

MANAGEMENT BRIEF

A Tribute to Tributaries: Endangered Fish Distributions within Critical Habitat of the San Juan River, USA

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Abstract

The extent of fish movements in contemporary river networks can depend on spatial position relative to attractive features that may provide food and refuge, such as tributary mouths, or restrictive features, such as barriers. From the San Juan River basin in New Mexico and Utah, we integrated remote summertime PIT tag detections at two tributary mouths (McElmo Creek and Chaco Wash) with main-stem recapture data from 2012 to 2015 to determine if two endangered species, Colorado Pikeminnow *Ptychocheilus lucius* and Razorback Sucker *Xyrauchen texanus*, differed in tributary use, demography, and seasonal ranges. Razorback Suckers were more abundantly detected ($n = 266$ individuals) and recaptured ($n = 145$) than were Colorado Pikeminnows ($n = 96$ detected; $n = 55$ recaptured). Despite the San Juan River flowing uninterrupted between the tributary mouths, individuals of each species separated into tributary-specific groups. Razorback Suckers had very similar sizes and ages at each tributary, reflecting a homogeneous augmented population. Colorado Pikeminnows separated into tributary-specific groups of either adult (Chaco Wash) or subadult (McElmo Creek) fish based on total length and age. Analyses suggested that fish size was a significant factor explaining the extent of seasonal ranges for both species. Although the

ranges of both species exhibited a tributary effect, this effect was more significant in explaining Razorback Sucker ranges than Colorado Pikeminnow ranges, which were explained best by season. Understanding how mobile species interact with attractive and inhibitive river features can help managers identify potential sampling biases along with possible consequences of spatially structured populations. Managers should consider extending sampling upstream of barriers, installing additional permanent antenna arrays, and maintaining perennial flows in these tributaries.

Understanding the spatial extent of freshwater fish movements has captivated ecologists, guided management, and challenged our perception of how fish use a defined area (Cooke et al. 2013). Within a species' home range, defined by Gerking (1959) as the area in which a species normally travels, riverine fishes often need multiple different habitats to fulfill their needs, and these habitats may be scattered across the landscape, necessitating movement (Schlosser 1991). Home ranges may change as fish mature and habitats change. Monitoring the use of multiple

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habitat types by multiple life stages—often across broad spatial scales—can more accurately portray population-wide movement patterns or define them within seasonal bounds (Fausch et al. 2002).

To many fish biologists, river networks are managed as multiresource waterbodies that provide human needs (i.e., municipal water, irrigation) and fish habitat (Koster and Crook 2017; Pennock et al. 2018). To fish, a contemporary river network may present natural or artificial features that restrict movements along with features that attract them. Waterfalls, dams, and diversions are widespread in North American streams and often restrict fish movements that would be advantageous for specific life history or population functions, such as outmigration to downstream rearing habitats or upstream migrations that counter egg or larval drift (Marschall et al. 2011; Perkin and Gido 2011; Perkin et al. 2015). Attractive features, such as tributary confluences, can also structure the distribution, diversity, and abundance of fish in a river network depending on species, body size, and life history (Osborne and Wiley 1992). Choosing locations attractive to fish within a river network can be advantageous for fish biologists to better capture broadscale movement patterns and define seasonal ranges of fishes (Webber et al. 2012; Bottcher et al. 2013).

The Colorado River basin is a large river network altered by dams, diversions, native fish eradication, and establishment of nonnative species (Minckley and Deacon 1968). These factors contributed to the listing of several native fishes and have resulted in decades of adaptive management that seeks to maintain endemic, large-river, large-bodied, long-lived, and mobile fishes, such as the federally endangered Colorado Pikeminnow *Ptychocheilus lucius* and Razorback Sucker *Xyrauchen texanus* (Minckley and Deacon 1968). Although larger tributaries, such as the White River in the upper Colorado River basin, have been demonstrated to support spawning and use by endangered fishes tagged in main-stem rivers, small tributaries and their confluences may also offer important habitats for the conservation of endemic and imperiled fishes (Webber et al. 2013). For example, small tributaries in the Colorado River basin retain larvae (Haynes et al. 1984), offer productive subadult growth (Webber et al. 2012), connect habitats for spawning migrations (Weiss et al. 1998), and provide refugia or foraging outside of main-stem environments (Cathcart et al. 2018a). While tributary systems are recognized as crucial habitats for native desert fishes (Fraser et al. 2017; Laub et al. 2018; Hooley-Underwood et al. 2019), most studies do not explore how small tributaries may affect main-stem distributions of fishes. This perspective is important because tributary systems and their junctions with main-stem rivers impart strong ecological forces that spatially structure fish populations (Fernandes et al. 2004; Lopes et al. 2019), communities (Osborne and Wiley 1992), and geomorphological processes

throughout river networks (Benda et al. 2004; Kiffney et al. 2006).

Fish tagged with transmitting tags allow biologists to track them through various habitat types (Durst and Franssen 2014; Cathcart et al. 2018a). However, different tracking methods present trade-offs to managers and researchers in that active tracking of tagged fish can cover an expansive area that requires greater effort, whereas remote monitoring may be continuous and less human intensive but usually lacks extensive spatial coverage (Cooke et al. 2013). One way to mitigate the shortcomings of one monitoring method is to combine active and passive monitoring methods. For example, remote passive detection can be combined with active physical captures to more accurately investigate the interactions among movement or habitat use and demography (Webber and Beers 2014).

We integrated these concepts, river features, and tools to study Razorback Sucker and Colorado Pikeminnow populations from a tributary-mouth perspective within their critical habitat of the San Juan River, a major tributary to the Colorado River. Our main objectives were to delineate seasonal ranges and to understand the spatial structure of endangered fishes by linking tag detection data from two contrasting tributaries to physical recapture events in the main-stem San Juan River. We hypothesized that tributaries would share individuals of each species with similar traits because Razorback Suckers and Colorado Pikeminnows have been heavily augmented by stocking in the San Juan River, the main-stem San Juan River is unfragmented between the tributary mouths, and both species have exhibited long-distance movements that can exceed 100 km (Tyus and McAda 1984; Tyus and Karp 1990; Durst and Franssen 2014; Cathcart et al. 2018b).

METHODS

Study area.—As a major tributary to the Colorado River, the San Juan River flows through Colorado, New Mexico, Arizona, and Utah, where it meets Lake Powell 365 km downstream of Navajo Dam (Figure 1). Recently, an upstream barrier in the form of the Piute Farms Waterfall (hereafter referred to as the waterfall) has formed since the late 1980s (Ryden and Ahlm 1996; Franssen and Durst 2013). Critical habitat for the endangered fishes in the San Juan River begins ~22 km upstream of the Public Service Company of New Mexico (PNM) weir for Colorado Pikeminnow at the mouth of the Animas River (339 km total) or at the Hogback Diversion for Razorback Sucker (305 km total) and extends about 48 km downstream of the waterfall in an area still partially inundated by Lake Powell. Besides the Animas River (mean annual flow > 20 m³/s), there are five small tributaries (mean wetted widths < 10 m, mean annual

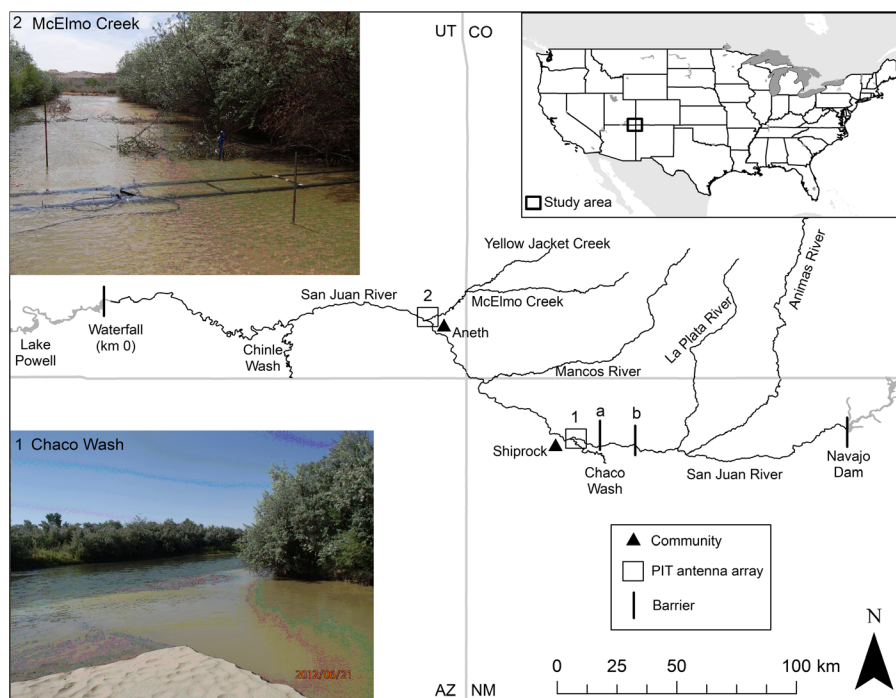


FIGURE 1. Locations of PIT antenna arrays used in Chaco Wash and McElmo Creek relative to notable features within the San Juan River drainage, such as barriers. The locations of Hogback Diversion (a) and the Public Service Company of New Mexico weir (b) are also shown. Numbers at PIT antenna arrays correspond to pictures of each tributary mouth from 2012.

flows $< 1.42 \text{ m}^3/\text{s}$) to the San Juan River downstream of Navajo Dam, two of which provide $> 100 \text{ m}$ of perennial habitat upstream from the main-stem San Juan River: McElmo Creek and Chaco Wash (Figure 1).

Chaco Wash (drainage area = $11,396 \text{ km}^2$, confluence location = 244 km upstream of the waterfall) is an intermittent stream yet perennially large backwater in northwestern New Mexico near Shiprock, New Mexico. McElmo Creek drains an area of $1,818 \text{ km}^2$ in Colorado and Utah and joins the San Juan River 163 km upstream of the waterfall near Aneth, Utah (Cathcart et al. 2015). The tributary confluences are separated by 81 km of the San Juan River. Common land uses in the drainages include livestock ranching, agriculture, coal power generation (Chaco Wash), and fossil fuel extraction (McElmo Creek). Fish predators, such as river otters *Lontra canadensis*, were observed at Chaco Wash (2012, 2013, and 2015), and great blue herons *Ardea herodias* were observed at both tributary mouths across all years. Riparian zones are dominated by nonnative Russian olive *Elaeagnus angustifolia*, with native eastern cottonwood *Populus deltoides* being rare.

Chaco Wash and McElmo Creek both have perennial tributary connections with the San Juan River, but they offer contrasting confluence morphology, flow regimes, and spatial position that may affect fish occurrence and movement (Cathcart et al. 2015; Jones and Schmidt 2017). Chaco Wash has a short overall length of perennial

stream habitat ($< 2 \text{ km}$), notably the confluence backwater that extends $> 600 \text{ m}$, whereas McElmo Creek has much greater perennial stream habitat ($> 50 \text{ km}$ of connected stream), with flows enhanced by transbasin diversions for irrigation. Water velocity is five-fold faster at McElmo Creek (0.551 m/s) compared with the backwater-like flow at Chaco Wash (summer time water velocity $\sim 0.1 \text{ m/s}$). Thus, substrates are finer (e.g., deep silt-covered bedrock) at Chaco Wash compared with more coarse sands and gravel at McElmo Creek. The average wetted widths are similar between Chaco Wash and McElmo Creek, but the mouth of Chaco Wash averages over twice as deep ($\sim 50 \text{ cm}$) as the mouth of McElmo Creek ($\sim 20 \text{ cm}$). Maximum depths exceeded a meter at the mouth of Chaco Wash, whereas they rarely surpassed 40 cm in McElmo Creek. Secchi disk depths measured in low-flow periods at Chaco Wash ($< 10 \text{ cm}$) were considerably less than those in McElmo Creek, which exceeded 30 cm (C. N. Cathcart, unpublished data). Chaco Wash enters the San Juan River in an area with backwater habitats prevalent for about 10 km immediately adjacent to its mouth in either direction compared with McElmo Creek, where larger backwater habitats are farther away ($> 8 \text{ km}$). McElmo Creek enters a reach of the San Juan River that has faster water velocity compared with where Chaco Wash enters.

PIT antennas and tagging.—Continuously operating PIT antenna systems collected our data by recording tag

identification with date and time of detection. To passively monitor seasonal occurrence of endangered fishes at Chaco Wash, we deployed a self-contained submersible PIT antenna overnight in 2012 (August 7–8), for 31 d in 2013 (June 16 to July 17), and for 16 d in 2015 (July 12–28). In 2012 and 2013, the system comprised a rectangular PIT antenna system (3.05×0.76 m) installed in a “swim-through” fashion whereby the antenna was positioned vertically in the water column (with the top of the antenna at the water surface) and perpendicular to the riverbank with block nets on either side to funnel fish through the antenna. In 2015, we used a circular PIT antenna (~1 m in diameter) that rested on the streambed at the same location as in 2012 and 2013 but with no block nets. The McElmo Creek antenna array was installed approximately 150 m upstream from the confluence with the San Juan River in May 2012 and ran continuously throughout the project. This array involved five antennas fastened to the streambed that spanned the width of the stream in two rows (Cathcart et al. 2018a).

Endangered fish were PIT tagged (12-mm full-duplex, 134.2 kHz; Biomark, Boise, Idaho) as part of both ongoing research and monitoring efforts funded through the San Juan River Basin Recovery and Implementation Program. We linked detection data to tag records in the Species Tagging, Research and Monitoring System (STRaMS), hereafter referred to as “the database,” to identify individuals. Generally, Razorback Suckers were already PIT tagged prior to stocking and were >350 mm TL, whereas Colorado Pikeminnows are stocked as juveniles (<100 mm TL) and PIT tagged at first capture by main-stem San Juan River monitoring efforts (STRaMS 2017) and occasionally from tributary sampling (Cathcart et al. 2015). From 2000 through 2015, more than 140,000 PIT-tagged Razorback Suckers were entered into the database following either stocking or recapture events of tagged fish from about the mouth of the Animas River to Lake Powell (Furr 2016; STRaMS 2017). Since 2007, over two million age-0 or age-1 Colorado Pikeminnows have been stocked from the mouth of the Animas River to Lake Powell, contributing to >50,000 Colorado Pikeminnow tag records in the database (Furr 2016; STRaMS 2017). Participating organizations annually updated the database with new capture, tagging, or detection records from throughout the San Juan River and upper Colorado River basins.

Data analysis.—Analyses relied on tag detection and physical recapture data. To compare McElmo Creek tag detection data with those from the Chaco Wash antennas, we used seasonal (summer) tag detections from June, July, and August in 2012, 2013, 2014 (McElmo Creek only), and 2015. For each tag detected by our PIT antennas, we queried the STRaMS database for main-stem recaptures and the associated demographic data. These values

included total length at recent recapture (only fish recaptured during the study period were analyzed further), stocking or tagging year (i.e., age to determine potential maturity), and number of recapture encounters. Individual fish data were pooled across all years for analyses. Individual tags could be detected across numerous years, but for our analyses only one detection at a tributary was needed to assign it to a tributary group. Main-stem recapture events were compiled with data from annual large-bodied fish monitoring and nonnative fish removal efforts by Utah Division of Wildlife Resources and the U.S. Fish and Wildlife Service using single-pass raft electrofishing (Smith-Root 5.0 GPP) from March through October. These events occurred within a 261 km reach from the PNM weir 266 km upstream (or 25 km upstream of Chaco Wash) to a boat landing 5 km upstream from the waterfall (158 km downstream of McElmo Creek).

Demographic analyses used detections to assign fish to tributaries and then used all recapture records. We performed one-way ANOVAs to test differences in total length at last recapture and total length at first capture or stocking. For other variables where we violated assumptions of normality based on a Pearson's correlation test, we used a nonparametric Kruskal–Wallis ANOVA test for independence among species groups in the number of recaptures, month of first encounter (Colorado Pikeminnow only), month of last recapture (both species), and year-classes.

Range analyses also used tributary tag detections to assign a tributary for individual fish. Then, these summer-time-detected fish were linked to the most recent recapture location (if present) separated by season (summer versus nonsummer captures) that allowed us to explore their seasonal ranges relative to their tributary of detection. Recaptured fish were pooled into two seasons whereby “summer” events mirrored antenna sampling (June, July, and August) and any recaptured fish from outside these months were classified into “nonsummer.” Individual fish could potentially be recaptured multiple times in a season or both seasons during this study, but we restricted our range analyses to the distance between a tributary at which a fish was detected and their most recent recapture. This means individuals could have both summer and nonsummer captures, but the most recent capture would void the other one (and the other season) to prevent pseudoreplication of individuals in analyses. Lastly, we compared tag detection history from both tributaries to identify any overlapping tag detections that would indicate expansive travels through the San Juan River to access multiple small tributaries. Direction of seasonal ranges (upstream versus downstream), distances from tributary mouths, and seasonal ranges based on total fish length were compiled. We used multiple linear regression to test how distance away (range) from the tributary of detection was affected by total length (continuous variable), season

(categorical; summer or nonsummer), tributary (categorical; Chaco Wash or McElmo Creek), and their interactions at a level of significance of $\alpha = 0.05$. Then, we performed ANCOVA to test whether total length covaried with stream and season.

RESULTS

In total, we detected 362 unique individuals between the two tributary antenna arrays, with 203 of those fish having recapture histories that could be linked to a season or both seasons (Table 1). At Chaco Wash, we identified tags from 205 unique endangered fish. Unique fish detected at Chaco Wash comprised 154 Razorback Suckers and 51 Colorado Pikeminnows. Of these, 83 Razorback Suckers and 35 Colorado Pikeminnows were recaptured between 2012 and 2015. Unique fish detected at McElmo Creek comprised 112 Razorback Suckers and 46 Colorado Pikeminnows. Of these, 20 Colorado Pikeminnows and 62 Razorback Suckers were recaptured between 2012 and 2015. Two Colorado Pikeminnows were detected at both Chaco Wash and McElmo Creek antenna systems. One was detected in July 2012 at McElmo Creek, then in July 2013 at Chaco Wash, and had a recapture event in March 2009 at river kilometer 29 of the San Juan River (measuring from the waterfall downstream near Lake Powell at river kilometer 0). The other one was detected at McElmo Creek in November 2014 and then at Chaco Wash in July 2015 but was recaptured between those detections in March 2015 at river kilometer 77 of the San Juan River. Due to the infrequency of this multitributary movement type in the data, both were removed from further analyses. No Razorback Suckers were detected at both tributaries. Only fish with both detection and recapture events were used in further analyses.

Endangered fish exhibited contrasting demographics between tributaries. Colorado Pikeminnows detected at

Chaco Wash were recaptured more in addition to being significantly larger and older than those detected at McElmo Creek according to total length and tagging year (Figure 2). Conversely, Razorback Suckers demonstrated no significant differences in total length, age, or number of recaptures between the two tributaries. Seasonal ranges varied between and within species depending on direction, extent, season, and tributary (Table 1). Seasonal ranges of Razorback Suckers showed greater upstream distances from McElmo Creek compared with those from Chaco Wash (Figure 3). Chaco Wash had a much higher frequency of Razorback Suckers that had a limited range (<5 km) based on all recapture seasons compared with McElmo Creek.

Colorado Pikeminnows exhibited similar patterns of a greater upstream end of ranges by McElmo Creek fish compared with those from Chaco Wash. They also had more distinct downstream-directed ranges in the nonsummer compared with summer (Figure 4). From visualizing linear regression of ranges plotted against total length, tributary effects by season were apparent (Figure 5). There were three notable instances where total length was an important explanatory variable. First, Colorado Pikeminnows detected at McElmo Creek and recaptured in the summer showed that larger fish had ranges farther upstream than smaller fish. Second, Colorado Pikeminnows detected at Chaco Wash and recaptured in the nonsummer season showed a pattern of smaller fish with ranges far downstream compared with larger fish that maintained positions closer to the mouth. Third, Razorback Suckers detected at McElmo Creek and recaptured in the nonsummer showed that smaller fish had ranges farther upstream than larger individuals that stayed near the mouth. Otherwise, Razorback Sucker ranges were not well explained by total length—especially at Chaco Wash where they exhibited limited ranges across both seasons.

TABLE 1. Descriptive statistics of PIT-tagged endangered fish detected by PIT antennas at McElmo Creek or Chaco Wash and recaptured in the San Juan River between 2012 and 2015. Season codes include S (summer; June, July, and August) and NS (nonsummer). Downstream (%) indicates the percentage of detected fish seasonally recaptured downstream of the tributary they were detected at.

Species	Tributary	Season	<i>n</i>	Distance from mouth (km)		Downstream (%)	Total length (mm)	
				Mean	Range		Mean	Range
Colorado Pikeminnow	Chaco	NS	15	-30	-167 to +6	80	481	162-695
	Chaco	S	20	-2	-63 to +24	40	464	264-712
	McElmo	NS	12	-30	-120 to +61	67	297	193-540
	McElmo	S	6	29	-13 to +80	33	314	193-383
Razorback Sucker	Chaco	NS	38	-2	-25 to +10	79	473	348-545
	Chaco	S	45	-2	-51 to +6	69	448	353-570
	McElmo	NS	31	14	-36 to +101	55	453	347-555
	McElmo	S	31	5	-34 to +87	58	463	370-526

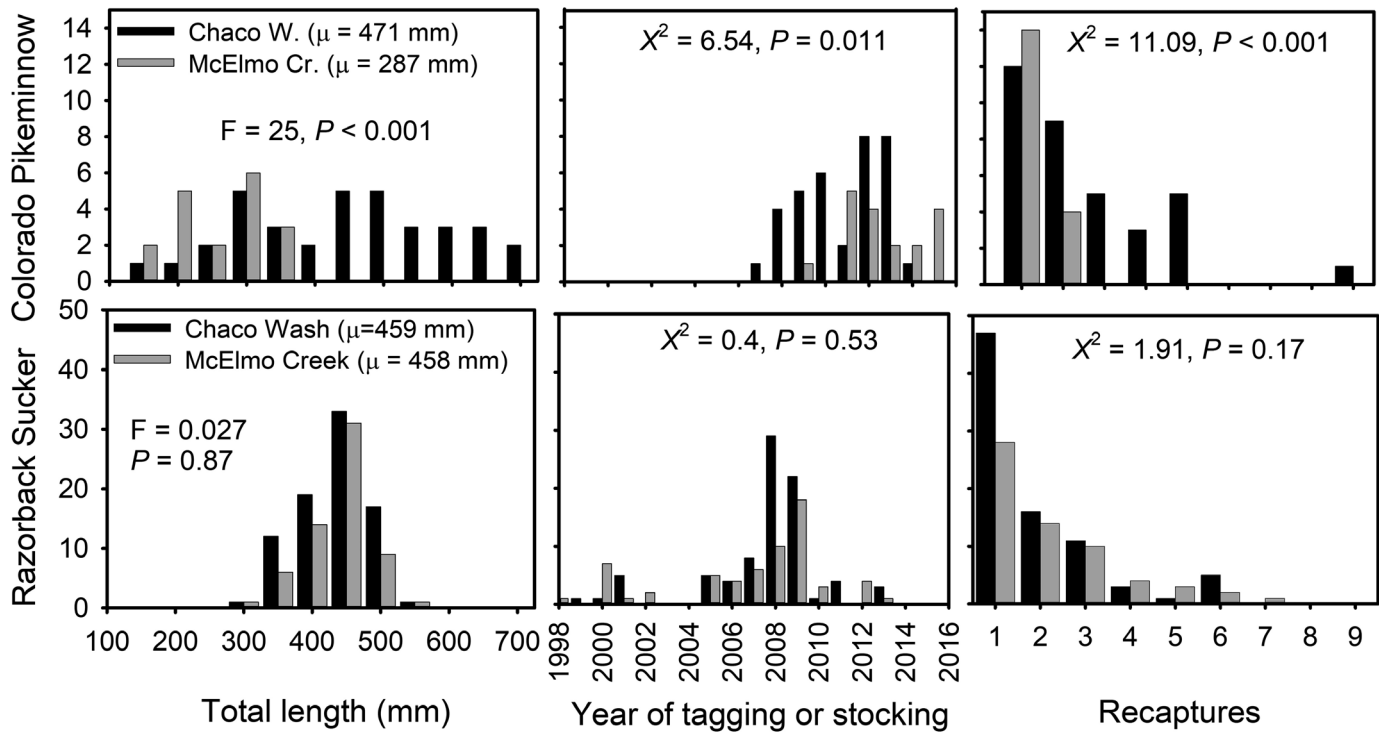


FIGURE 2. Total lengths at last recapture, year of tagging (Colorado Pikeminnow) or stocking year-class (Razorback Sucker), and number of recaptures for groups of PIT-tagged endangered fish detected by PIT antennas at Chaco Wash or McElmo Creek and recaptured between 2012 and 2015. At $\alpha=0.05$, differences in total lengths were tested with ANOVAs, while differences in tag year and recaptures were tested with Kruskal–Wallis ANOVAs.

Statistical analyses identified significant factors and interactions explaining main-stem San Juan River seasonal ranges of endangered fishes detected in tributaries (Table 2). In the multiple regression model, there was a significant relationship between Razorback Sucker ranges and the tributary from where it was detected. The interaction between total length and stream was also a significant explanatory variable for Razorback Sucker range. Alternatively, in the multiple regression model for Colorado Pikeminnows, total length, season, and the interaction between these variables were identified as significant covariates explaining their seasonal range. Although the ranges of Colorado Pikeminnows did not vary according to tributary detection origin, a positive relationship existed between range and total length; their ranges significantly differed by season due to upstream-oriented ranges in summer and downstream-oriented ranges in nonsummer. For Razorback Suckers, the results of the ANCOVA indicated that average ranges are significantly different between streams when controlling for total length ($F_{2, 142} = 10.23$, $P = 0.001$) but not significantly different between seasons ($F_{2, 142} = 5.7$, $P = 0.12$). Conversely, for Colorado Pikeminnows, the results of the ANCOVA indicated that average ranges are significantly different between seasons when controlling for total length ($F_{2, 50} = 4.8$, $P = 0.007$)

but not significantly different between streams ($F_{2, 50} = 1.4$, $P = 0.28$).

DISCUSSION

Overall, our data did not support our general hypothesis that groups of endangered fish were similar between Chaco Wash and McElmo Creek. Even though both Colorado Pikeminnows and Razorback Suckers originate from stocked populations in the San Juan River, groups separated themselves between the two small tributaries. For the most part, Colorado Pikeminnows occupied tributary mouths depending on size and age, whereby the upstream, deep, backwater-like mouth of Chaco Wash supported large, adult fish and the more downstream, shallow, flowing mouth of McElmo Creek was occupied occasionally by small subadults. The exceptions were two Colorado Pikeminnows that used both tributaries, showing the potential for expansive movements in the San Juan River by this renowned migrator.

The general patterns of smaller Colorado Pikeminnows using downstream reaches and larger ones using upstream reaches was also seen in the upper Colorado River basin (Osmundson et al. 1998). Even though Chaco Wash is near barriers that limit upstream movements, recovery

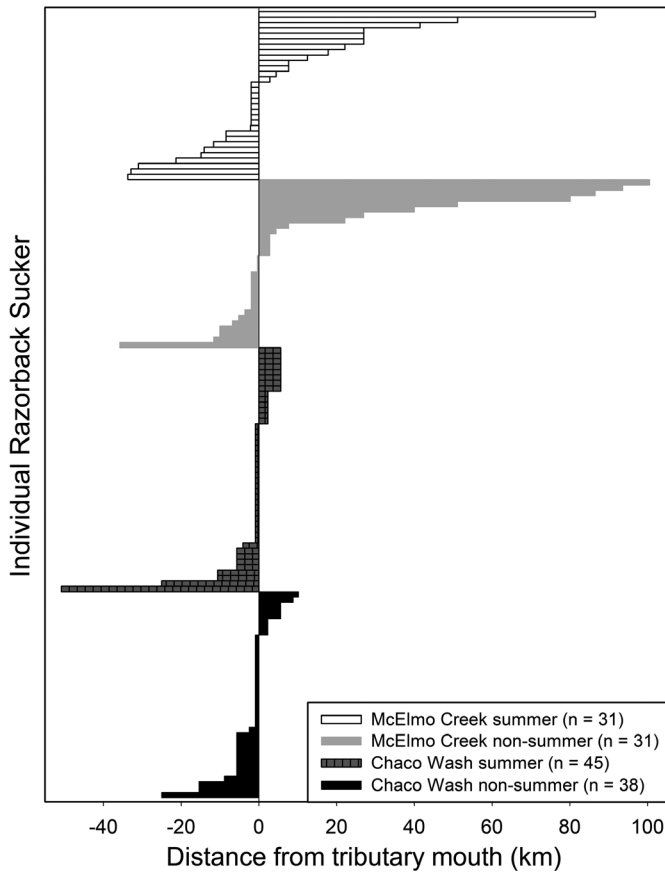


FIGURE 3. Nonsummer and summer ranges for PIT-tagged Razorback Suckers detected by PIT antennas during summer at Chaco Wash (2012, 2013, 2015) and McElmo Creek (2012, 2013, 2014, 2015). Negative values indicate downstream movements and positive values indicate upstream movements.

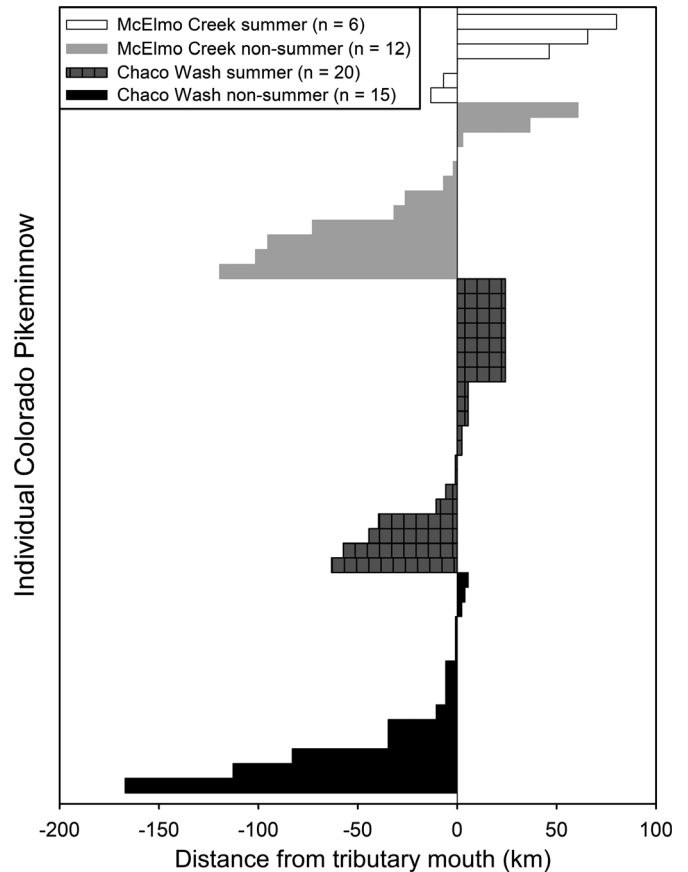


FIGURE 4. Nonsummer and summer ranges for PIT-tagged Colorado Pikeminnows detected by PIT antennas during summer at Chaco Wash (2012, 2013, 2015) and McElmo Creek (2012, 2013, 2014, 2015). Negative values indicate downstream movements and positive values indicate upstream movements.

actions could benefit by determining how these older individuals persist in upstream reaches without meeting a similar fate as subadult fish that largely disappear from the system after age 3 (Durst and Franssen 2014). Backwater or tributary use may offer alternatives to main-stem habitats and promote more sedentary behavior in mature Colorado Pikeminnows of the San Juan River (i.e., Ryden and Ahlm 1996), despite them being a mobile species with observed expansive home ranges in the upper Colorado River basin (Tyus and McAda 1984; Irving and Modde 2000). Given the variable movements among populations of Colorado Pikeminnows in the Colorado River basin and different tributary use by them in the San Juan River, revived consideration of alternative life history tactics (i.e., movers versus stayers) is warranted. For example, testing “moving” versus “staying” tactics in the context of the San Juan River Colorado Pikeminnow could demonstrate that a staying strategy promotes retention of individuals in the system and a potentially smaller viable population

compared with the movers (especially subadults) that may swim too far downstream and pass over the waterfall, never to return (sensu Durst and Franssen 2014).

Razorback Suckers provide a different example whereby—despite homogenous demographics—the absence of mixing among tributary groups, maturity of individuals, and limited seasonal ranges potentially indicate these tributary mouths are within home ranges that include off-channel refugia (Cathcart et al. 2018a), main-stem spawning habitat (Farrington et al. 2016), and feeding arenas peripheral to the main stem (Tyus and Karp 1990). While more confined by time, this finding is contrary to recent studies showing long-distance movements throughout the Colorado River basin by Razorback Suckers (Durst and Francis 2016; Cathcart et al. 2018b). Limited seasonal evidence of fish using the main stem to access both tributary confluence zones could arise from mismatches among confluence habitats, habitat ranges, the needs of fish, and our detection timeframes.

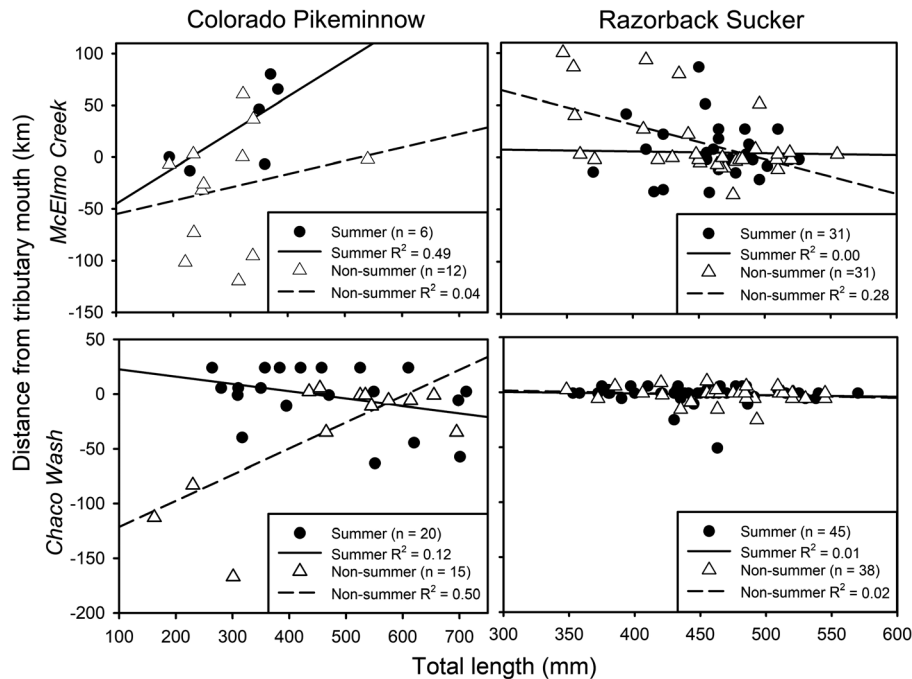


FIGURE 5. Seasonal recapture distance from the tributary of detection (kilometers on y -axis) by total length for individual Razorback Suckers (right panels) and Colorado Pikeminnows (left panels) captured in the main-stem San Juan River and detected in Chaco Wash (bottom panels) or McElmo Creek (top panels). Fish were detected at the mouths of Chaco Wash or McElmo Creek during summer of 2012, 2013, 2014 (McElmo Creek only), and 2015. Along the y -axis, negative values indicate downstream movements and positive values indicate upstream movements.

TABLE 2. Multiple regression model results testing whether total length (TL), stream, season (summer or nonsummer), and their interactions explained range (distance [km] moved away from the tributary of detection) for each species based on tag detections from Chaco Wash and McElmo Creek and seasonal recapture location in the San Juan River between 2012 and 2015. Asterisks indicate variables are significant at $P < 0.05$.

Species	Parameter estimates ^a							R^2
	Intercept	TL	Stream	Season	TL \times stream	TL \times season	Stream \times season	
Razorback Sucker	39.46	-0.09	98.3*	-54.7	-0.19*	0.12	-6.53	0.18
Colorado Pikeminnow	-128.6	0.21*	24.54	145.7*	0.05	-0.02*	-14.71	0.27

^aFull model: range (km) \sim TL + stream + season + (TL \times season) + (TL \times season) + (stream \times season).

Our multiple regression analyses identified drivers of seasonal ranges in Razorback Suckers (ranges explained by stream) and Colorado Pikeminnows (ranges explained by season). Smaller Razorback Suckers tended to move farther away (e.g., upstream) from the mouth of McElmo Creek—maybe to search for better habitat, such as low-velocity habitat that is less prevalent within that area—compared with more limited movements around Chaco Wash (Bliesner and Lamarra 2000). Movement distances of Colorado Pikeminnows were best explained by season (e.g., downstream in nonsummer) and to some extent size, similar to other findings that indicate greater movement in main-stem and tributary habitats during nonsummer periods by subadult individuals (Durst and Franssen 2014; Cathcart et al. 2018a). Since our analyses relied on rare

fish being both detected and captured, our small sample sizes (e.g., low number of McElmo Creek samples for Colorado Pikeminnows) may prevent higher confidence in results compared with a study with a larger sample size over a broader spatial scale. Future work would benefit by incorporating remote monitoring of main-stem movement corridors in neutral locations (i.e., ideally places with neither inhibitive or attractive features) to achieve a more precise measure of networkwide interactions of populations and communities.

In the absence of expanded sampling, unlimited funding, and superior technology for monitoring, many data, such as PIT tag records from passive monitoring and active captures collected by various stakeholders, will require synthesis—and creativity—to gain useful information (sensu

Webber and Beers 2014). In this study, collaborative efforts and large centralized databases of diverse fish encounter types (e.g., STReAMS in this study) enabled syntheses and analysis of disparate studies. Although we did not meet the challenge of reconstructing the complete movement histories of all fish (e.g., use all recapture data linked to tag detection), further synthesis of these data could provide a more accurate, fine-scale approximation of seasonal or home ranges in these species.

While the use of small tributaries by Colorado Pikeminnows (e.g., Fresques et al. 2013) and Razorback Suckers (Cathcart et al. 2015) is often noteworthy, seldom do studies test how these habitats may benefit them beyond seasonal and opportunistic occupancy or movements, especially in a comparative manner. This is important to consider since riverine fish populations and communities worldwide have been shown to be structured by tributaries and their confluences that can provide migratory routes, spawning or rearing locations, and refugia connected to main-stem streams (Brown and Coon 1994; Fernandes et al. 2004; Thornbrugh and Gido 2010; Zeigler and Whitley 2011; Fraser et al. 2017). Possible factors to consider in future research could include exploring diets (do confluences provide equal opportunity in terms of diet for endangered fishes?), main-stem spawning (can they spawn and recruit nearby?), movement habits (do individuals annually return to the same tributary?), and negative effects of confluence attraction, such as predation (to what extent do river otter, great blue heron, or nonnative fishes consume endangered fishes?).

Perspectives that incorporate tributary mouths enable managers to identify what could promote persistence of a species within a system bounded by barriers upstream (diversions and a large dam) and downstream (waterfall). Durst and Franssen (2014) acknowledged that barriers may impede seasonal movements by Colorado Pikeminnows, especially upstream movements. The upstream extent of seasonal ranges is limited by the barriers upstream of Chaco Wash and downstream of the mouth of the Animas River. Two diversions exist in this stretch: PNM weir (25 km upstream of Chaco Wash) and Hogback Diversion (13 km upstream of Chaco Wash). However, sampling and monitoring efforts are lacking in upstream reaches and bias our interpretations of upstream fish passage and range. This should be mitigated in the future with expanded sampling and the recent PIT antenna installations at those diversions that were outside the period of this study (i.e., PNM weir antenna installed in spring of 2015). Alternatively, due to hypolimnetic releases from Navajo Dam, upstream reaches may not be productive for endangered fishes due to cold water or be suitable conservation targets since the tailwater reach supports a popular, albeit nonnative, Rainbow Trout *Oncorhynchus mykiss* fishery (Gido et al. 2000). The waterfall that divides the San Juan River from Lake Powell

blocks migratory fish that may swim downstream over the barrier from returning (Cathcart et al. 2018b). Movement studies that estimate ranges of fish populations can be useful to identify, and mitigate, potential effects of barriers and connectivity in contemporary rivers (Koster and Crook 2017; Lopes et al. 2019).

Applying a tributary-oriented perspective to understanding the main-stem movements of endangered fishes can be beneficial when species groups segregate themselves to specific tributaries. However, variable geomorphological and flow patterns among tributary confluences (and between tributaries and the main-stem river) can limit how these areas support one or several life stages of fish, which can then affect their river network distributions (Jones and Schmidt 2017). Understanding the spatial structure of fish populations can alert managers of potentially important interactions with tributary confluences, barriers, and other animals. Given the rarity of tributaries in the San Juan River yet the demonstrated use of them by endangered fishes, managers should consider installing permanent, or seasonally long-term, PIT antenna arrays in perennial tributaries, such as Chaco Wash, and maintaining flows in these important habitats. Additional monitoring would provide better comparisons with antenna arrays in other tributary systems or at diversions, as well as greater longitudinal coverage of tag monitoring relative to critical habitat within the San Juan River.

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