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RESEARCH ARTICLE

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Waterfall formation at a desert river–reservoir delta isolates endangered fishes

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Abstract

Unforeseen interactions of dams and declining water availability have formed new obstacles to recovering endemic and endangered big-river fishes. During a recent trend of drying climate and declining reservoir water levels in the Southwestern United States, a large waterfall has formed on two separate occasions (1989–1995 and 2001–present) in the transition zone between the San Juan River and Lake Powell reservoir because of deposited sediments. Since recovery plans for two large-bodied endangered fish species, razorback sucker (*Xyrauchen texanus*) and Colorado pikeminnow (*Ptychocheilus lucius*), include annual stockings in the San Juan River, this waterfall potentially blocks upstream movement of individuals that moved downstream from the river into the reservoir. To quantify the temporal variation in abundance of endangered fishes aggregating downstream of the waterfall and determine population demographics, we remotely monitored and sampled in spring 2015, 2016, and 2017 when these fish were thought to move upstream to spawn. Additionally, we used an open population model applied to tagged fish detected in 2017 to estimate population sizes. Colorado pikeminnow were so infrequently encountered (<30 individuals) that population estimates were not performed. Razorback sucker captures from sampling (335), and detections from remote monitoring (943) showed high abundance across all 3 years. The razorback sucker population estimate for 2017 alone was 755 individuals and, relative to recent population estimates ranging from ~2,000 to ~4,000 individuals, suggests that a substantial population exists seasonally downstream of this barrier. Barriers to fish movement in rivers above reservoirs are not unique; thus, the formation of this waterfall exemplifies how water development and hydrology can interact to cause unforeseen changes to a riverscape.

KEYWORDS

climate change, Colorado River Basin, endangered species, fragmentation, razorback sucker, river–reservoir inflow, waterfall

1 | INTRODUCTION

Connectivity of freshwater systems and conservation of freshwater animals are challenged worldwide by increasing drought and pervasive water development, often in the form of large dams and excessive water use (Ruhi, Olden, & Sabo, 2016). Dams and reservoirs disrupt the continuity of rivers (Stanford & Ward, 2001) where they create abrupt shifts in physical and biological properties at the junctions of rivers and reservoirs (Galay, 1983; Poff et al., 1997; Sabo, Bestgen, Graf, Sinha, & Wohl, 2012). Once impaired, fragmented rivers often experience declines or extinctions of fishes disconnected from habitats necessary for the fulfilment of life histories (Minckley & Deacon, 1991; Moyle, 1995). Ultimately, these disconnections and alterations have contributed to the listing of many fishes or populations under the Endangered Species Act, including a high percentage of native fishes from the Colorado River Basin (Minckley & Deacon, 1991; Osmundson, 2011). Despite the intrinsic value of native fish and cost of recovery, conservation programs must often consider barriers (especially dams or diversions) as permanent structures to the landscape because of their economic value and importance to water security (Coutant & Whitney, 2006; Lackey, 2013; Propst & Gido, 2004).

Research perspectives have primarily focused on downstream effects of dams, with limited attention paid to changes occurring upstream of impoundments in both fish populations and stream function (Falke & Gido, 2006; Pringle, 1997). Inundated lotic habitat upstream of dams can reduce habitat availability, restrict migration, and diminish population viability for riverine species (Hudman & Gido, 2013; Osmundson, 2011). An upstream perspective may be particularly useful to understand the importance of the river–reservoir interface for both lentic and lotic adapted species (Birnie-Gauvin, Aarestrup, Riis, Jepsen, & Koed, 2017; Minckley & Deacon, 1991; Stanford & Ward, 2001). In addition, dynamic reservoir volume alters geomorphological processes structuring delta formation and location (Galay, 1983; Stevens et al., 2001; Johnson, 2002). Specifically, as reservoir levels recede from decreasing basin water availability or seasonal dam operations, vegetation sequesters sediments in the inflow area (raising elevation of the river channel) slowing inflow and depositing sediment on higher surfaces (Johnson, 2002; Pasternack & Brush, 1998). In the Colorado River Basin, receding reservoir levels have exposed river–reservoir deltas, altering river channels in alluvial sediments.

Lake Powell, created in 1963, is the second largest reservoir in the United States, covering 400–660 km^2 (1.5–3.0 million hectare metres of storage) and includes the historical confluence of the San Juan and Colorado rivers (Figure 1). Combined sediment deposition and water level declines in Lake Powell have resulted in a geomorphic barrier at the San Juan River inflow to Lake Powell, Utah between 1989 and the present. Lake Powell reservoir experienced dynamic inflows since reaching capacity in 1980, which subsequently led to delta formation and the eventual emergence of waterfall barriers on the San Juan River (Figure 2). These barriers to fish movement, which first appeared as late as 1989, were described by Ryden and Ahlm (1996) as being >10 m tall depending on river flows. The reservoir then experienced a period of greater storage from higher inflows throughout the mid-1990s, inundating the waterfall by 1995. After further water level

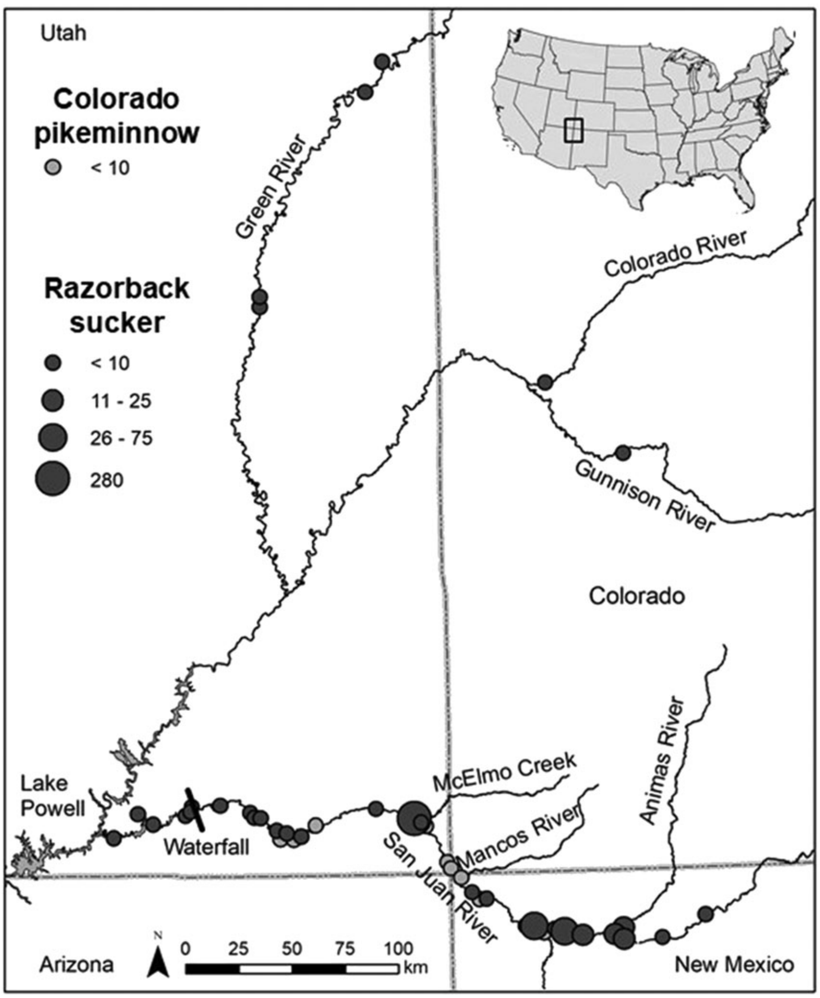

FIGURE 1 Study area showing the stocking or tagging event location and relative abundance of passive integrated transponder-tagged endangered fishes detected or captured downstream of the waterfall (shown by black line labelled "waterfall") in 2015, 2016, or 2017. Tags were matched to records in the Species Tagging Research and Monitoring System (STReamS 2017, accessed 7/20/2017, https://streamsystem.org). Lake Powell is shown at full pool

recession in the late 1990s, the river channel again shifted through the newly formed delta and a new waterfall formed in 2001 approximately 3 km downstream from the prior waterfall (Figure 3). This process, referred to as superimposition, involves the river cutting through new deposited sediments as reservoir levels recede, thus creating a new channel. The current waterfall is >6 m tall and is a complete barrier to upstream fish movement in an area referred to as Piute Farms, UT (Figure 4). Since emerging in 2001, the current waterfall has only been inundated (thus passable) once, in 2011 for 2 weeks in late July and mid-August (Durst & Francis, 2016).

Two intensively managed endangered species are likely affected by the emergent waterfall. Colorado pikeminnow (*Ptychocheilus lucius*) and razorback sucker (*Xyrauchen texanus*) are large-bodied (>1 m long), long lived (>30 years old), highly fecund (mature individuals regularly have >60,000 eggs), and migratory fishes endemic to large river habitats in the Colorado River Basin that typically spawn in late spring to mid-summer after snowmelt run-off (Hamman, 1985). Colorado pikeminnow have a non-augmented wild population in the Upper Colorado River and a stocked population in the San Juan River and are highly migratory in both systems (Osmundson, 2011; Durst & Franssen, 2014). Besides rivers, razorback sucker inhabit (and spawn in) all major Colorado River Basin reservoirs (Mead, Mohave, Havasu, and Powell). Razorback sucker often spawn on the ascending limb of the hydrograph from mid-March through June at water temperatures between 9°C and 17°C (Tyus & Karp, 1990). Successful recruitment to adulthood has only been documented in Lake Mead, and we do not understand how reservoir-dwelling razorback sucker life histories may interact with inflowing rivers (Albrecht et al., 2017; Albrecht, Holden, Kegerries, & Golden, 2010; Marsh, Dowling, Kesner, Turner, & Minckley, 2015). Lake Powell is both a movement corridor connecting the Upper Colorado River and San Juan River basins and a habitat for razorback sucker that are known to make substantial downstream movements after stocking or during larval drift (Albrecht et al., 2017; Durst & Francis, 2016; Zelasko, Bestgen, & White, 2010). Current management for both species involves stocking (Zelasko et al., 2010), mimicking natural flow regimes (Propst & Gido, 2004), and removing nonnative fishes (Franssen, Davis, Ryden, & Gido, 2014).

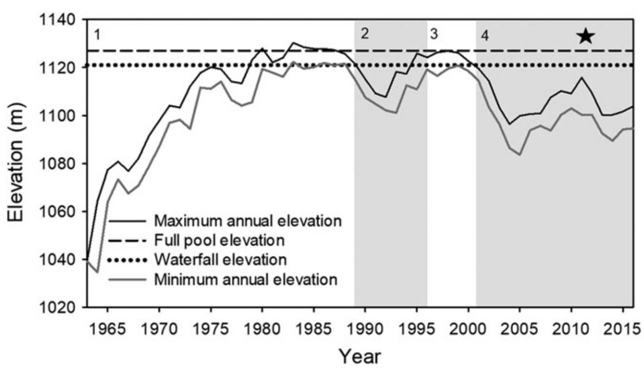

FIGURE 2 Lake Powell reservoir surface elevation metrics (maximum and minimum annual elevation) and thresholds (full pool and waterfall elevations) since Glen Canyon Dam operations began. Lake Powell and the San Juan River inflow are characterized by four phases since 1963: (1) filling to capacity, (2) elevation declines leading to emergence of first waterfall, (3) refilling of reservoir inundating the initial waterfall, and (4) subsequent declines and prolonged water shortage leading to the current waterfall. The star indicates a 2-week period of waterfall inundation in July–August 2011 that was not captured by mean annual reservoir elevation. Shaded phases indicate times when the waterfall is present and a barrier to fish passage

Over 140,000 razorback sucker and over 50,000 Colorado pikeminnow have been implanted with passive integrated transponder (PIT) tags in the San Juan River basin during stocking or on-river tagging events between 2000 and 2017 (Figure 1). In the Upper Colorado River Basin upstream of Lake Powell (e.g., Colorado, Green, and Gunnison rivers), ~424,000 razorback sucker and ~50,000 Colorado pikeminnow have been PIT tagged and could travel through the reservoir to the waterfall. With few exceptions, razorback sucker are stocked in these rivers with a PIT tag at ~300-mm total length (TL). Colorado pikeminnow are stocked in the San Juan River as juveniles (<100-mm TL) and are PIT tagged at first capture. Intense sampling of tagged endangered fishes in the San Juan River upstream of the waterfall within and across years has allowed population estimates of endangered fishes in the river (U.S. Fish and Wildlife Service [USFWS], 2017) but does not account for fishes that move downstream to the reservoir. Our main objectives were to measure sex ratios, quantify temporal patterns of abundance, and estimate population sizes of Colorado pikeminnow and razorback sucker downstream of the waterfall. This research shows how unforeseen fragmentation alters endangered fish population connectivity and, ultimately, their recovery.

2 | METHODS

2.1 | Fish sampling

Because of limited historical sampling downstream of the Piute Farms waterfall, we performed pilot sampling in 2015 to assess the occurrence of endangered fishes. After confirming the presence of endangered fish, more rigorous sampling in the localized area (0–500 m downstream of the waterfall) was conducted during spring of 2016 (March and April) and 2017 (February and March) with raft-mounted electrofishing. Amount of habitat and sampling effort (two 15-min "passes") were similar across days, although total days sampled varied across years (6–13 days). Endangered species were identified, measured for TL, and sexed when possible through observation of sexually dimorphic traits (i.e., gamete expression, tubercle presence, and razorback sucker anal fin shape) and were scanned with a PIT tag reader for the presence of prior tags. If a tag was absent, we implanted the fish with a PIT tag (Biomark, Boise, Idaho, 12-mm full-duplex, 134.2 kHz). All individual fish captured in 2015, 2016, and a subset in 2017 were translocated upstream of the waterfall barrier as a conservation action to assist migration and promote spawning.

2.2 | Temporal variation in abundance

To detect PIT-tagged fishes, we deployed a circular (1-m diameter) submersible PIT tag antenna (Biomark, Boise, Idaho) from March 21 to July 6, 2015 (107 days), March 2 to April 7, 2016 (36 days), and

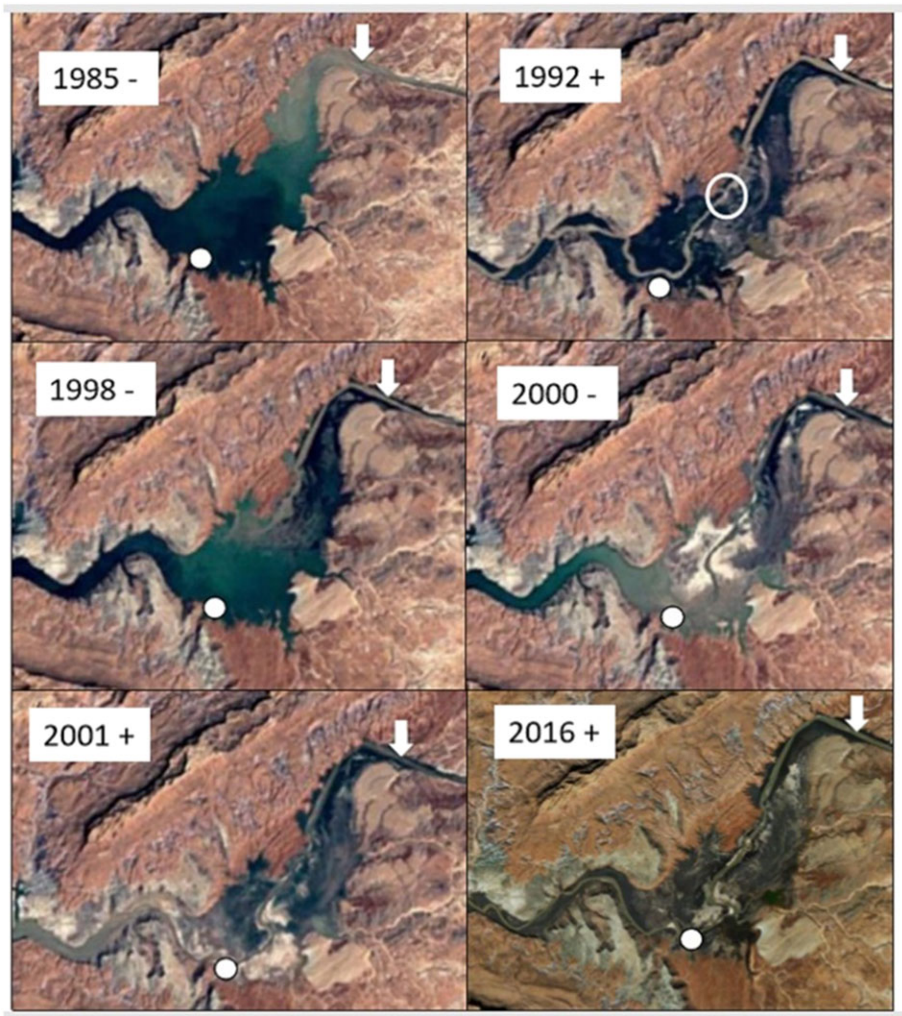

FIGURE 3 Time series of photos of the San Juan River arm of Lake Powell showing the dynamic water levels at the inflow area since 1985. The location of the current waterfall, shown in all photos, is indicated by the white-filled circle. The plus and minus signs next to years indicate the presence (+) or absence (−) of a waterfall, respectively. Open circle in 1992 indicates location of the first waterfall that existed from the late 1980s to the mid-1990s. Arrow indicates Clay Hills Crossing, UT [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 4 A photo of the Piute Farms waterfall in 2015 looking downstream towards Lake Powell reservoir (~177 km upstream of Glen Canyon Dam) [Colour figure can be viewed at wileyonlinelibrary.com]

February 12 to June 3, 2017 (111 days). The antenna was deployed in an eddy approximately 10 m downstream of the waterfall on the right bank, over sand and bedrock substrates in water depths from 70 to 160 cm. The antenna typically detected tags within 0.5 m. Detected individuals were identified by relating them to a PIT tag database compiled by the San Juan River and Upper Colorado River recovery programs (STReaMS, 2017).

To illustrate environmental cues commonly correlated with fish spawning migrations, we show the relationship of tag detections with mean daily discharge (m^3 s^{-1}) and mean daily water temperature (°C) from the U.S. Geological Survey gauge near Bluff, UT (gauge number 9375000), approximately 85 km upstream from the waterfall.

2.3 | Population estimates

Extremely low detections of Colorado pikeminnow downstream of the waterfall prevented their population estimation, but we estimated population size of razorback suckers in 2017. Capture data from

2015 were inadequate to estimate population size, and the sampling period changed between 2016 and 2017; it was March 02 to April 07 in 2016 and February 12 to June 03 in 2017. We lengthened the sampling period (physical capture plus antenna resight period) in 2017 to increase sample sizes; sampling period was 3.6 months in 2017 compared with 1.2 months in 2016. The longer sampling period yielded a greater number of unique fish captured, which was 32% higher for 2017 compared with 2016. Thus, we only estimated population size for 2017 as it reasonably encompassed an entire spawning season and had adequate sample size. Translocated fish were not used in the open population size estimates because they could not be recaptured. Due to the long detection period (February 12 to June 03), we tested the assumption of population closure for the antenna detection data using Program CloseTest (Stanley & Burnham, 1999). This test indicated the assumption of closure was not met. Fish were entering and leaving the study area during the detection period; thus, we estimated population size using POPAN (Schwarz & Arnason, 1996), an open population model implemented in Program MARK (Cooch & White, 2016). POPAN is a Jolly-Seber model and assumes equal catchability (or detection) among individuals, which means we did not expect there could be a behavioural response to being detected by the antenna.

For the POPAN model, a previously PIT-tagged fish was considered "unmarked" until it was first detected by the antenna, after which it was considered a marked fish. Marked fish could be detected by the antenna continuously during the sampling period. On the basis of the proportions of unique fish detected, we grouped the data into four periods; February 12 to March 15, March 16 to March 31, April 01 to April 15, and April 16 to June 03 (the proportions of unique fish detected for each occasion were 0.24, 0.30, 0.23, and 0.23). To account for differences in period length, we used unequal time intervals in Program MARK. The cumulative number of tags detected across the time periods used in the model indicated that longer antenna deployment did not result in greater numbers of unique tags detected (Figure S1). We constructed a set of models with capture probability (p), apparent survival probability, which in this situation is the probability of leaving the waterfall area (φ), and probability of initial entrance to the waterfall area (p_{ent}) modelled as constant across the four sampling periods and variable from period to period. We constructed eight initial models for all possible combinations of these three parameters. We used the "gross" population size from POPAN (Schwarz & Arnason 1996), which is the number of PIT-tagged razorback sucker using the waterfall area over the entire study period and includes fish who arrived and departed between occasions. We added the count of translocated fish to the model-averaged estimated population size from POPAN to estimate a minimum total population size of razorback sucker using the waterfall area during the sampling period. This estimate allowed for comparison to razorback sucker population size in the San Juan River upstream of the waterfall (USFWS, 2017).

3 | RESULTS

3.1 | Fish sampling

Below the waterfall, we captured 167 razorback sucker in 2016 and 183 in 2017 (Table 1). Razorback sucker ranged from 403 to 618-mm TL with a minimum weight of 550 g and a maximum of 2,800 g. In 2016, about 10% of females and 77% of males that were handled were freely expressing gametes. Sampling was performed earlier in 2017, and ripe fish were rare. Twenty-four Colorado pikeminnow were captured, and most were subadults except for a 571-mm TL fish in 2016.

3.2 | Temporal variation in abundance

Over 3 years, we detected 967 unique endangered fish downstream of the waterfall (Table 1). Razorback sucker made up a large proportion (98%) of detected fishes across all years. The majority of detected (and captured) fish were either stocked or tagged in the San Juan River upstream of the waterfall, but several razorback sucker came from the Upper Colorado River Basin (Figure 1), which involves a minimum of 220 km to traverse Lake Powell. The PIT antenna ran continuously during study periods in all 3 years, except for 5 days (May 28 to June 3) in 2015 and again in 2017, when ~1 m of sediment buried the operating antenna for six consecutive days in late February.

Some fish were detected in multiple years for both species. Of razorback sucker detected in 2015, 51% (n = 255) were also detected

TABLE 1 Number of individual fish detected by a passive integrated transponder antenna or captured during sampling efforts downstream of a waterfall barrier on the San Juan River, Utah

Species	Year	Days detecting	Days sampling	Number detected	Number captured	Number unique	Per cent female	Total length (mm) ($M \pm SD$)	Weight (g) ($M \pm SD$)
Razorback sucker	2015	107	6[a]	499	16	507	—	—	—
	2016	36	6	472	167	523	53	483 ± 39	1,251 ± 323
	2017	111	13	615	183	689	48	502 ± 36	1,340 ± 348
	Total unique			943	335	1,015			
Colorado pikeminnow	2015			15	6	19	—	—	—
	2016			8	6	13	—	330 ± 126	418 ± 613
	2017			7	6	13	—	214 ± 95	122 ± 186
	Total unique			24	18	39			

Note. Because fishes could be both detected and sampled, the "number unique" column indicates the total number of unique fishes recorded from all sampling and detection data.

[a]Sampling in 2015 was a pilot effort of multiple gears including castnets, gillnets, and beach seines but not raft electrofishing. Consequently, effort was less intensive compared with 2016 and 2017.

in 2016, and 64% (n = 302) of fish detected in 2016 were then detected in 2017. Eighteen per cent (167) of razorback sucker were detected in all three years. Concomitant with their relatively low detection numbers, few Colorado pikeminnow were detected in multiple years. One fish was detected in all three years, one fish each was detected in both 2015–2016 and 2016–2017, and a single individual detected in 2015 was detected in 2017.

Water temperatures and flows showed similar patterns across all 3 years. Water temperatures during antenna deployments included observed spawning temperatures for razorback sucker (Figure 5). Generally, patterns of unique daily razorback sucker detections were similar across all 3 years. Each year, daily detections were variable but higher earlier in the study period and declined over time with increasing water temperature and river discharge. Peak razorback sucker abundances at the waterfall occurred, whereas when water temperatures were below 16°C until warming in mid-April when razorback sucker abundance decreased.

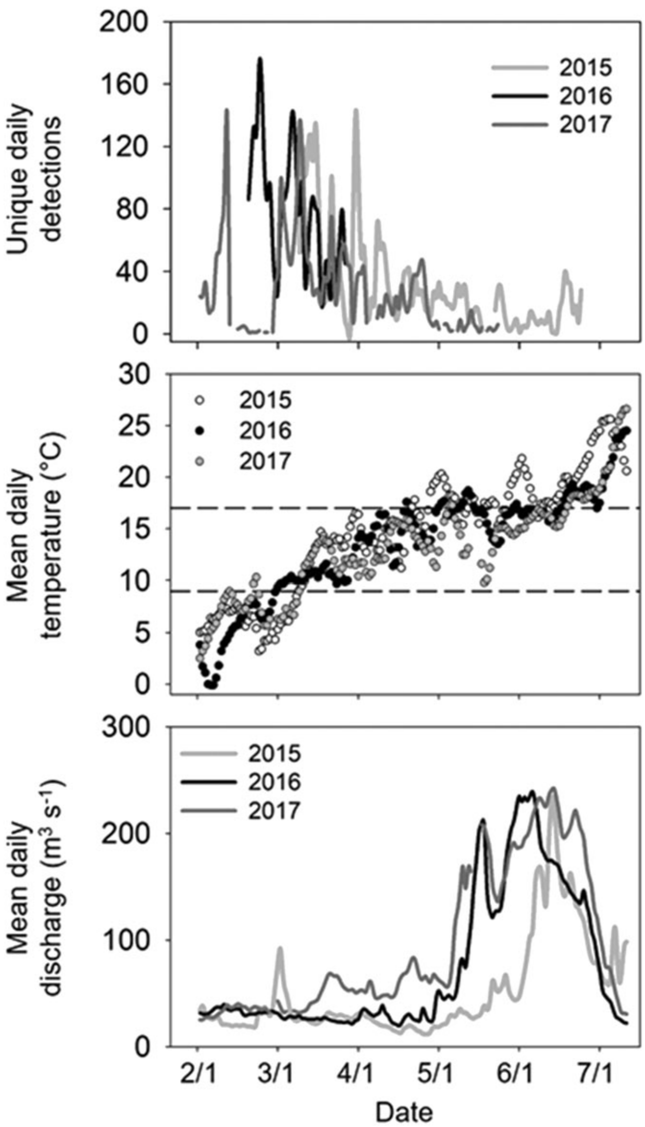

FIGURE 5 Passive integrated transponder tag detections of razorback sucker at a submersible passive integrated transponder tag antenna stationed immediately downstream of the Piute Farms waterfall (top) and coinciding environmental conditions of the San Juan River from 2015, 2016, and 2017. Dashed lines in the middle panel represent the upper and lower bounds of observed spawning temperatures for razorback sucker (Tyus & Karp, 1990)

3.3 | Population estimates

In 2017, we captured and/or detected 689 unique individual razorback sucker. Of these, 183 were physically captured (27%) and 506 were PIT tagged but only detected by the antenna (73%). Of the 183 fish physically captured, 34 did not have a PIT tag (19%). All physically captured fish were moved upstream of the waterfall area. The eight candidate models estimating razorback sucker population using fish only detected by the antenna were ranked by Akaike's information criterion. The top POPAN model included $\varphi(.)$ $p(t)$ $p_{\mathrm{ent}}(t)$ and had a model weight (w_i) of 0.81 (Table S1). Detection probabilities were high, ranging from 0.64 to 0.91. The model-averaged estimated population size for 2017 was 572 (SE = 11.7; 95% CI [549, 595]). Adding the minimum count of physically captured fish indicated that at least 755 razorback suckers used the waterfall area in 2017.

4 | DISCUSSION

Although we expected to capture endangered fish downstream of the waterfall based on past occurrence records, the large number of razorback sucker we sampled was surprising and showed that a substantial proportion of the fish stocked in the river moved downstream to the reservoir. Using PIT antennas continuously in a novel, albeit discrete and fine-scaled, location within the Colorado River Basin further illustrated how remote sensing can more accurately measure populations compared with spatially continuous yet temporally discrete active sampling events (Webber & Beers, 2014). That these fish migrated back upstream and aggregated below the waterfall in spring enhanced our ability to detect individuals and then accurately represent and estimate the population of razorback suckers here. USFWS (2017) population estimates from 112.5 km of the upper river in 2015 ranged from 2,296 to 4,073 fish compared with our 2017 population estimate of 755 fish. Thus, the proportion of the San Juan River population using habitat downstream of the waterfall was between 19% and 33%. Given that 5,800 adult razorback sucker in the San Juan River are necessary for downlisting them from endangered to threatened, the cumulative populations in habitats upstream and downstream of the waterfall represent significant progress towards reaching that recovery criterion. Barring rare waterfall inundation during high river flow events synchronized with elevated reservoir pool such as late summer 2011 (that would not assist spring spawning migrations anyway), this >6 m tall waterfall is a barrier to all fishes attempting to swim upstream (see Meixler, Bain, & Walter, 2009). Although it seems limited, quantifying spawning habitat (i.e., confluences of washes and areas with coarse substrates) in the ~25-km reach between Lake Powell and the waterfall would be a considerable first step towards understanding the potential of this river–reservoir transition area to support the life history of razorback sucker isolated from the upper San Juan River.

Although the waterfall certainly impedes connectivity of adult fishes, recruitment of early life stages upstream of the waterfall could also be compromised by this fragmentation. The abundance of mature, gamete-spewing razorback sucker repeatedly detected and captured coincident with observed spawning temperatures implies the waterfall blocks annual spawning migrations into the upper San Juan River. Historical and contemporary monitoring indicates the presence of young-of-the-year (larval and transformed juvenile) razorback sucker and Colorado pikeminnow just upstream of the waterfall as well as in the inflow area where the San Juan River transitions into Lake Powell (Platania, Bestgen, Moretti, Brooks, & Propst, 1991; Pennock, unpublished data). Larval fish could accumulate in the inflow following drift from hatching locations upstream in the San Juan River and over the waterfall. Flow regulation and invasive Russian olive (*Elaeagnus angustifolia*) have channelized the river, thereby reducing larvae-retaining habitats (inundated floodplains and backwaters) and increasing larval drift distance (e.g., Robinson, Clarkson, & Forrest, 1998). Generational losses to upstream reaches from isolated downstream populations could also occur when upstream migrations cannot occur to offset larval drift (e.g., Perkin & Gido, 2011).

Ryden and Ahlm (1996) suggested the first waterfall in the San Juan River disrupted Colorado pikeminnow migrations. Our sampling from late winter to early summer may have missed movements to or over the waterfall that could occur at other times of year. Given their tendency for long-distance migrations as adults (Tyus & McAda, 1984), downstream winter migrations as subadults (Durst & Franssen, 2014), and the fact they are stocked at small sizes without PIT tags, the Piute Farms waterfall presents a major challenge to Colorado pikeminnow recovery in the San Juan River if downstream migrating fish swim too far and become “trapped” below the waterfall.

The discontinuity of a desert river caused by an emergent waterfall in a reach between two large dams is likely reconcilable. Connecting habitats through fish passage (including barrier removal, bypass, or capture and translocate) could allow hundreds of endangered fish to move seasonally (*sensu* Pess, Quinn, Gephard, & Saunders, 2014). Fish passage systems mitigate barriers to migratory fish if designed correctly, but they can also negatively interact with some species, including suckers, by preventing or delaying movements (Hatry et al., 2016; McLaughlin et al., 2013). Regardless, total functional connectivity of the river is not necessarily preferred by recovery programs that devote substantial resources to removing nonnative fish that are considered a primary threat to endangered Colorado River Basin fishes (Franssen et al., 2014; Minckley & Deacon, 1991). In fact, the Piute Farms waterfall also blocks upstream movement of nonnative predatory fishes such as striped bass (*Morone saxatilis*) and walleye (*Sander vitreus*). Thus, alternative methods (e.g., selective fish passage such as translocation) would maintain downstream isolation of nonnative fishes (Rahel, 2013). Lake Powell requires >85% fullness to inundate the waterfall, suggesting this will likely remain a barrier to fish movement for the foreseeable future (Bureau of Reclamation, unpublished data). If connectivity is desired, our study pinpoints effective times to manage for passage, especially for razorback sucker.

The barrier-forming geomorphological processes described here (and in Ryden & Ahlm, 1996) are not unique to the San Juan River and are currently creating fragmentation issues upstream of another large south-western American reservoir. A volatile large rapid formed via interactions of reservoir volume and superimposition processes in the mid-2000s at the Colorado River inflow to Lake Mead where the river exits the Grand Canyon at Pearce Ferry (Martin & Whitis, 2013). Formation of this rapid created such a hazard to river runners that the National Park Service constructed a multi-million-dollar road and takeout area upstream of the rapid to allow users to exit safely (Video S1). Pearce Ferry Rapid is younger than Piute Farms waterfall but may be approaching a similar result: a barrier to endangered fish movements between Lake Mead and the Grand Canyon. The importance of connectivity between Lake Mead and Grand Canyon to razorback sucker is unknown and should be considered as Pearce Ferry Rapid develops.

The effects (and threat) of fragmentation on freshwater fishes are well documented and include community structure changes, population reduction, enhanced negative species interactions, and species extirpation upstream and downstream of barriers (Gido, Whitney, Perkin, & Turner, 2016; Guy et al., 2015; Perkin & Gido, 2011; Sanches et al., 2006). Despite the acknowledgment of fragmentation effects in conceptual models of riverine function (e.g., Stanford & Ward, 2001) and negative interactions of reservoirs with large river fish recruitment (Guy et al., 2015), current models treat reservoirs separately from the rivers they impound, which could explain the limited number of studies assessing upstream effects of reservoirs. Studies on fish distributions between or within reservoir and riverine habitats treat reservoirs as strictly lentic habitats and often consider these artificial systems as barriers themselves (Buckmeier, Smith, Fleming, & Bodine, 2014; Falke & Gido, 2006; Taylor, Knougt, & Hiland, 2001). In reality, there is not an abrupt change from riverine to reservoir environments but more gradual change as one moves through the riverine, transition, and lacustrine zones within a reservoir (Thornton, 1990). This gradient of ecosystem novelty (e.g., Gandy & Rehage, 2017) along the river–reservoir continuum could provide productive habitats (e.g., floodplain connectivity) no longer seen in upstream portions of regulated rivers (Volke, Scott, Johnson Carter, & Dixon, 2015) and benefit fish (e.g., razorback sucker) able to utilize the lentic–lotic interface (Da Silva et al., 2015; Gido et al., 2002). However, the consequences of being isolated in these habitats are largely unknown. These contemporary barrier formation events illustrate how fragmentation and isolation can metastasize in alluvial rivers when delta formation processes interact with increased water use, historical fragmentation, and natural topography. Depending on when, where, and what these emergent features can affect (such as fish or public safety), awareness and action can assist resource managers in adapting to them.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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