period. Monsoonal rainstorms may interrupt spawning by depressing water temperatures, and recruitment may be diminished by displacement from nursery or optimal habitats. Flow spikes associated with localized storms also transport fine sediments from the adjacent watershed into the main-stem San Juan River via ephemeral tributary streams (Heins et al. 2004). These sediments cover spawning substrates and fill nursery habitats, such as backwaters (Bliesner and Lamarra 2000).

Our overarching objective was to evaluate this general framework of how native fish recruitment varies with flows and interactions with nonnative species by using long-term correlative data from the San Juan River, New Mexico and Utah. Data collected over an 18-year period were used to make these

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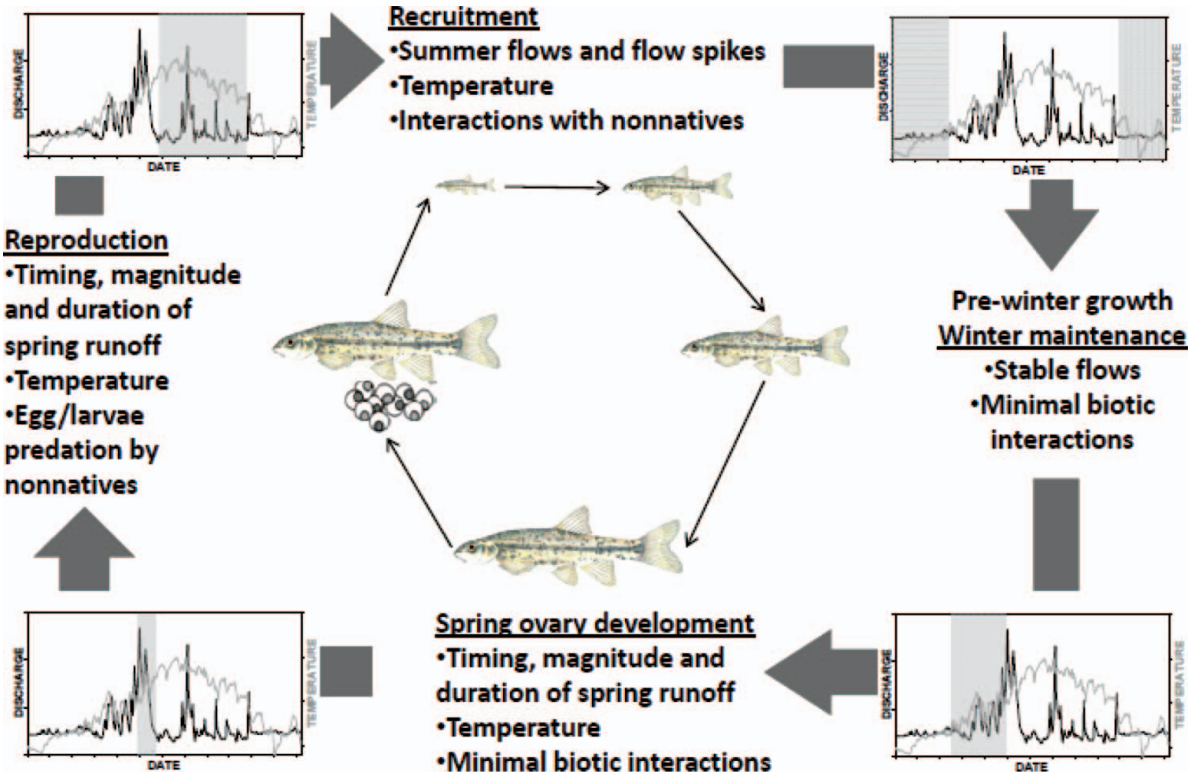


FIGURE 1. Conceptual model of flow and thermal regime attributes (and environmental correlates of those attributes) that might influence survival of fishes through different life stages in the San Juan River, New Mexico and Utah. Hydrograph and temperature data are from 2010 and represent a flow year with both elevated spring discharge and monsoon-induced discharge during summer. Shading indicates the time period addressed in the flow diagram. [Figure available online in color.]

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evaluations and provide general recommendations on the efficacy of flow manipulations and control of nonnative populations to benefit native fishes. Previously, we characterized the response of native and nonnative fishes to several attributes of a managed flow regime (Propst and Gido 2004). Revisiting these relationships with nine more years of data plus the consideration of nonnative predators as a driving factor enabled a more robust evaluation of the relative strengths of long-term data sets and to evaluate the efficacy of our initial interpretations of the relationships among flow attributes and species responses. We expected that doubling the time frame of the study would (1) help to identify more complex interactions, such as time-lagged effects or responses to climate cycles; (2) provide greater resolution to relationships discerned from 9 years of data; and (3) potentially discount or dismiss interactions perceived from a study of briefer duration. Moreover, the additional years of study (2002–2010) included an extensive drought, and the collapse of several numerically dominant nonnative species was observed. Specific objectives in the current study were to (1) characterize the relationships among annual flow attributes, abundance of nonnative fishes, and recruitment of native fishes; and (2) determine whether conclusions from our previous study (1993–2001) characterizing flow–recruitment relationships were preserved with twice as many years of monitoring data.

## STUDY AREA

A description of the study area was provided in our previous paper (Propst and Gido 2004), but an overview of relevant details is provided herein. Navajo Dam, about 120 river kilometers (rkm) upstream from our study reaches, regulates the majority of the discharge of the San Juan River, but flows from the Animas River, an unimpounded tributary that joins the San Juan River in Farmington, New Mexico (Figure 2), contributes about 40% of its total discharge. Releases from Navajo Reservoir (constructed in the early 1960s and operated primarily as a water storage and irrigation delivery reservoir) have been manipulated since 1993, when possible, to simulate a natural flow regime by synchronizing spring reservoir releases with peak snowmelt runoff in the Animas River. Mean daily spring discharge (March–June) of the San Juan River at a gauging station upstream of the Animas River confluence (Archuleta, U.S. Geological Survey [USGS] station 09355500) was higher before impoundment (1955–1962; mean $\pm$ SD = 61 $\pm$ 47 $m^3/s$) than after impoundment, both before (1963–1992; 39 $\pm$ 18 $m^3/s$) and during (1993–2010; 39 $\pm$ 31 $m^3/s$) our study. Mean maximum annual discharge was greatest before impoundment (177 $m^3/s$), lowest after impoundment but prior to our study (73 $m^3/s$), and intermediate during our study (112 $m^3/s$). Mean daily spring flow in our study reaches below the confluence of the Animas

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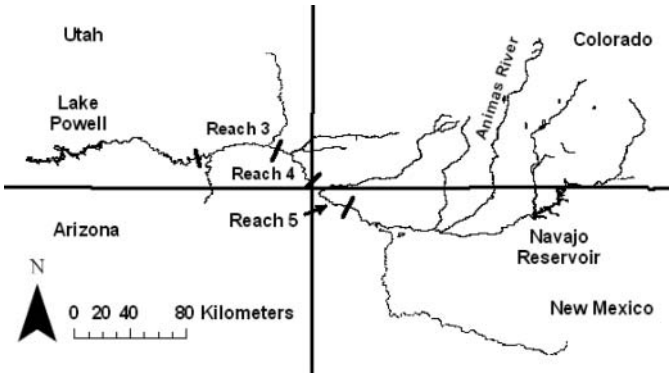


FIGURE 2. San Juan River map, with major perennial and ephemeral tributaries. Three reaches where secondary fish communities were sampled are indicated on the map.

River (Shiprock, USGS station 09368000) before impoundment also was higher (113 ± 91 $m^3/s$) than postdam flow before (73 ± 39 $m^3/s$) and during (75 ± 54 $m^3/s$) our study. Maximum flows at this location also were greater before impoundment (360 $m^3/s$) than after impoundment (before our study: 198 $m^3/s$; during our study: 219 $m^3/s$). Overall, water releases from Navajo Dam during our study resulted in higher discharge peaks and greater discharge variability than water releases between 1963 and 1992, prior to efforts to mimic a natural flow.

Because physical differences along the San Juan River might influence the response of fishes to flows, we used previously established geomorphic reaches of the San Juan River between Navajo Dam and Lake Powell (Bliesner and Lamarra 2000) to partition our study reach. Our study area encompassed three of the eight established reaches (Figure 2) that were sampled consistently between 1993 and 2010: reach 3 (rkm 110 to rkm 173), reach 4 (rkm 173 to rkm 211), and reach 5 (rkm 211 to rkm 248; rkm 0 is at Piute Farms, Utah, about 80 km upstream from the historical confluence of the San Juan and Colorado rivers). Channel braiding was extensive in reaches 3–5, with flow often divided between the primary and secondary channels. Fish community data were unavailable from other reaches because secondary channels were rare or absent. Cobble and gravel were predominant substrata in most reach 5 secondary channels. Reach 4 was geomorphically transitional between reaches 5 and 3; sand was common, but cobble and gravel were present in most reach 4 secondary channels. Sand and silt were the most common substrata in reach 3, but some cobble and gravel were present. Fish collections from secondary channels were the focus of this study because they have been consistently sampled for the longest period of time and provide abundant low-velocity habitats for age-0 native and nonnative fishes (Gido and Propst 1999). Secondary channels were defined as those with 25% or less of discharge (visually estimated) at the time of sampling and measuring 200 m or longer.

## METHODS

*Flow attributes*.—Discharge data were from the USGS gauge located in reach 5 at Shiprock, New Mexico (station 09368000). Nine flow attributes (Table 1) for two periods were selected for analyses: spring (native fish spawning period) and summer (nonnative fish spawning and rearing period; native fish rearing period). Although we considered a suite of other flow attributes used by Mathews and Richter (2007) to generally characterize flow regimes, ours were selected to index events we deemed likely to influence critical life stages of resident fishes (Figure 1). To minimize multicollinearity among these attributes, we evaluated all pairwise correlations of variables and selected a subset that explained a large proportion of variation ($r > 0.70$ or $r < -0.70$) of other variables.

*Fish collections*.—Fish were collected each year between 1993 and 2010 during daylight from an average of 27 (range = 13–45) secondary channels per year between mid-September and mid-October, a period when flows are relatively stable. Each habitat (e.g., pool, shoal, run, and riffle) present in a secondary channel was sampled with a drag seine (4.6 × 1.8 m, 3.2-mm mesh) in rough proportion to its availability, except that uncommon habitats (e.g., pools and riffles) tended to be sampled more completely than common habitats (e.g., runs and shoals). Although discharge during sampling was somewhat variable

TABLE 1. Annual variation in flow ($Q$) attributes of the San Juan River (data from U.S. Geological Survey gauging station 09368000 near Shiprock, New Mexico). Variables were selected based on their potential association with the recruitment of fishes. Flow attributes include measures of mean, variance, maximum, minimum, timing at which high flows occur (day of year $Q > 56$ $m^3/s$), and duration of high ($Q > 56$ $m^3/s$) and low ($Q < 14$ $m^3/s$) flows.

| | Year | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Flow attribute | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 |
| Mean spring $Q$ ($m^3/s$) | 147 | 80 | 128 | 38 | 109 | 74 | 69 | 44 | 73 | 17 | 26 | 44 | 115 | 42 | 74 | 134 | 57 | 37 |
| SD of spring $Q$ ($m^3/s$) | 61 | 75 | 83 | 28 | 94 | 58 | 63 | 30 | 63 | 4 | 23 | 26 | 92 | 46 | 62 | 65 | 49 | 23 |
| Maximum spring $Q$ ($m^3/s$) | 278 | 259 | 331 | 101 | 351 | 215 | 224 | 144 | 229 | 229 | 260 | 135 | 374 | 192 | 257 | 314 | 172 | 134 |
| Day of year $Q > 56$ $m^3/s$ | 55 | 124 | 69 | 133 | 77 | 115 | 135 | 125 | 118 | 254 | 142 | 94 | 98 | 136 | 121 | 43 | 121 | 147 |
| Duration (d) $Q > 56$ $m^3/s$ | 148 | 72 | 150 | 40 | 135 | 74 | 139 | 36 | 63 | 3 | 18 | 47 | 93 | 36 | 69 | 146 | 45 | 29 |
| Mean summer $Q$ ($m^3/s$) | 36 | 33 | 66 | 16 | 69 | 31 | 124 | 15 | 22 | 17 | 24 | 19 | 29 | 29 | 35 | 29 | 17 | 27 |
| SD of summer $Q$ ($m^3/s$) | 25 | 27 | 52 | 11 | 38 | 21 | 47 | 6 | 15 | 30 | 38 | 17 | 17 | 15 | 23 | 15 | 6 | 15 |
| Minimum summer $Q$ ($m^3/s$) | 13 | 8 | 22 | 4 | 14 | 9 | 21 | 7 | 9 | 7 | 6 | 8 | 9 | 13 | 15 | 9 | 9 | 14 |
| Duration (d) $Q < 14$ $m^3/s$ | 5 | 23 | 0 | 47 | 0 | 14 | 0 | 45 | 19 | 74 | 41 | 48 | 16 | 0 | 0 | 10 | 26 | 1 |

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among years (range = 13–70 $m^3/s$), there was little, if any, relation with species densities ($r = -0.31$ to 0.02) and its inclusion in regression models predicting species densities did not significantly improve the fit or alter model selection. Thus, because the fishes we sought generally occupied shallow habitats (Gido and Propst 1999) that were easily sampled with seines, we assumed that discharge at the time of sampling had a minimal influence on sampling efficiency. The majority of the fish captured were identified, counted, and released alive. Total length (TL, mm) and mass (g) were determined for most individuals greater than 100 mm TL. All remaining specimens (as vouchers) were preserved in 10% formalin and returned to the laboratory for identification and enumeration. The area of each seine haul was measured after fish sampling was completed. Data from 18 annual fish collections were grouped by three geomorphic reaches (i.e., $n = 54$), and fish density was the number of specimens of a species collected per total area ($m^2$) sampled in that reach in a given year. To reduce effects of disproportionately large values in the analyses, fish densities were $\log_{10}(x + 0.001)$ transformed.

In autumn, age-0 fish numerically dominated secondary channel fish communities because the majority of adults of small-bodied native and nonnative species and age-1 and older individuals of large-bodied fishes were rarely captured in these shallow-water habitats (Gido et al. 1997; Gido and Propst 1999). Although small numbers of age-1 and older fish were captured, interannual variation in density was primarily attributed to densities of age-0 fish. Thus, we considered autumn densities of fish in secondary channels as an index of recruitment of age-0 fish prior to overwintering.

To estimate abundance of nonnative predators, we relied on annual monitoring of the main channel that occurred in the same reaches and at the same time using raft-mounted electrofishing gear (D. Ryden, U.S. Fish and Wildlife Service, unpublished data). Fish were captured by netters on platforms mounted on the bow of two or three electrofishing rafts that were rowed parallel downstream, typically sampling shoreline habitats. Catch rates as catch per unit effort (CPUE) were standardized to the number of minutes electrofished. We only included channel catfish *Ictalurus punctatus* greater than 300 mm TL (adult) in our analysis because this size-class is more likely to be predaceous (Bailey and Harrison 1945) and other predators were rare in comparison. Largemouth bass *Micropterus salmoides* was the next most abundant predator, with 364 individuals (all size-classes) captured over the study period in comparison with 21,365 adult channel catfish captured.

*Data analysis*.—Least-squares regression was used to evaluate the influence of flow attributes and biotic interactions on recruitment of fishes in the San Juan River. We excluded uncommon species that had mean densities less than 0.02 individuals/$m^2$ and that occurred in less than 80% of secondary channels sampled over the course of the study. Thus, three native fishes (speckled dace *Rhinichthys osculus*, bluehead sucker *Catostomus discobolus*, and flannelmouth sucker *Catostomus latipinnis*) and five nonnative fishes (red shiner *Cyprinella lutrensis*, common carp *Cyprinus carpio*, fathead minnow *Pimephales promelas*, western mosquitofish *Gambusia affinis*, and channel catfish) were used in our analyses. We

TABLE 2. List of candidate least-squares regression models used to evaluate the influence of flow attributes, nonnative competitor density (Nonnative Comp), and nonnative predator CPUE (Nonnative Pred) on fish assemblages in the San Juan River, New Mexico and Utah. Independent variables representing flow attributes are mean spring daily discharge (Mean_sp), mean summer daily discharge (Mean_su), and number of days on which summer discharge was less than 14 $m^3/s$ (Day_less_14).

| Model number | Model description |
|---|---|
| | **Models for native species** |
| 1 | Species density ~ Reach |
| 2 | Species density ~ Mean_sp + Reach |
| 3 | Species density ~ Mean_su + Reach |
| 4 | Species density ~ Day_less_14 + Reach |
| 5 | Species density ~ Nonnative Comp + Reach |
| 6 | Species density ~ Nonnative Pred + Reach |
| 7 | Species density ~ Nonnative Pred + Nonnative Comp + Reach |
| 8 | Species density ~ Mean_sp + Nonnative Comp + Reach |
| 9 | Species density ~ Mean_su + Nonnative Comp + Reach |
| 10 | Species density ~ Day_less_14 + Nonnative Comp + Reach |
| 11 | Species density ~ Mean_sp + Nonnative Pred + Reach |
| 12 | Species density ~ Mean_su + Nonnative Pred + Reach |
| 13 | Species density ~ Day_less_14 + Nonnative Pred + Reach |
| 14 | Species density ~ Mean_sp + Nonnative Comp + Nonnative Pred + Reach |
| 15 | Species density ~ Mean_su + Nonnative Comp + Nonnative Pred + Reach |
| 16 | Species density ~ Day_less_14 + Nonnative Comp + Nonnative Pred + Reach |
| | **Models for nonnative species** |
| 1 | Species density ~ Reach |
| 2 | Species density ~ Mean_sp + Reach |
| 3 | Species density ~ Mean_su + Reach |
| 4 | Species density ~ Day_less_14 + Reach |
| 5 | Species density ~ Nonnative Pred + Reach |
| 6 | Species density ~ Mean_sp + Nonnative Pred + Reach |
| 7 | Species density ~ Mean_su + Nonnative Pred + Reach |
| 8 | Species density ~ Day_less_14 + Nonnative Pred + Reach |

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used an information theoretic approach (Burnham and Anderson 2002) to rank a series of candidate models (Table 2) for each species that included three representative flow attributes (of nine considered), nonnative competitor density, and nonnative predator CPUE. Nonnative competitor density was calculated by summing the densities of nonnative western mosquitofish, red shiners, and fathead minnow. Whereas flow attributes did not vary by reach, nonnative competitor densities and nonnative predator CPUEs were reach-specific values. Candidate models for nonnative fishes did not include nonnative competitor density. To account for potentially different dynamics among three distinct geomorphic reaches, we included a categorical variable delineating these reaches in all candidate models. Finally, we included a null model with only the reach variable to give a total of 16 competing models for native fishes and eight models for nonnative fishes (Table 2). Akaike's information criterion (AIC) was used to select the best-approximating models by comparing each of the candidate models simultaneously. The AIC scores were adjusted for bias due to small sample size ($AIC_c$), and Akaike weights ($w_i$) were calculated. Models with the lowest $AIC_c$ and the highest $w_i$ were considered to have the best support. Following model selection, bivariate plots of fish densities and model parameters were examined to evaluate the direction and magnitude of the relationships that were identified in top candidate models.

To test for serial autocorrelation in our time series, we used a Durbin–Watson statistic followed by an examination of plots of autocorrelation functions. If there was strong evidence for autocorrelation, we used generalized least-squares regression and specified an autoregressive moving average (ARMA) correlation structure in the model. We expected stronger temporal autocorrelation for fishes with rapid turnover rates (i.e., nonnative red shiner, fathead minnow, and western mosquitofish) because a strong year-class for these species was most likely to influence densities (reproductive output) the following year. All statistical analyses were performed with R software (R Development Core Team 2007).

## RESULTS

### Flows

Discharge patterns during our study period varied considerably among years (Figure 3), ranging from a mean daily discharge of 80 $m^3/s$ in 1993 to 18 $m^3/s$ in 2002. There were

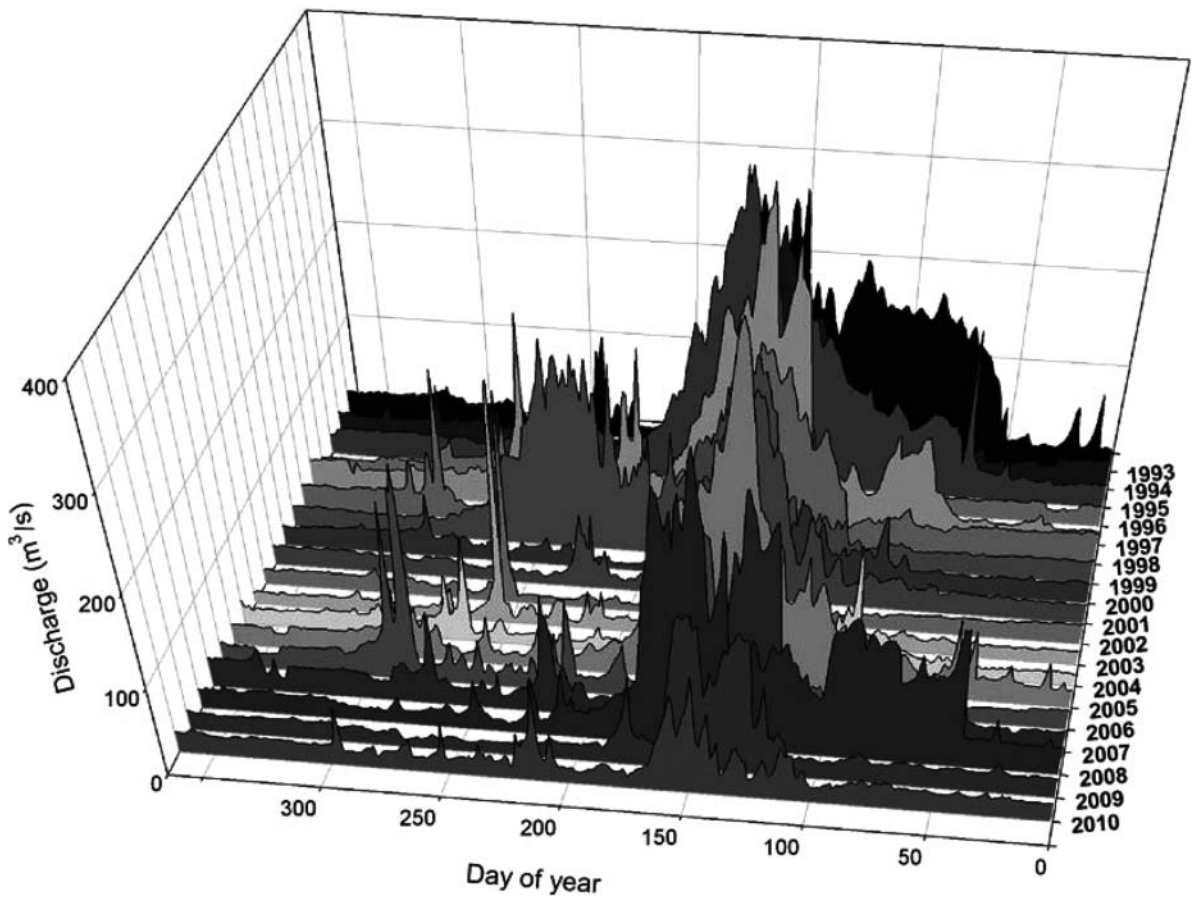


FIGURE 3. Annual variation in mean daily discharge in the San Juan River (data from U.S. Geological Survey gauging station 09368000 at Shiprock, New Mexico).

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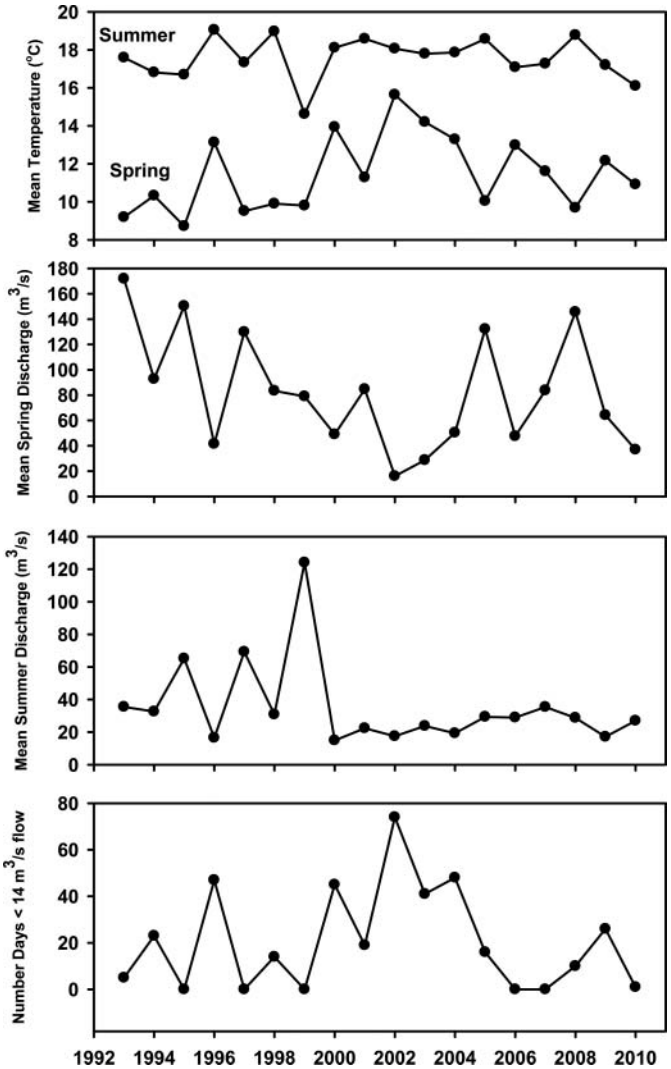


FIGURE 4. Annual variation in mean temperature of the San Juan River near Farmington, New Mexico (R. Bliesner, Keller-Bliesner Engineering, unpublished data), and three flow regime attributes (mean spring discharge, mean summer discharge, and mean number of days on which discharge was less than 14 $m^3/s$; flow data are from U.S. Geological Survey gauging station 09368000 at Shiprock, New Mexico).

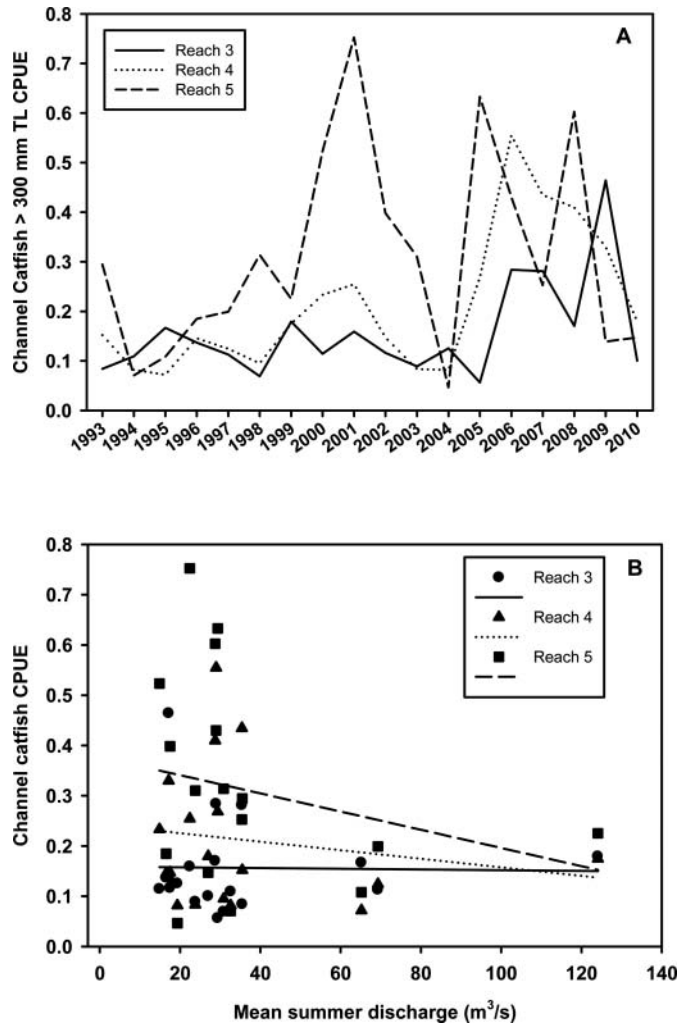


FIGURE 5. **(A)** Annual variation in CPUE (fish/min of electrofishing) of channel catfish larger than 300 mm TL captured from the primary channel of the San Juan River; and **(B)** relationship between mean summer daily discharge and autumn CPUE of channel catfish.

notable climatic cycles, with a wet period occurring early in the study (1993–1999; mean annual discharge = 61 $m^3/s$) followed by a dry period in the latter part of the study (2002–2010; mean annual discharge = 39 $m^3/s$; Table 1). This pattern was particularly evident when mean summer daily discharge was consistently no more than 35 $m^3/s$ after 1999 (Figure 4). Individual flow attributes were often highly correlated (Table 3). After removing highly correlated attributes ($r > 0.70$ or $r < -0.70$), we retained three variables (mean spring daily discharge, mean summer daily discharge, and number of days on which the summer discharge was less than 14 $m^3/s$) to use as indices of interannual variation in flow and temperature in our regression models. The inclusion of more variables in our analysis (increasing our cutoff for removal to $r > 0.80$ or $r < -0.80$) yielded similar results, so we retained the simpler set of variables. These three variables reflected a large range in variation in flow attributes and temperature among the years that were hypothesized to influence recruitment of fishes.

## Nonnative Predators

Catch rates of channel catfish greater than 300 mm TL were variable among the three reaches and over time (Figure 5A). Starting in 2003, there was an active nonnative removal effort in the primary channel for adult common carp and channel catfish that included the upper 10 km of reach 5 (J. E. Davis, U.S. Fish and Wildlife Service, unpublished data). However, the only potential effect of the removal efforts relevant to this study was that catch rates of channel catfish greater than 300 mm TL initially declined in abundance in reach 5 during 2004 and increased in abundance in all reaches after 2006, perhaps

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TABLE 3. Correlation coefficients between annual flow ($Q$) attributes measured between 1993 and 2010 in the San Juan River. Attributes in bold text (column and row headings) indicate the three attributes that were used to index annual variation in flow and temperature. The $r$-values in bold italics are significant ($P < 0.05$).

| Flow attribute | **Mean spring $Q$** | SD of spring $Q$ | Maximum spring $Q$ | Day of year $Q >$ 56 m$^3$/s | Duration (d) $Q >$ 56 m$^3$/s | **Mean summer $Q$** | SD of summer $Q$ | Minimum summer $Q$ | **Duration (d) $Q <$ 14 m$^3$/s** |
|---|---|---|---|---|---|---|---|---|---|
| **Mean spring $Q$** | 1.000 | | | | | | | | |
| SD of spring $Q$ | ***0.819*** | 1.000 | | | | | | | |
| Maximum spring $Q$ | ***0.743*** | ***0.761*** | 1.000 | | | | | | |
| Day of year $Q > 56$ m$^3$/s | ***−0.812*** | −0.669 | −0.414 | 1.000 | | | | | |
| Duration (d) $Q > 56$ m$^3$/s | ***0.911*** | ***0.787*** | 0.657 | ***−0.757*** | 1.000 | | | | |
| **Mean summer $Q$** | 0.331 | 0.482 | 0.357 | −0.190 | 0.657 | 1.000 | | | |
| SD of summer $Q$ | 0.253 | 0.310 | 0.525 | −0.026 | 0.475 | ***0.748*** | 1.000 | | |
| Minimum summer $Q$ | 0.442 | 0.491 | 0.371 | −0.292 | 0.644 | ***0.807*** | 0.650 | 1.000 | |
| **Duration (d) $Q < 14$ m$^3$/s** | −0.607 | ***−0.701*** | −0.419 | 0.588 | −0.658 | −0.544 | −0.255 | ***−0.749*** | 1.000 |

owing to a compensatory response to removal of larger channel catfish. The highest CPUE for large channel catfish typically occurred in reaches 4 and 5 in years with low summer flows, but this was not always the case (Figure 5B).

## Recruitment of Fishes

In general, native fish densities in secondary channels were lower but more stable than nonnative fish densities (Figure 6). Densities of nonnative red shiners, common carp, fathead minnow, and western mosquitofish peaked in 2000 and then declined by several orders of magnitude, with lowest densities occurring in 2007 and 2008. As predicted, serial autocorrelation in the time series was greater for small-bodied nonnative fishes with an earlier age at maturity than other species; the Durbin–Watson statistic ranged from 0.68 to 1.03 ($P$-values $< 0.001$), whereas that for native species ranged from 1.47 to 1.75 ($P$-values $> 0.03$). Thus, we used generalized least-squares regression and specified ARMA correlation structure for red shiners, fathead minnow, and western mosquitofish. Strength of regression models was rather low, with $R^2$ ranging from 0.208 to 0.439 (Table 4). There were generally more competing models with reasonable support ($\Delta AIC_c < 2$; $w_i > 0.10$) for native fishes than for nonnative fishes. Top candidate models predicting densities of age-0 bluehead suckers included nonnative predator CPUE, nonnative competitor density, and mean summer daily discharge in addition to reach (Table 4). In general, densities of bluehead suckers were positively associated with mean summer daily discharge and nonnative competitor density and negatively associated with nonnative predator CPUE (Figure 7). Nonnative competitor density was included in the top-three regression models for flannelmouth suckers, mean spring daily discharge was included in two models, and nonnative predator CPUE was included in one candidate model (Table 4). Flannelmouth sucker densities were positively associated with nonnative competitor density and mean spring daily discharge and negatively associated with nonnative predator CPUE. The top candidate model for speckled dace included positive associations with mean spring daily discharge and nonnative competitor density and negative associations with nonnative predator CPUE (Figure 7). Although densities of native fishes were greatest in the upstream-most reach (reach 5) in the majority of years, there was notable variation, particularly for catostomids, across years (Figure 6). Nonetheless, annual fluctuations in densities were generally synchronous across reaches.

Top-ranked candidate models that obtained the majority of support for predicting densities of nonnative species other than age-0 channel catfish included a positive association with the number of days on which discharge was less than 14 m$^3$/s during summer (Figure 8). However, nonnative fish densities also generally declined with nonnative predator CPUEs (Figure 8), and models that included this variable also received notable support (Table 4). Densities of age-0 channel catfish collected from secondary channels varied considerably by reach, with increasing densities downstream. Candidate models that included catch rates of channel catfish greater than 300 mm TL and low mean summer daily discharge were twice as likely to be the best-approximating model than candidate models that included mean spring daily discharge (not shown) and number of days on which discharge was less than 14 m$^3$/s. Densities of age-0 channel catfish generally declined with increasing catch rates of large channel catfish, but relationships with mean summer daily discharge were variable by reach (Figure 8). As with native fishes, annual variation in densities of nonnative fishes other than age-0 channel catfish was variable among

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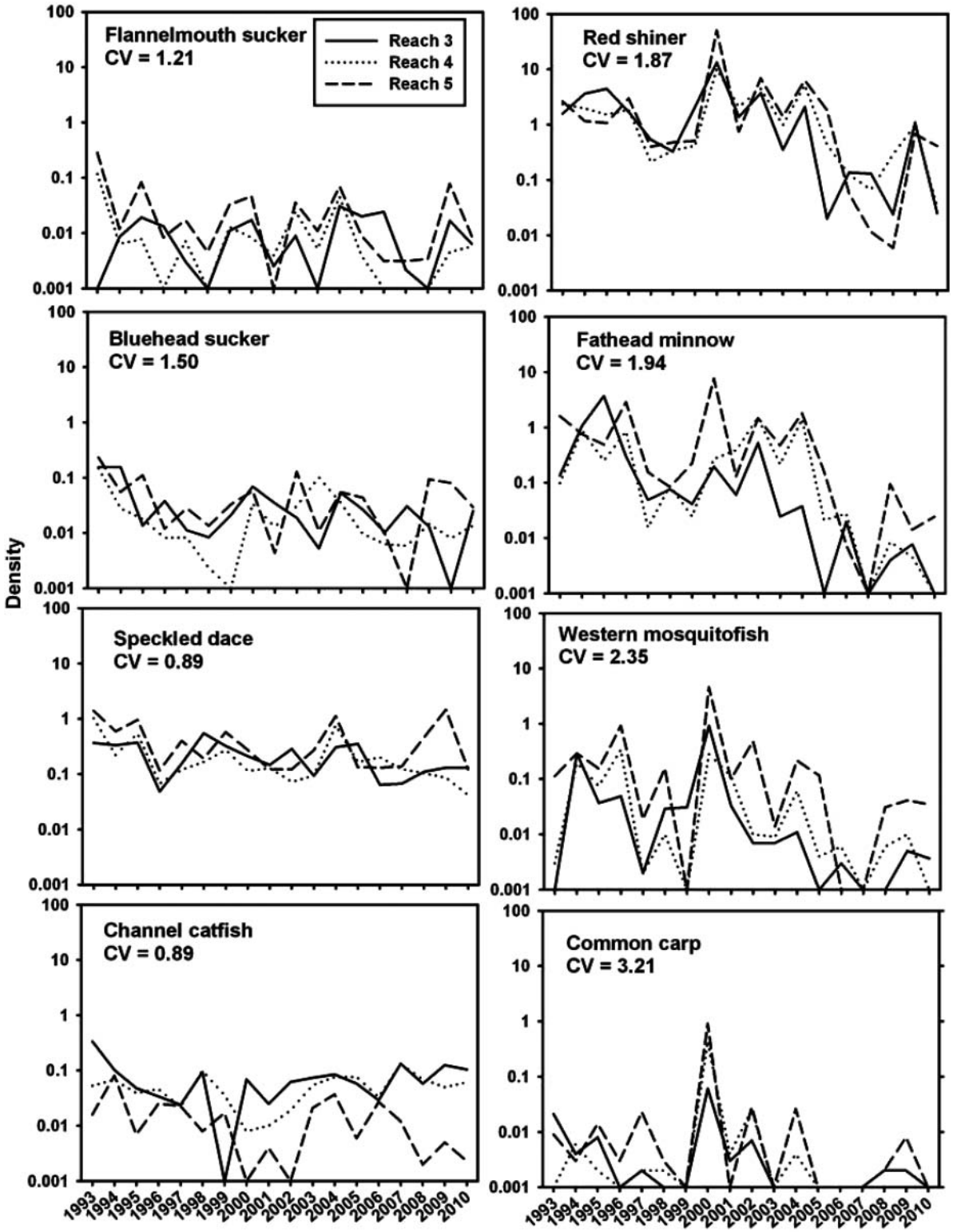


FIGURE 6. Mean densities (individuals/m$^2$) of native and nonnative fishes captured from secondary channels in three reaches of the San Juan River, New Mexico and Utah. Coefficient of variation (CV = 100·[SD/mean]) of $\log_{10}$-transformed density data is provided as an index of variability over time.

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TABLE 4. Regression models, ranked by corrected Akaike's information criterion ($AIC_c$) scores, that explain annual variation in densities of three native fishes (bluehead sucker, flannelmouth sucker, and speckled dace) and five nonnative fishes in secondary channels of the San Juan River, 1993–2010 (Nonnative Pred = nonnative predator CPUE; Nonnative Comp = nonnative competitor density; $Q$ = discharge; Day_less_14 = number of days on which summer $Q$ was less than 14 $m^3/s$). Only models with Akaike weights ($w_i$) greater than 0.10 are presented. The $R^2$ value for the top candidate model is given in parentheses for each species. Species identified by an asterisk (*) exhibited notable autocorrelation; thus, general least-squares regression with an autoregressive moving average correction for correlation structure was used. $K$ represents the number of parameters in the model.

| Model | $K$ | $AIC_c$ | $\Delta AIC_c$ | $w_i$ | Cumulative $w_i$ |
|---|---|---|---|---|---|
| **Bluehead sucker ($R^2 = 0.273$)** | | | | | |
| Nonnative Pred + Nonnative Comp + Reach | 5 | 183.61 | 0 | 0.27 | 0.27 |
| Mean summer $Q$ + Nonnative Comp + Nonnative Pred + Reach | 6 | 184.44 | 0.83 | 0.18 | 0.44 |
| Mean summer $Q$ + Nonnative Comp + Reach | 5 | 184.98 | 1.37 | 0.13 | 0.58 |
| Nonnative Comp + Reach | 4 | 185.29 | 1.68 | 0.12 | 0.69 |
| **Flannelmouth sucker ($R^2 = 0.286$)** | | | | | |
| Mean spring $Q$ + Nonnative Comp + Reach | 5 | 171.73 | 0 | 0.35 | 0.35 |
| Mean spring $Q$ + Nonnative Comp + Nonnative Pred + Reach | 6 | 172.37 | 0.64 | 0.26 | 0.61 |
| Nonnative Comp + Reach | 4 | 173.74 | 2.01 | 0.13 | 0.74 |
| **Speckled dace ($R^2 = 0.439$)** | | | | | |
| Mean spring $Q$ + Nonnative Comp + Nonnative Pred + Reach | 6 | 119.55 | 0 | 0.76 | 0.76 |
| **Red shiner ($R^2 = 0.351$)*** | | | | | |
| Day_less_14 + Reach | 5 | 192.73 | 0 | 0.67 | 0.67 |
| Day_less_14 + Nonnative Pred + Reach | 6 | 194.16 | 1.43 | 0.33 | 1.00 |
| **Fathead minnow ($R^2 = 0.340$)*** | | | | | |
| Day_less_14 + Reach | 5 | 203.17 | 0 | 0.66 | 0.66 |
| Day_less_14 + Nonnative Pred + Reach | 6 | 204.56 | 1.39 | 0.33 | 0.99 |
| **Western mosquitofish ($R^2 = 0.335$)*** | | | | | |
| Day_less_14 + Reach | 5 | 208.67 | 0 | 0.65 | 0.65 |
| Day_less_14 + Nonnative Pred + Reach | 6 | 210.26 | 1.59 | 0.29 | 0.94 |
| **Common carp ($R^2 = 0.208$)** | | | | | |
| Day_less_14 + Reach | 4 | 196.46 | 0 | 0.70 | 0.70 |
| Day_less_14 + Nonnative Pred + Reach | 5 | 198.48 | 2.02 | 0.26 | 0.96 |
| **Channel catfish ($R^2 = 0.395$)** | | | | | |
| Mean summer $Q$ + Nonnative Pred + Reach | 5 | 168.36 | 0 | 0.29 | 0.29 |
| Nonnative Pred + Reach | 4 | 168.36 | 0.33 | 0.25 | 0.54 |
| Mean spring $Q$ + Nonnative Pred + Reach | 5 | 170.21 | 1.85 | 0.12 | 0.65 |
| Day_less_14 + Nonnative Pred + Reach | 5 | 170.35 | 1.99 | 0.11 | 0.76 |

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reaches, but temporal patterns were synchronous across reaches (Figure 6).

## DISCUSSION

Results from our study clearly demonstrate that native and nonnative fishes responded differently to key attributes of the annual flow regime—specifically flow magnitude during either spring or summer. Native fishes generally responded positively to elevated spring discharge, and densities of nonnative fish increased in years that had extended periods of low flow during summer. It is likely that high spring discharge generally favors recruitment of native fishes through increased quantity and quality of spawning habitat (Osmundson and Burnham 1999) and food resources (Paukert and Rogers 2004). The bluehead sucker was an exception to the spring discharge–density relationship owing to its successful recruitment in several years with low spring discharge. For example, moderate to high densities of bluehead suckers occurred in 2002 (Figure 6), the year with the lowest mean spring daily discharge and the longest duration of low flows during summer (Figure 4). This pattern, along with the generally low amount of variation in species densities explained by our models ($R^2 < 0.50$), indicated that factors other than high spring discharge may influence recruitment of native fishes in the San Juan River.

Overall, the relationships we found with 9 years of data (Propst and Gido 2004) were affirmed with 18 years of data, and these similarities held despite substantial differences in flow between study periods, most notably lower summer flows during the latter half of the study. The consistent pattern of increased

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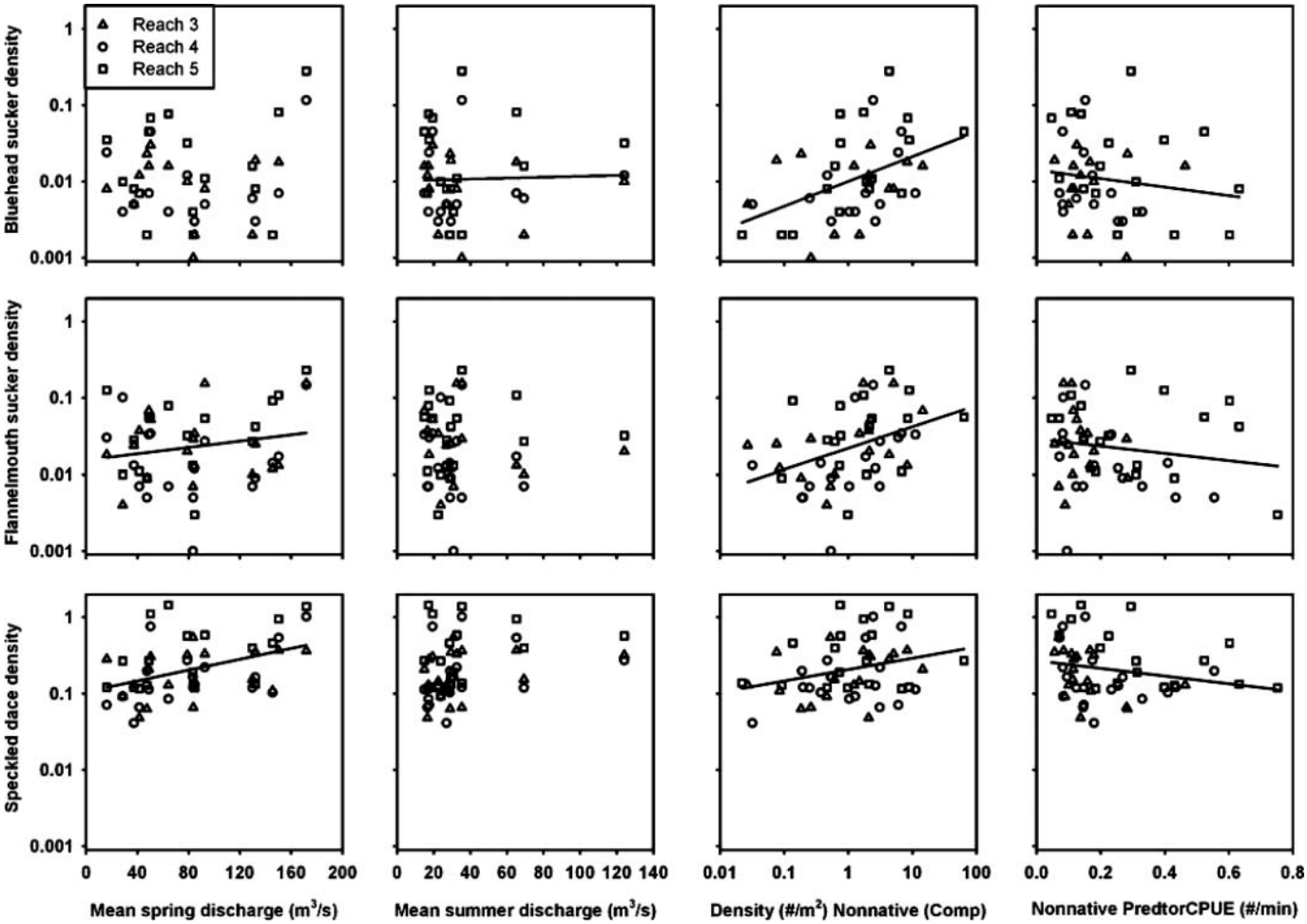


FIGURE 7. Bivariate relationships between native fish densities (individuals/m$^2$) and variables evaluated in regression models (Density Nonnative Comp = density of nonnative competitors; Nonnative PredtorCPUE = catch of predatory adult channel catfish [>300 mm TL] per min of electrofishing). Least-squares regression lines are shown for variable combinations that were included in the top-ranked candidate model for each species (Table 4).

densities of flannelmouth suckers and speckled dace in years of high spring discharge in our long-term study accords with observations for similar species within the Colorado River basin (e.g., Brouder 2001; Stefferud et al. 2011). In our previous study, the number of days when summer discharge was less than 14 m$^3$/s negatively affected speckled dace autumn density; however, with 18 years of data, this flow attribute was not included in top candidate models for any native fish. Mean summer daily discharge had no measurable effect on any native or nonnative species in the 1993–2001 period but was considered in top-performing bluehead sucker and channel catfish models for the extended 1993–2010 period. In our initial study, we found a positive relationship between the number of summer days on which discharge was less than 14 m$^3$/s and the autumn densities of red shiners, common carp, and western mosquitofish, and this relationship held with an additional 9 years of data for these species as well as for the fathead minnow, which was not considered in our earlier study.

Biotic interactions may have obscured the relationship between spring discharge and native fish densities, a factor not considered in our previous study (Propst and Gido 2004). For example, catch rates of large channel catfish were rather low in 2004, which also had low spring flows and comparatively high densities of bluehead suckers. It is possible that the response of native fishes to nonnative predators is contingent on flow, such that low-flow years were only detrimental to native fishes when nonnative predators were abundant and consumption was greatest. A similar phenomenon was hypothesized for fishes in the Gila River basin, New Mexico (Propst et al. 2008; Stefferud et al. 2011). Assuming that the interaction between flows and nonnative predators is a key driver of recruitment success, an understanding of factors (e.g., flows and harvest) regulating abundance of nonnative predators is necessary to inform management of native species.

Factors driving recruitment and abundance of age-0 channel catfish, the main nonnative predator in the San Juan River, are not well understood and were possibly influenced by removal efforts since 2003. In contrast to other nonnative species, densities of age-0 channel catfish collected in secondary channels were not positively associated with durations of low flows. Rather, age-0

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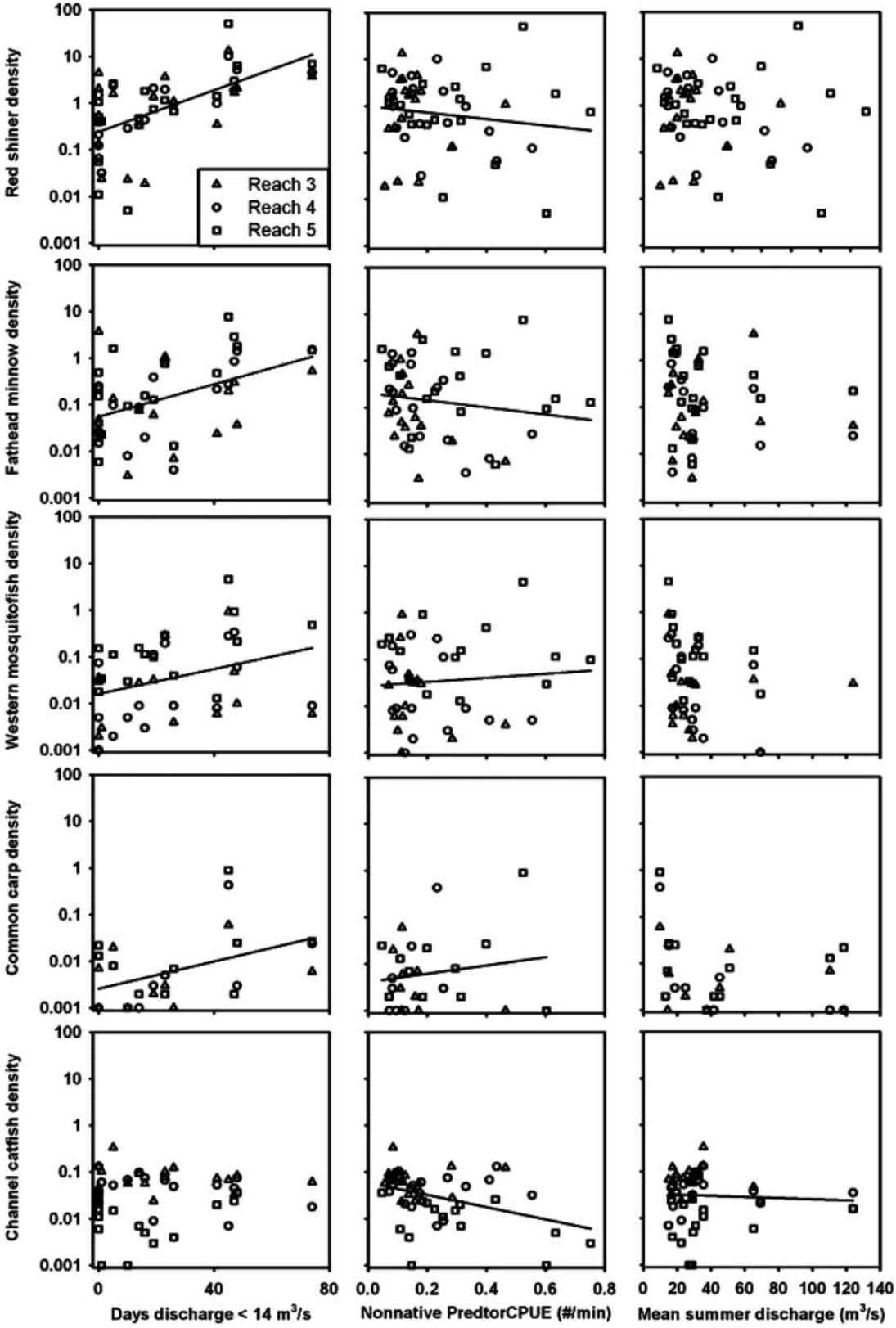


FIGURE 8. Bivariate relationships between nonnative fish densities (individuals/m$^2$) and variables evaluated in regression models (Nonnative PredtorCPUE = catch of predatory adult channel catfish [>300 mm TL] per min of electrofishing). Least-squares regression lines are shown for variable combinations that were included in the top-ranked candidate model for each species (Table 4).

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channel catfish densities were greatest in downstream reaches and were negatively associated with catch rates of large channel catfish. Other studies have suggested that channel catfish dynamics in rivers are driven both by stochastic variation in flows and intraspecific interactions (Colombo 2007; Sakaris and Irwin 2010). In contrast to other common San Juan River nonnative fishes, channel catfish spawn mainly during the latter phases of spring runoff rather than during summer low-flow periods. However, prior to (or in concert with) developing management strategies for reducing populations of channel catfish, experiments that test the potential mechanisms responsible for the negative association between native fish recruitment and catch rates of large channel catfish would be informative. For example, harvest strategies are likely to alter both channel catfish abundance and population size structure; therefore, understanding size-dependent interactions with native fishes would help focus management efforts.

The pattern of greater autumn densities of nonnative fishes in years with extended low flows might be linked to water temperature and sediment dynamics. Higher water temperatures were positively associated with summer low flows and probably favored earlier and more prolonged spawning periods for most nonnative fishes (Gido et al. 1997; Gido and Propst 1999). The absence of monsoonal storms that caused sediment transport from tributary watersheds to main-stem spawning substrates also might favor recruitment of these species by maintaining clean substrates used for nesting (Mueller 1984; Vives 1993) and increased invertebrate production (Feminella and Resh 1990). The strength of this relationship indicates that flow management (i.e., elevated summer discharge and reservoir-induced flow spikes) could be used to diminish populations of nonnative fishes, but it is important to first establish that these nonnative fishes interfere with the success of native fishes.

The introduction and spread of small-bodied nonnative species such as the red shiner are thought to be detrimental to native species, as indicated in several studies (e.g., Karp and Tyus 1990; Rinne 1991; Ruppert et al. 1993; Douglas et al. 1994; Brandenburg and Gido 1999). However, the positive association between densities of nonnative and native fishes was not consistent with the presumed negative interactions among these species. Our data suggested that environmental conditions (e.g., high spring flows and low predator abundance) that favor native species might also have beneficial effects on populations of some nonnative species. For example, the elevated spring flows that mobilize fine sediments, thereby improving spawning habitat for native species such as speckled dace, also might benefit red shiners, which spawn in riffles. Moreover, differences in spawning chronology among native and nonnative fishes probably reduce interactions related to use of spawning and nursery habitats.

Strong correlations among flow attributes and temperature made it difficult to isolate specific attributes associated with recruitment of fishes. For example, although low-flow duration was positively associated with recruitment of most nonnative species in secondary channels, this attribute was negatively associated with other flow attributes, including mean spring daily discharge and variability in spring discharge (Table 3). Warm summer temperatures associated with low summer flows constitute the most parsimonious explanation for successful reproduction and recruitment by nonnative fishes, but cooler water temperatures associated with high spring flows also shortened the spawning period for nonnative species by postponing spawning, sometimes by a month or more (Gido et al. 1997; Gido and Propst 1999). Assuming that water temperature was the main factor driving recruitment of nonnative species, flow management strategies to limit their reproductive success while benefitting native fishes might include extending spring runoff or providing elevated or pulsed discharge during summer. Conducting such flow experiments and monitoring their associations with other environmental factors (e.g., temperature and sediment loads) are logical next steps toward developing a robust strategy for managing flows to benefit native fish assemblages in the San Juan River.

The overarching goal of current management of flows from Navajo Reservoir is to mimic a natural flow regime to benefit native fishes, especially federally protected species (Colorado pikeminnow *Ptychocheilus lucius* and razorback sucker *Xyrauchen texanus*), after obligations to water users have been met (San Juan River Basin Recovery Implementation Program, www.fws.gov/southwest/sjrip/). Federal protection of the Colorado pikeminnow and razorback sucker was prompted, in part, by negative interactions with nonnative species and reservoir-regulated flow regimes. Because of their rarity during much of this study and annual augmentation with hatchery stocks for the past 15 years, neither the Colorado pikeminnow nor the razorback sucker was included in our analysis. Nonetheless, our results illustrate how flows influence other members of the assemblage and may have bearing on flow management for these federally protected species. Although we do not have the appropriate controls (i.e., pre- or postmanipulation) to test the effects of the natural flow regime mimicry, it is possible that the stability of native fishes and the declines in nonnative fishes were responses to this management strategy.

Sound ecological understanding of how fish species respond to flows in the San Juan River is essential to refine management strategies because of the increasing demands on water resources (e.g., recent construction of Lake Nighthorse, which is maintained by water withdrawals from the Animas River). Our correlative data are a first step in evaluating biotic response to flows, but mechanistic understanding of proximal factors affecting fishes at different life stages, such as those outlined in Figure 1, could help inform management strategies (Lancaster and Downes 2010). There are several ongoing efforts in the Colorado River basin that are providing this critical information. For example, experiments testing how flow modifications and resulting changes in thermal regimes influence growth and survival of early life stages (Bestgen 2008) will help identify bottlenecks to recruitment. Predator–prey studies that evaluate

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the influence of prey availability on predator growth and survival (Franssen et al. 2007) or that use bioenergetics to evaluate consumptive demands (Johnson et al. 2008) will help characterize important biotic interactions and how they interact with flow regimes. Investigations such as these, however, are best understood and interpreted within the context of long-term data sets that include common climatic phenomena (e.g., extended drought) and shifts in abundances of dominant taxa.

## ACKNOWLEDGMENTS

Field work was accomplished with the assistance of numerous colleagues, most notably L. A. Ahlm, T. Bingham, M. J. Buntjer, S. M. Carman, T. Chart, S. Davenport, J. E. Davis, S. Durst, N. Franssen, D. W. Furr, C. W. Hoagstrom, A. L. Hobbes, J. A. Jackson, R. D. Larson, M. Mata, A. M. Monié, Y. M. Paroz, T. J. Pilger, C. Roberstson, J. Wick, and N. Zymonas. Dale Ryden graciously provided channel catfish data. Our research benefited from discussions with K. R. Bestgen, J. E. Brooks, F. K. Pfeifer, and S. P. Platania. Helpful hydrological and geomorphological insights were provided by S. Cullinan. Earlier drafts of the manuscript were improved by W. Brandenburg, R. Clarkson, S. Durst, E. Martin, M. Troia, J. Whitney, three anonymous reviewers, and the associate editor. Fish illustrations in Figure 1 were provided by W. H. Brandenburg. Funding for this study was provided by the U.S. Bureau of Reclamation, the New Mexico Department of Game and Fish (State Wildlife Grants), and the U.S. Fish and Wildlife Service. Much of the work reported herein was conducted under the auspices of the San Juan River Basin Recovery Implementation Program. Scientific collecting permits were provided by the Navajo Nation, the states of Utah and New Mexico, and the U.S. Fish and Wildlife Service.

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