Evaluating the Conservation Potential of Tributaries for Native Fishes in the Upper Colorado River Basin

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We explored the conservation potential of tributaries in the upper Colorado River basin by modeling native fish species richness as a function of river discharge, temperature, barrier-free length, and distance to nearest free-flowing main-stem section. We investigated a historic period prior to large-scale water development and a contemporary period. In the historic period, species richness was log-linearly correlated to variables capturing flow magnitude, particularly mean annual discharge. In the contemporary period, the log-linear relationship between discharge and species richness was still evident but weaker. Tributaries with lower average temperature and separated from free-flowing main-stem sections often had fewer native species compared to tributaries with similar discharge but with warmer temperature and directly connected to free-flowing main stems. Thus, tributaries containing only a small proportion of main-stem discharge, especially those at lower elevations with warmer temperatures and connected to free-flowing main stems, can support a relatively high species richness. Tributaries can help maintain viable populations by providing ecological processes disrupted on large regulated rivers, such as natural flow and temperature regimes, and may present unique conservation opportunities. Efforts to improve fish passage, secure environmental flows, and restore habitat in these tributaries could greatly contribute to conservation of native fish richness throughout the watershed.

INTRODUCTION

Many fish species move throughout drainage basins to fulfill their life-history requirements, using large rivers and small tributaries at different times for spawning, feeding, and dispersal (Fausch et al. 2002). Many species exhibit metapopulation dynamics, in which connectivity between populations is crucial for overall population persistence (Fagan et al. 2002; Falke et al. 2012). The long-term persistence of fish populations is further enhanced through portfolio effects, in which populations inhabiting different tributaries in large river systems respond uniquely to regional forcing, such as climate change (Schindler et al. 2010). Maintaining viable populations and suitable habitat in both main-stem and tributary rivers will likely enhance the resilience of species to large-scale threats and increase the likelihood of persistence (Gyllenberg and Hanski 1997; Hilborn et al. 2003). Thus, when developing conservation plans for native riverine fish communities, managers should adopt a catchment-scale perspective, which considers conservation potential throughout the river network.

Opportunities for habitat restoration and ecological flow provisions are often available in different locations throughout river networks, from smaller tributary headwater streams to larger main-stem rivers. Differing political, economic, and regulatory circumstances across drainage networks require that conservation and management activities be tailored to individual rivers and streams. For example, in some river systems, compliance with the Endangered Species Act (ESA) provides incentive for provision of environmental flows targeting species recovery. Rivers that receive little recreational or angling use may provide opportunities for management efforts, such as habitat restoration and nonnative species removal, due to fewer potential conflicts with other stakeholders (Clarkson et al. 2005; Pracheil et al. 2013). Clearly, opportunities for native fish conservation can be identified throughout river networks, but prioritizing locations where actions can have the greatest benefit is necessary to ensure efficient use of limited resources (Linke et al. 2011).

One criteria for assessing the relative conservation potential for species richness is simply mean discharge (Xenopoulos and Lodge 2006) because richness in fish assemblages most often increases from smaller headwater streams to larger rivers (Oberdorff et al. 1995). Previous work in the Mississippi River system has demonstrated that there is a threshold mean discharge above which tributaries are likely to hold a similar species richness as the Mississippi River main stem and that this threshold relationship could be used to prioritize fish passage barriers for modification (Pracheil et al. 2013). Attributes of peak flood discharges, such as magnitude, timing, and duration, can also serve as useful indicators of ecological integrity across river systems as flood flows provide spawning cues for many species (e.g., Nesler et al. 1988), provide access to productive off-channel habitats, and create and maintain habitat necessary for successful recruitment (Arthington and Balcombe 2011). Even streams inaccessible to large adult fish during base flow or low-water periods can provide productive spawning and rearing habitat during flood periods, and subadult fish produced in such tributary streams during peak flows can then migrate to larger rivers as flows decline. In addition, peak annual discharge was previously found to be a significant predictor of local extinction probability for three species of native fishes in the upper Colorado River basin (UCRB; Budy et al. 2015). Rivers that maintain other aspects of a natural flow regime, such as discharge variability and the timing, frequency, duration, and rate of change of flood and drought events are also important in native fish conservation (Poff et al. 1997).

In this article, we relate discharge to species richness in the UCRB, as has been done for other drainage basins (e.g., Xenopoulos and Lodge 2006; Pracheil et al. 2013). Our goal was to investigate the occurrence of endangered and other state-listed sensitive native fishes in rivers and their tributaries throughout the UCRB and inform conservation and restoration planning efforts. Specifically, we wanted to determine if discharge metrics might provide an initial assessment of whether rivers throughout the drainage network support or have the potential to support high native species richness. We supplemented discharge-richness relationships with several covariables, including temperature, distance to movement barriers, and whether tributaries were connected to free-flowing river reaches or reservoirs, to help further explain contemporary richness patterns across the UCRB. Identifying initial flow criteria would help supplement management efforts in main-stem rivers by providing a first step toward prioritization of management actions, such as instream flow management, nonnative fish removal, and barrier removal projects, in tributaries across the UCRB. Although other factors such as habitat availability and nonnative fish abundances would need to be considered to fully gauge conservation potential of different rivers, the analysis presented here could also serve as a guide for development of similar criteria on other desert river systems.

METHODS

We investigated relationships between discharge and native fishes in 28 eight-digit U.S. Geological Survey (USGS) hydrologic unit codes (HUCs), i.e. subwatersheds, in the UCRB (Figure 1). We defined the geographic extent as HUCs that were historically occupied by at least six of seven native large-bodied

Figure 1. Map of eight-digit U.S. Geological Survey hydrologic unit code watersheds within the upper Colorado River basin that comprised the study region. The Colorado, Green, and San Juan main-stem rivers are shown by the dark bold lines; tributaries are shown in lighter lines. Inset shows location of study region.

riverine fish (Table 1), and tributaries to these systems at the eight-digit HUC level. We used six species as the cutoff, rather than seven, because few HUCs contained all seven species and

using seven species would have severely reduced the geographic extent of the study and the number of data points for analyses. Tributary rivers included in this study did not support all native

Table 1. Fish species used in this study and whether they were present (P) or absent (A) in each 8-digit HUC for both the historic (H) and contemporary (C) periods. Species abbreviations as follows: FMS = Flannelmouth Sucker *Catostomus latipinnis*, BHS = Bluehead Sucker *Catostomus discobolus*, RTC = Roundtail Chub *Gila robusta*, CPM = Colorado Pikeminnow *Ptychocheilus lucius*, RBS = Razorback Sucker *Xyrauchen texanus*, BT = Bonytail *Gila elegans*, HBC = Humpback Chub *Gila cypha*. Colorado Pikeminnow, Razorback Sucker, Bonytail, and Humpback Chub are all federally listed endangered species. Flannelmouth Sucker, Bluehead Sucker, and Roundtail Chub are each considered threatened by state agencies and are currently managed as a complex under an interstate conservation agreement (UDNR 2006). Primary sources used for presence/absence data include the NatureServe database (explorer.natureserve.org), the Upper Colorado River Endangered Fish Recovery program and associated documents (coloradoriverrecovery.org), the San Juan River Recovery Implementation Program and associated documents (fws.gov/southwest/sjrip), Bezzerides and Bestgen (2002), and Bottcher et al. (2013).

	FMS		BHS		RTC		CPM		RBS		BT		HBC		Richness	
	H	C	H	C	H	C	H	C	H	C	H	C	H	C	H	C
HUC subwatershed																
Uncompahgre	P	P	P	P	P	P	A	A	P	A	A	A	A	A	4	3
Lower Gunnison	P	P	P	P	P	P	P	P	P	P	P	P	P	A	7	6
Colorado Headwaters-Plateau	P	P	P	P	P	P	P	P	P	P	P	A	P	P	7	6
Lower Dolores	P	P	P	P	P	P	P	A	P	A	P	A	A	A	6	3
HUC																
Colorado: Westwater Canyon	P	P	P	P	P	P	P	P	P	P	P	A	P	P	7	6
Blacks Fork	P	P	P	P	P	P	A	A	A	A	A	A	A	A	3	3
Upper Green: Flaming Gorge	P	P	P	P	P	P	P	P	P	P	P	A	P	A	7	5
Little Snake	P	P	P	P	P	P	P	P	A	A	A	A	P	P	5	5
Lower Yampa	P	P	P	P	P	P	P	P	P	P	P	P	P	P	7	7
Lower Green: Diamond	P	P	P	P	P	P	P	P	P	P	P	P	P	P	7	7
Duchesne	P	P	P	P	P	P	P	P	P	P	P	P	A	A	6	6
Upper White	P	P	P	P	P	P	P	P	P	A	P	A	A	A	6	4
Piceance	P	P	A	A	A	A	P?	P?	A	A	A	A	A	A	2	2
Lower White	P	P	P	P	P	P	P	P	P	P	P	P	P	A	7	6
Willow	P?	P?	A	A	P?	P?	A	A	A	A	A	A	A	A	2	2
Price	P	P	P	P	P	A	P	P	P	P	P	P	A	A	6	6
Lower Green	P	P	P	P	P	P	P	P	P	P	P	P	P	P	7	7
San Rafael	P	P	P	P	P	P	P	P	P	P	P	P	A	A	6	6
Dirty Devil	P	P	P	P	P	P	A	A	P?	A	A	A	A	A	4	3
Escalante	P	P	P	P	P	P	A	A	P?	A	A	A	A	A	4	3
Piedra	P	P	P	P	P?	P?	A	A	A	A	P?	A	A	A	4	3
Upper San Juan	P	P	P	P	P	P	P	A	P?	A	P?	A	A	A	6	3
Animas	P	P	P	P	P	P	P	P	P?	P	A	A	A	A	5	5
Middle San Juan	P	P	P	P	P	P	P	P	P?	P	P?	A	A	A	6	5
Mancos	P	P	P	P	P	P	A	A	A	A	A	A	A	A	3	3
McElmo	P	P	P	P	P	P	P	P	P	P	A	A	A	A	6	6
Chinle	P?	P?	P?	P?	P?	P?	A	A	A	A	A	A	A	A	3	3
Lower San Juan: Four Corners	P	P	P	P	P	P	P	P	P	P	P?	A	A	A	6	5

species but historically were hydrologically connected to main-stem rivers and were at least accessible to all species, even if other factors such as habitat suitability and temperature were limiting. The Colorado River, Green River, and San Juan River were defined as main-stem rivers, and all other rivers used in our analysis were defined as tributaries.

Recognizing that current relationships between discharge and native species richness were likely modified by water development and management, we examined whether species-discharge relationships have changed over time by comparing relationships in a period prior to widespread, large-scale hydrologic development (1957 and earlier) and a contemporary period (1996–2011). Hydrologic development has significantly impacted flow regimes across the basin. In particular,

operation of dams for electricity generation and irrigation has reduced the magnitude and duration of spring snowmelt peak discharge and increased base flow magnitude on many rivers (Schmidt 2010). The year 1957 was chosen as the end of the historic period because it marks a transition to large-scale hydrologic development (the Colorado River Storage Project was authorized in 1956), and it also marks the end of an earlier period of hydrologic record, data of which were summarized in an early USGS report assessing the water resources of the UCRB (Iorns et al. 1965). As such, although discharge metrics changed on most rivers from the historic to contemporary period, what we define as the historic period is not a prealteration period because dam-building and water use was well underway throughout the basin before 1957.

Although the seven study species are a subset of the native species present in the UCRB (14 species), they represent the contingent of Colorado River main-stem species currently the focus of most management and recovery efforts (USFWS 1993; UDNR 2006). Occurrence of native fishes for both the historic and contemporary periods was initially determined by using data on species distribution from the NatureServe database (explorer.natureserve.org). We used the distribution maps found in individual species records on the NatureServe database to identify whether each species was considered present or absent in each eight-digit HUC in the contemporary period. Species were considered present historically in each eight-digit HUC if the species was either present in the contemporary period or was listed as extirpated or possibly extirpated within the HUC in the NatureServe database. The NatureServe distribution maps are based on state Natural Heritage Program records, scientific literature, and expert consultation. We amended NatureServe records by collecting scientific literature, reports, and sampling records from state and federal natural resource agencies. We attempted to verify all capture records of the species within the contemporary and historic periods. In cases where species occurrence was not verified, and it was not clear the species had existed historically and been extirpated in the contemporary period, we considered the species occurrence as unknown and ran data analysis with the species as present and absent. For example, Bonytail *Gila elegans* have not been conclusively documented in the San Juan River even though they are thought to have occurred widely throughout the Colorado River basin historically and are listed as possibly extirpated in the NatureServe database. In some cases, we added additional species to rivers in the contemporary period that were not included in the NatureServe database when there was verified capture of the species. For example, detections of passive integrated transponder (PIT)-tagged fish in the San Rafael River indicated that several species detected in this tributary were not listed in the NatureServe database (Bottcher et al. 2013). Local capture records included multiple sampling methods, primarily electrofishing, seining, and detections of previously tagged fish by stationary tag-detection antennas. Sampling effort was unevenly distributed across all watersheds in the study area, and to help mitigate potential sampling biases, we considered a species to be present in a watershed if there was at least one recorded detection of a species any time during the 1996–2011 contemporary period. To further account for potential errors in presence–absence records, we simulated varied richness values to determine whether discharge-richness relationships were sensitive to exact richness values used (analysis described below).

Discharge data for the historic period (1957 and earlier) were available for some parameters in some HUCs from a USGS report assessing the water resources of the UCRB (Iorns et al. 1965) and in published recreations of historic discharge, which were based on correlations between the gauge of interest and an upstream or downstream gauge that was operating during the historic period (Gaeuman et al. 2005; Grams and Schmidt 2005; Manners et al. 2014). Where these sources were unavailable, we obtained discharge records for all water years (i.e., from October 1 to September 30) up to and including 1957 from the downstream-most USGS stream gauge with data available for 1957 and earlier. We also collected discharge records for the contemporary period (1996–2011) from the downstream-most USGS stream gauge with data covering the contemporary time period. In most rivers, the contemporary and historic gauge were at the same location, but in a few cases,

the contemporary gauge was located within 35 km upstream or downstream of the historic gauge (Table 2). In one case (lower Yampa River), we estimated historic discharge records at the site of the contemporary gauge (USGS gauge number 09260050) by combining discharges from an upstream gauge (USGS gauge number 09251000) and a major tributary (Little Snake River) gauge (USGS gauge number 09260000). The length of discharge records in the historic period was variable, with some records extending as far back as the late 1800s and others only extending back to the early 1950s. With this variability, there was a potential for some rivers to be biased toward drought years or wet years because the early 1900s were a wet period throughout much of the UCRB and the 1950s were a dry period (e.g., Gaeuman et al. 2005; Manners et al. 2014). To address this possible bias, we explored how excluding rivers without discharge data extending back to at least the 1920s altered discharge-native richness relationships in the historic period.

We calculated several discharge metrics using the discharge records with the goal of incorporating information on all components of the natural flow regime, including mean discharge, discharge variability, and magnitude, frequency, duration, predictability, and rate of change of flood and drought events (Supplementary Table S.1). In selecting metrics, we applied recommendations from previous analyses that assessed the ability of different metrics to capture relevant variation in discharge regimes (Olden and Poff 2003). We calculated mean annual discharge (MAQ) as the grand mean of mean daily discharge across all water years and peak annual discharge (PAQ) as the mean of the instantaneous peak discharges from each water year (highest flow in a water year regardless of timing). We also calculated the average frequency and duration of high flow events, with high flow events determined as flows above the 75th percentile of all daily flows. We assessed variability in discharge using the mean coefficient of variation of mean daily discharge (CVMAQ), the coefficient of variation of high flow events, and discharge skewness, defined as the mean annual flow over the median annual flow across all water years (Olden and Poff 2003). To assess whether low-discharge periods may limit the number of species present in a tributary, we also calculated the mean minimum annual discharge (MINQ) for each tributary and the frequency and duration of low flow spells, defined as flows below the 25th percentile of all daily flows. Timing of flow occurrence was assessed using metrics of constancy, a measure of temporal variance, and predictability (Colwell 1974), and rate of change of flows was assessed using rise rate, the mean magnitude of increase between consecutive daily flows scaled by MAQ. Many rivers in the UCRB historically had an annual PAQ associated with spring snowmelt runoff from high elevations. However, the UCRB also spans a north–south gradient in the amount of precipitation during the North American summer monsoon (Mock 1996; Higgins et al. 1997), which influences streamflow patterns, including the timing of PAQ. For example, the Escalante River is one of the southernmost watersheds in the UCRB, and PAQ occurred between July 1 and October 31 in all years but one across both the contemporary and historic periods. In contrast, PAQ occurred between March 1 and June 30 in all but 4 years (out of 31) in the Duchesne River, located in the northern portion of the study area. To capture the potential impact of PAQ timing, we calculated peak discharge for both the spring snowmelt component (instantaneous peak discharge between March 1 and June 30; PAQ_{spring}) and the monsoon component (instantaneous peak discharge between 1 July and 31 October; PAQ_{mon}). We used mean daily flows for all metric calculations,

Table 2. Mean annual discharge (MAQ) at the indicated U.S. Geological Survey (USGS) gauge for each hydrologic unit code (HUC) subwatershed and the associated river in the contemporary period (1996–2011) and a prior historic period. In some cases in the historic period, only peak flow data was available for some years. NA = not available. See Supplementary Tables S.1 and S.2 for additional discharge metrics and covariables.

HUC subwatershed	River	USGS gauge location and number	Contemporary MAQ (m³/s)	Historic MAQ (m³/s)	Range of historic period
Uncompahgre	Uncompahgre	At Delta, CO (09149500)	9.2	8.1	1903–1931, 1939–1957
Lower Gunnison	Gunnison	Near Grand Junction, CO (09152500)	65.3	73.6[a]	1914–1957
Colorado Headwaters-Plateau	Colorado	Near CO–UT state line (09163500)	169	172	1951–1957
Lower Dolores	Dolores	Near Cisco, UT (09180000)	15	26[a]	1937–1957[b]
Colorado: Westwater Canyon	Colorado	Near Cisco, UT (09180500)	179	234[a]	1914–1957
Blacks Fork	Blacks Fork	Near Little America, WY (09224700)	7.1	NA	NA
Upper Green: Flaming Gorge	Green	Near Greendale, UT (09234500)	51	67	1951–1957[c]
Little Snake	Little Snake	Near Lily, CO (09260000)	17	17	1922–1957
Lower Yampa	Yampa	At Deerlodge Park, CO (09260050)	61	59[d]	1923–1957
Lower Green: Diamond	Green	Near Jensen, UT (09261000)	115	132	1904, 1906, 1947–1957
Duchesne	Duchesne	Near Randlett, UT (09302000)	12	23[e]	1943–1957
Upper White	White	Near Meeker, CO (09304500)	17	18[a]	1914–1957
Piceance	Piceance	At White River, CO (09306222)	0.8	NA	NA
Lower White	White	Near Watson, UT (09306500)	19	21	1904–1905, 1923–1957
Willow	Willow	Near Ouray, UT (09308000)	NA	0.8	1947–1955
Price	Price	At Woodside, UT (09314500)	2.3	2.8	1909–1910, 1946–1957
Lower Green	Green	At Green River, UT (09315000)	151	180[a]	1914–1957
San Rafael	San Rafael	Near Green River, UT (09328500)	2.4	4.9	1909–1918, 1946–1957
Dirty Devil	Dirty Devil	Above Poison Spider Wash Near Hanksville, UT (09333500)	2.9	2.9	1948–1957
Escalante	Escalante	Near Escalante, UT (09337500)	0.3	0.3[a]	1943–1955
Piedra	Piedra	Near Arboles, CO (09349800)	10	9.3	1940–1957[f]
Upper San Juan	San Juan	Near Archuleta, NM (09355500)	24	39	1928–1957[g]
Animas	Animas	At Farmington, NM (09364500)	22	26	1913–1957
Middle San Juan	San Juan	At Shiprock, NM (09368000)	43	67	1928–1957
Mancos	Mancos	Near Towaoc, CO (09371000)	1.0	1.7[a]	1921–1943, 1952–1957

(continues)

except for PAQ in both the contemporary and historic periods and MINQ and seasonal PAQ metrics in the contemporary period for which we used instantaneous flows.

Similar to Pracheil et al. (2013), we identified the location of complete fish passage barriers closest to the main stem for each tributary to indicate the potential river length available to fish within the tributaries (Supplementary Table S.2). We also included barrier-free length (unimpeded length from the mouth to the first barrier) in models relating discharge to relative richness as a potential explanatory variable for tributaries that had lower

Table 2. (Continued)

HUC subwatershed	River	USGS gauge location and number	Contemporary MAQ (m³/s)	Historic MAQ (m³/s)	Range of historic period
McElmo	McElmo	Near CO-UT state line (09372000)	1.4	1.0	1952–1957
Chinle	Chinle	Near Mexican Water, AZ (09379200)	0.4	NA	NA
Lower San Juan: Four Corners	San Juan	Near Bluff, UT (09379500)	45	80.5[a]	1914–1957

[a]Directly from Iorns et al. (1965).

[b]Historic data for years 1937–1954 was from upstream gauge Dolores River at Gateway, CO (09179500).

[c]Historic peak flow data was taken from Grams and Schmidt (2005) and included years 1894–1898, 1901–1906, and 1915–1957.

[d]Historic data from Manners et al. (2014) using Yampa River near Maybell, CO (09251000) and Little Snake River near Lily, CO (09260000).

[e]Historic data for MAQ was from Gaeuman et al. (2005) and included years from 1912 to 1957.

[f]Historic data was from upstream gauge near Piedra, CO (09349500).

[g]Historic data for years 1928–1954 was from upstream gauge near Blanco Canyon (09356500).

native species richness than expected given the discharge relationships. We also identified the next complete barrier upstream of the complete barrier closest to the main stem on each tributary in order to calculate the amount of stream kilometers that could be made available by barrier removal, modification, or installation of fish passage facilities. We identified barrier locations through a combination of mapped dams and diversions available from the USGS National Hydrography Dataset and through conversations with local resource managers familiar with the structures on each tributary in relation to fish passage potential.

We also included distance of each tributary to a source population as a covariate in models relating discharge to richness for the contemporary period (Supplementary Table S.2). This metric was included because, for example, several tributary rivers (e.g., Escalante and Blacks Fork rivers) now flow into large reservoirs (e.g., Lake Powell, Flaming Gorge). While reservoirs do support populations of some native species, particularly in the main-stem inflow areas, they usually do not support all native species and often act as a significant geographic barrier to movement between tributaries. Therefore, richness could potentially be lower in these discontinuous systems due to lack of available colonists from larger main-stem rivers, relative to main-stem-connected tributaries. We determined distance to source populations as the distance through the reservoir to the nearest free-flowing section of the main-stem river, which was still connected to populations of at least six of the seven species. We chose to use distance to source populations instead of a categorical connection variable (i.e., connected or not connected) because source populations were often located upstream of the mouth of disconnected tributaries, such that fish had to swim through a reservoir but did not have to pass through a dam to reach the disconnected tributary.

Finally, we included a measure of mean August water temperature as a covariate in discharge-richness models for the contemporary period (Supplementary Table S.2). Modeled mean August temperatures were available on each study river for the period 1993–2011 (Isaak et al. 2016). Temperatures were available for 1-km segments of river, and we used the mean of all 1-km sections as our temperature metric for each river. Temperature data were not consistently available for the historic period.

STATISTICAL ANALYSIS

We analyzed relationships between relative richness and discharge variables using generalized linear models (McCullagh and Nelder 1989). All models were analyzed using the glm function in program R (R Development Core Team, Vienna, Austria). We conducted separate analyses for the historic and contemporary period, though we did compare modeled relationships between the two periods. We also conducted an analysis for the historic period in which only rivers with data extending back to the early 1900s were included to ensure our results were not biased by favoring the inclusion of rivers only gauged during drought years due to short historical records. Each of the 28 eight-digit HUCs with sufficient hydrological data were included in these analyses. We estimated relative richness as the number of species present in a HUC divided by seven, the total number of potential species. We first analyzed regression relationships between relative richness and single discharge variables. We then built nested models, akin to multiple regression (Cohen et al. 2003), by adding other discharge variables into the best-performing single metric models to determine whether combining different components of the flow regime improved model fit. When nested models significantly improved model fit, we examined the relationship between residual variance from the single-variable model and the added variable by plotting residual variance from the discharge model versus the added variable. To determine whether discharge-relative richness relationships were log-linear, as has been found for other river systems (e.g., Xenopoulos and Lodge 2006), we compared linear and log-linear model fit.

We performed an additional analysis to determine whether three environmental variables could explain some residual variance in the richness-discharge models: (1) distance to source population, (2) barrier-free length, and (3) mean August temperature. To do this, we built nested multiple regression models that included barrier-free length, distance to source population, and mean August temperature as covariables in discharge regressions. We determined whether the nested models had improved fit compared to discharge-only models. When nested models significantly improved model fit, we examined the relationship between residual variance from the discharge-only model and the added variable. We excluded the historic period and main stem HUCs from analyses of barrier-free length, distance to source population, and temperature effects because many barriers and large reservoirs did not exist in the historic period (e.g., Flaming Gorge, Lake Powell, and Navajo Lake) and modeled temperature data were unavailable for the historic period. The analysis was performed to determine whether the covariables could explain

why some tributaries had lower or higher richness than expected based on fitted discharge relationships. For example, we hypothesized that if two tributaries had equal mean discharge, richness would be lower in the tributary with lower temperature because cold temperatures may limit occurrence of warmwater desert fish species.

We compared model fit using Akaike's information criterion (AIC), which computes the goodness-of-fit of a model to a data set, with a penalty for increasing model parameters (Burnham and Anderson 2004). Using the difference between the AIC value of a given model and the model with the lowest AIC value (ΔAIC), values less than 2 indicate equally supported models (Burnham and Anderson 2004).

Given the possibility of errors in species richness values due to potential inaccuracies in the NatureServe database and potential data omissions in the literature review, we assessed sensitivity of model results to different species richness values by rerunning MAQ-relative richness models for both the historic and contemporary period with varying relative richness values. First, we reran the models, assuming that all unverified presence records were false presences (see Table 1). Second, we ran a simulation in which we added or subtracted one species to one-half of the rivers, selected randomly. The random selection was chosen by rounding random draws from a uniform distribution (−1−1) for each river to the nearest whole number (−1, 0, or 1) and adding the value to the number of species, except that rivers with seven species never had species added. We then reran the MAQ-relative richness model and determined the model *P*-value. We ran 10,000 simulations for each of the historic and contemporary periods and determined how often the *P*-value became nonsignificant.

RESULTS

All of the investigated rivers had at least two of the seven species present in the contemporary time period (*N* = 27), and no rivers added species between the historic and contemporary periods (Table 1). Flannelmouth Sucker *Catostomus latipinnis* was found in all river sections in both time periods. Of all species considered, Humpback Chub *Gila cypha* was found in the fewest river sections in both time periods.

In the historic period (*N* = 25), the model relating relative richness to MAQ had the best fit of all single variable models (lowest AIC value; Table 3). Models relating relative richness to MINQ and PAQ$_{spring}$ had similar model support (ΔAIC <2; Table 3). Higher values of MAQ, MINQ, and PAQ$_{spring}$ correlated with greater relative richness, and each relationship showed greater model fit as a log-linear relationship than as a linear relationship (all ΔAIC values comparing linear to log-linear models were >10; Figure 2). Relationships between discharge and relative richness were nearly identical whether rivers without discharge data extending back to the 1920s were included in the analysis or not (Supplementary Figure S.1).

Most multivariable models had equal or lower support compared to best-supported single variable models, and only one had an AIC value more than 2 units below the best-supported single-variable model. The exception was the model relating relative richness to MINQ and CVMAQ (Table 3). The residual plot from the MINQ and CVMAQ nested model showed that rivers with higher CVMAQ had higher richness than expected based on MINQ alone (Supplementary Figure S.2).

Models relating relative richness to MAQ, PAQ, and PAQ$_{spring}$ had the best fits of all single variable discharge models in the contemporary period (Table 4). In all cases,

Table 3. Akaike's information criterion (AIC) for log-linear relationships between flow metrics and relative richness in the historic period (Number of HUCs = 25). Only those multivariable models that were more than 2 AIC units lower than the top single-variable model are reported. Also given are AIC values for the corresponding linear relationships for single-variable models. Flow variables are mean annual discharge (MAQ), mean peak annual discharge (PAQ), mean minimum annual discharge (MINQ), mean peak annual discharge in the spring (PAQ$_{spring}$) and monsoon (PAQ$_{mon}$) periods, mean annual coefficient of variation of mean daily flows (CVMAQ), mean annual discharge scaled by the median annual discharge (Skewness), discharge predictability and constancy (see Colwell 1974), average rate of positive changes between mean daily discharges scaled my the mean annual discharge (rise rate), frequency of discharge events below the 25th percentile of mean daily discharges (FL1), frequency of discharge events above the 75th percentile of mean daily discharges (FH9), average duration of low discharge events (DL16), average duration of high discharge events (DH15), and the coefficient of variation in duration of high discharge events (DH16).

Model	AIC	Linear AIC
MAQ	−29.22	−16.16
PAQ	−26.73	−15.94
MINQ	−29.11	−12.91
PAQ$_{spring}$	−28.25	−16.90
PAQ$_{mon}$	−18.05	−11.85
CVMAQ	−6.49	−5.82
Skewness	−4.33	−4.08
Predictability	−9.99	−10.45
Rise rate	−17.41	−13.67
Constancy	−9.64	−8.95
FL1	−4.18	−4.16
FH9	−11.36	−9.49
DL16	−4.24	−4.34
DH15	−11.23	−12.07
DH16	−9.58	−9.68
MINQ + CVMAQ	−31.35	NA

log-linear relationships had lower AIC scores than linear relationships, but both received nearly equal support (all ΔAIC values comparing linear to log-linear models were <2; Figure 2). Relationship trends were the same as in the historic period, with relative richness increasing with increasing discharge metrics. No multivariable discharge models had AIC values less than 2 compared to the best-supported single variable model for the contemporary period.

The log-linear relationships between MAQ and relative richness were robust to potential errors in species presence–absence values. Eight tributaries of 25 in the historic analysis and 2 tributaries of 27 in the contemporary analysis had at least one unverified presence value (Table 1). The relationships remained significant in both periods when all unverified presence records were marked as absences. In addition, the historic log-linear relationship was significant in 100% of simulations adding or subtracting one species from half of the randomly selected rivers. The contemporary log-linear relationship was only nonsignificant in 0.06% of simulations.

Including temperature improved model fit in the contemporary MAQ-relative richness model (Table 4). Plotting residuals from the MAQ-relative richness relationship against temperature suggested that warmer rivers tended to have more species than expected based on MAQ alone (Supplementary
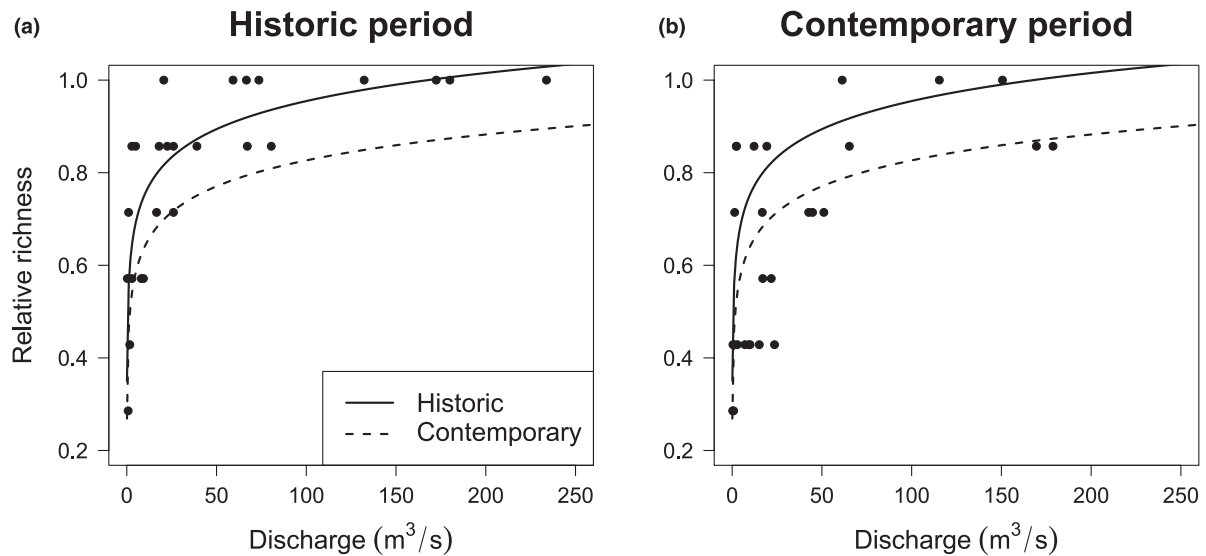
Figure 2. Relationship between mean annual discharge (MAQ) and relative richness for both the **(a)** historic and **(b)** contemporary periods. Both historic (*N* = 25) and contemporary (*N* = 27) log-linear model fits are plotted in each frame for comparison.

Table 4. Akaike's information criterion (AIC) for log-linear relationships between flow metrics, temperature, and relative richness in the contemporary period (Number of HUCs = 27). No multivariable models were more than 2 AIC units lower than the top single-variable model. Also given are AIC values for the corresponding linear relationships. Flow variables are mean annual discharge (MAQ), mean peak annual discharge (PAQ), mean minimum annual discharge (MINQ), mean peak annual discharge in the spring (PAQ_{spring}) and monsoon (PAQ_{mon}) periods, and mean annual coefficient of variation of mean daily flows (CVMAQ), mean annual discharge scaled by the median annual discharge (Skewness), discharge predictability and constancy (see Colwell 1974), average rate of positive changes between mean daily discharges scaled my the mean annual discharge (rise rate), frequency of discharge events below the 25th percentile of mean daily discharges (FL1), frequency of discharge events above the 75th percentile of mean daily discharges (FH9), average duration of low discharge events (DL16), average duration of high discharge events (DH15), and the coefficient of variation in duration of high discharge events (DH16).

Model	AIC	Linear AIC
MAQ	−16.47	−14.52
PAQ	−16.25	−14.53
MINQ	−10.86	−10.00
PAQ_{spring}	−17.02	−16.34
PAQ_{mon}	−11.2	−7.48
CVMAQ	−5.47	−4.28
Skewness	−1.41	−1.79
Predictability	−1.95	−2.07
Rise rate	−6.22	−4.59
Constancy	−1.61	−1.42
FL1	−0.92	−0.85
FH9	−6.43	−6.07
DL16	−0.95	−1.13
DH15	−6.60	−6.52
DH16	−2.05	−1.81
Temperature	−5.54	−5.19
MAQ + Temperature	−20.09	

Figure S.3). Including distance to source population also improved model fit, though not significantly (∆AIC = 1.3). Of the four tributaries that joined main-stem rivers in reservoirs (Blacks Fork, Piedra, Dirty Devil, and Escalante rivers), three had lower richness than predicted based on the fitted MAQ-relative richness model (the Escalante River was the exception). All tributaries had at least 15 km of fish-passable connection to their associated main-stem rivers, and most had more than 50 km (Supplementary Table S.2). Providing fish passage on the first barriers on most tributaries would provide additional access to substantial amounts of potentially suitable habitat (assuming other factors are not limiting) with several tributaries, including the White River and the San Rafael River having more than 100 km of unobstructed river length above the downstream-most barrier. However, including barrier-free length in models relating MAQ to relative richness of tributary systems did not improve model fit.

When discharge metrics were compared between the historic and contemporary periods, the general pattern was a decline in MAQ (17 out of 24 HUCs with both historical and contemporary discharge), a decline in PAQ (21 out of 24), a decline in CVMAQ (23 out of 24), and an increase in MINQ (16 out of 24). The MAQ-species-richness relationship in the contemporary period showed a lower maximum richness compared to the historic period (i.e., lower richness at high MAQ values (Figure 2).

DISCUSSION

Our analyses show that simple discharge metrics provide an initial estimate of the species conservation potential of rivers throughout the UCRB. Combined with a more detailed assessment of other limiting factors such as habitat availability, water quality, and nonnative fish impacts, the results can potentially be used to help prioritize management across the river network. Successful conservation of fish diversity will likely require a watershed approach that considers the full river network (Saunders et al. 2002) because many fish species move between large rivers and smaller tributaries as part of their

life history (Fausch et al. 2002). Recent work has highlighted the importance of river systems throughout a species range, which collectively contribute to overall life-history diversity of fish stocks (Hilborn et al. 2003; Schindler et al. 2010). Furthermore, tributaries in the network with lower nonnative fish richness or abundance, with limited water development, or with more natural flow and temperature regimes can provide unique ecological settings compared to large regulated rivers (Pracheil et al. 2009; Sabo et al. 2012). In the UCRB, direct tracking of fish movement has provided evidence of the extensive use of tributaries by native fishes, including ESA-listed species (Bottcher et al. 2013; Cathcart et al. 2015; Fraser et al. 2017). Large main-stem rivers often provide permanent refuge habitat and a source of colonists to smaller tributary rivers, which may dry completely during drought events (Magoulick and Kobza 2003). Given these observations, and the analysis presented here, it is clear that opportunities to enhance native fish conservation can be found throughout the UCRB.

We base our analyses on previous work in the Mississippi River system, where a strong threshold response of native species richness to MAQ was used to identify tributary rivers with high conservation potential (Pracheil et al. 2013). In the Mississippi River system, tributaries above a discharge threshold of 166 m³/s MAQ, harbored most or all of the main-stem river species. In the UCRB, in the period before major dam construction, we found a similar, albeit weaker, relationship, with relative richness showing a positive log-linear relationship to MAQ, MINQ, and PAQ$_{spring}$. Including CVMAQ improved the MINQ model fit, and rivers with higher CVMAQ had higher species richness than predicted from MINQ alone. As we discuss below, the log-linear discharge-richness relationships can help identify tributaries with particularly high conservation potential and can therefore supplement previous efforts to prioritize management activities across the UCRB.

As with the Mississippi River system, tributaries in the UCRB with discharge levels much less than the main-stem rivers can still hold nearly an equal amount of fish species richness as the main-stem rivers. Based on the approximate inflection point of the historic discharge-richness relationship, tributaries that exceed a MAQ of 25 m³/s can potentially provide habitat for at least six species, if other factors are not limiting. Even tributaries at the low end of the discharge range investigated here offer a substantial opportunity for conserving native fish species richness. Based on the historic flow-richness relationship, tributaries that exceed a MAQ of as little as 0.6 m³/s are likely to provide habitat for more than half of the native species included in the analysis. In the UCRB, these smaller isolated tributaries offer unique management opportunities, as many have limited angling or other recreational use and thus could potentially be managed exclusively for native fishes (Clarkson et al. 2005). We are not suggesting that conservation efforts on tributaries come at the expense of main-stem conservation efforts. Rather, this analysis reaffirms that conservation efforts in large rivers can be enhanced by undertaking management activities in smaller, connected tributary systems.

Several data issues could cause the parameters of the flow-richness relationships to change. For one, sampling effort for local occurrence records was uneven between watersheds because we opportunistically used available data from resource agencies and published studies. However, sampling effort bias would likely make the relationships presented here conservative in terms of identifying the species richness potential of smaller rivers because species richness could only increase

with additional sampling effort and many of the largest rivers already had all seven species present. We also found that the shape of discharge-richness relationships was robust to some uncertainty in species richness data. The limited amount of discharge data in the historic period for some rivers could also have affected parameter estimates; however, the general log-normal form of the relationships is unlikely to change because errors in discharge estimates for one river are likely to be low compared to the full range of discharge across all rivers in the analysis.

The relatively strong relationship between basic discharge metrics and relative native species richness, in addition to other relationships presented here, can help supplement previous efforts to prioritize native fish management efforts throughout rivers in the UCRB (Tyus and Saunders 2001; Xenopoulos and Lodge 2006). A previous assessment of the role of tributaries in endangered species recovery in the UCRB emphasized the importance of rivers with natural hydrographs, high contributions of sediment, and high annual, base, and peak flows relative to the main-stem Colorado and Green rivers (Tyus and Saunders 2001). The log-linear relationship between discharge metrics and native fish richness presented here supports the previous assessment but also suggests that rivers with much lower mean discharge than the largest main-stem rivers hold substantial conservation value when considering overall native species richness. In the contemporary time period, we found that several tributaries connected to reservoirs had lower species richness than tributaries with similar MAQ but connected to free-flowing sections of main-stem rivers. In addition, as modeled river temperature increased from 15°C to greater than 20°C, rivers were more likely to have higher richness than predicted by MAQ alone, a result consistent with the fact that all seven species except the Bluehead Sucker *Catostomus discobolus* are considered to have warm water (>26°C) temperature preference (Olden et al. 2006). Together, these observations suggest an initial framework for identifying high-priority rivers for native fish species conservation in addition to those identified in endangered species recovery efforts. High-priority rivers would be those with MAQ above 0.6 m³/s, connected to free-flowing main stems, and in the warmer end of the temperature range investigated (>19°C). McElmo Creek and the San Rafael, Dolores, Price, and White rivers stand out as high-priority tributaries using these criteria. Barrier removal or modification projects on such high-priority tributaries are likely to offer substantial benefits for native fish conservation. For example, the amount of connected habitat on the San Rafael River would increase by at least threefold if passage were provided on the downstream-most barrier, although habitat suitability and tradeoffs regarding providing passage to nonnative species would need to be considered to fully evaluate the potential benefits (Fausch et al. 2009; Walsworth et al. 2013). Furthermore, efforts to provide flow augmentation in high-priority rivers that have shown declines in MAQ, minimum flows, or peak flows from the historic period would likely yield important benefits for native fish conservation, as emphasized previously (Tyus and Saunders 2001).

The use of discharge metrics to gauge the conservation potential of tributaries is only a first step in prioritizing management actions across the UCRB because other factors influence the occurrence of species in any particular river. The presence of dams and their impacts on flow variability, temperature regimes, and fish movement could limit the conservation potential of particular streams (Baxter 1977; Olden and

Naiman 2010). Indeed, many rivers with lower than expected richness values based on MAQ were isolated by movement barriers from other rivers in the basin, particularly the San Juan River, which has previously been fragmented by diversion dams (many have subsequently been retrofitted for fish passage) and is currently fragmented by an impassible waterfall near its inflow to Lake Powell. We also found that rivers with higher variability in mean discharge tended to support greater species richness than rivers with equivalent minimum flows, but lower discharge variability, suggesting dams and other river regulations that reduce discharge variability, may limit native species occurrence. A flow variability–native fish link is consistent with literature on desert rivers, in which variable flows often benefit native fish, in part by eliminating or reducing establishment of nonnative fish (e.g., Meffe 1984; Eby et al. 2003).

Although we did not include nonnative fish species as a potential explanatory factor for native richness in our analysis, this does not imply that nonnative species have little impact on native species. Indeed, nonnative species are known to be one of the major limiting factors for native species persistence in the Colorado River basin (Minckley 1991). Although we found strong relationships between discharge and native richness without including nonnative species, the result may be an issue of scale. Native and nonnative species may coexist at the scale of watersheds examined here, but nonnative species could still prevent native species from occupying preferred habitat at the reach or habitat unit scale (e.g., pool, riffle). In addition, nonnative species could potentially explain much of the residual variance in the discharge-richness models. We explored the potential for including nonnative fish abundance data as covariates in the current analysis; however, data on nonnative abundances are not always reported and different sampling methods across rivers of different sizes make abundance comparisons difficult. Coordinated efforts across the UCRB to collect comparable spatial data on nonnative fish richness and abundance could greatly help identify priority rivers for conservation and management action across the watershed.

Watershed land use and regional climatic patterns have also been linked to fish community composition in the lower Colorado River (Pool et al. 2010) and, in addition to discharge, could limit occurrence of some species. For example, natural and anthropogenic hydrologic alteration, combined with nonnative vegetation encroachment, has altered the size, shape, and habitat complexity of rivers throughout the UCRB (Birkeland 2002; Gaeuman et al. 2005; Manners et al. 2014), and habitat availability may be limiting in some rivers. In addition, municipal and agricultural wastewater can interact with geologic formations to raise metal and salt levels, such that water quality impacts may be a limiting factor in some tributaries in the UCRB (Tyus and Saunders 2001).

The relationships presented here can help identify where additional limiting factors should be investigated because they provide an assessment of whether individual rivers have higher or lower richness than expected, based on simple discharge metrics. Moreover, the fact that many tributaries support high native species richness despite extensive alteration to habitat and water quality from dams, land use, and nonnative species highlights the importance of including these rivers in native fish conservation efforts.

Conserving individual species is likely to require a life-history approach that accounts for reproductive, growth, and migration needs of each species (Pool et al. 2010). Discharge metrics such as frequency and duration of low and high discharge events may be more useful than mean annual metrics under a life-history approach because they capture more detailed aspects of discharge patterns to which native species' life-history patterns have evolved (Deacon and Minckley 1974). Indeed, native fish may benefit from low predictability disturbance events such as flash flooding because native fish have evolved behavioral patterns to survive these intense floods, whereas nonnative fish may experience population declines (Meffe 1984). However, an important aspect of a life-history approach is to understand how fish use different rivers throughout large basins to complete their life history (Pool et al. 2010). It is well documented that native species such as Roundtail Chub *Gila robusta*, Flannelmouth Sucker, and Bluehead Sucker use tributaries extensively (Fraser et al. 2017) and several endangered species use tributaries at least seasonally (Holden and Stalnaker 1975; Bottcher et al. 2013; Cathcart et al. 2015). Although mean annual discharge metrics are relatively coarse measures of discharge patterns, their ability to explain a relatively high proportion of variation in native species richness across the UCRB likely reflects the importance of both main-stem rivers and tributaries in the life history of native fishes. Annual metrics may be particularly useful for predicting the occurrence of species analyzed here because they are all relatively long-lived and have adapted to survive through periods of harsh conditions such as low water levels and flash floods. By demonstrating the strong relationship between discharge and species richness, the analysis presented here reinforces that rivers throughout the UCRB have great conservation potential and that native fish conservation can be enhanced by coupling efforts in main-stem rivers to available opportunities in smaller tributaries.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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