Received: 30 July 2019 | Revised: 12 February 2020 | Accepted: 13 May 2020
DOI: 10.1002/aqc.3399

RESEARCH ARTICLE

WILEY

Movement ecology of imperilled fish in a novel ecosystem: River-reservoir movements by razorback sucker and translocations to aid conservation

Casey A. Pennock[1] | Mark C. McKinstry[2] | Charles N. Cathcart[3] | Keith B. Gido[1] | Travis A. Francis[4] | Brian A. Hines[5] | Peter D. MacKinnon[6] | Skyler C. Hedden[1] | Eliza I. Gilbert[7] | Christopher A. Cheek[8] | David W. Speas[2] | Katherine Creighton[5] | Darek S. Elverud[4] | Benjamin J. Schleicher[4]

[1]Division of Biology, Kansas State University, Manhattan, Kansas
[2]Upper Colorado Regional Office, US Bureau of Reclamation, Salt Lake City, Utah
[3]Alaska Department of Fish and Game, Alaska Freshwater Fish Inventory, Anchorage, Alaska
[4]Grand Junction Fish and Wildlife Conservation Office, US Fish and Wildlife Service, Grand Junction, Colorado
[5]Moab Field Station, Utah Division of Wildlife Resources, Moab, Utah
[6]Department of Watershed Sciences, Utah State University, Logan, Utah
[7]New Mexico Ecological Services Field Office, US Fish and Wildlife Service, Albuquerque, New Mexico
[8]Department of Forestry and Natural Resources, Purdue University, West Lafayette, Indiana

Correspondence
Casey A. Pennock, Department of Watershed Sciences and The Ecology Center, Utah State University, Logan, UT 84322, USA.
Email: casey.pennock@usu.edu

Funding information
U.S. Bureau of Reclamation

Abstract

1. Reservoirs and associated river fragments are novel ecosystems not experienced by fishes in their evolutionary history, yet they are now commonplace across the globe. Understanding how fishes use these novel habitats is vital to conservation efforts in contemporary riverscapes.
2. Movement patterns of the endangered razorback sucker (*Xyrauchen texanus*) synthesized from tagging efforts in the upper Colorado River basin, USA, illustrate the applications of tagging technology and data sharing by multiple agencies to better understand the spatial ecology of large river fishes.
3. Tagging studies between 2014 and 2018 in Lake Powell and its two main tributary rivers, the Colorado (unfragmented) and San Juan (waterfall-fragmented), were used to quantify movement of razorback sucker within this river–reservoir habitat complex. In addition, facilitated translocations of fish upstream of a waterfall barrier in the San Juan River were assessed in 2016–2017.
4. Extensive movement of fish occurred within and across river and reservoir habitats. Of 722 fish captured in the Colorado River arm of Lake Powell, 36% of re-encounters occurred upstream in the Colorado or Green rivers, or fish dispersed through the reservoir and were detected in the San Juan River arm. Fourteen fish moved more than 600 km. In the San Juan arm of the reservoir, 29% and 20% of fish in 2017 and 2018, respectively, had moved ~30–40 km upstream below the waterfall in the San Juan River within a year. In 2016–2017, 303 fish were translocated upstream of the waterfall into the San Juan River, but 80% were re-encountered downstream of the waterfall within a year.
5. Long-distance movements by razorback sucker were common within and among rivers and reservoirs illustrating how large river fish, in general, might maintain population connectivity in highly altered ecosystems.

KEYWORDS
Catostomidae, Colorado River basin, connectivity, fragmentation, inflow areas

1 | INTRODUCTION

Many freshwater fishes occupy novel ecosystems (*sensu* Hobbs et al., 2006) that blend vestiges of natural landscapes with anthropogenic additions. The creation of novel aquatic ecosystems through damming and lentification of rivers is ubiquitous across the globe (Grill et al., 2019; Sabater, 2008), resulting in altered flow and temperature regimes, decreased floodplain connectivity, and restricted movement of aquatic organisms (Pelicice, Pompeu, & Agostinho, 2015; Reidy Liermann, Nilsson, Robertson, & Ng, 2012). Dams cause reductions in biodiversity (Reidy Liermann et al., 2012), population abundance (Junge, Museth, Hindar, Kraabol, & Vollestad, 2014), dispersal ability (Rolls, Ellison, Faggotter, & Roberts, 2013), and the capacity of populations to buffer themselves against environmental stochasticity (Dunham, Young, Gresswell, & Rieman, 2004; Perkin et al., 2019; Perkin, Gido, Costigan, Daniels, & Johnson, 2015). Reservoirs and river fragments between reservoirs consist of altered abiotic conditions and combinations of species that may not have shared an evolutionary history (Havel, Lee, & Vander Zanden, 2005; Hobbs et al., 2006). Given the prevalence (and perhaps permanence) of altered river systems, understanding how native species use these systems can improve management of their populations in contemporary riverscapes (Buckmeier, Smith, Fleming, & Bodine, 2014).

Although movement is a necessity for freshwater fish, it is understudied for many species and the scale at which movement occurs is unclear and difficult to ascertain (Cooke et al., 2016; Cooke, Paukert, & Hogan, 2012; Fausch, Torgersen, Baxter, & Li, 2002; Schlosser, 1991). Populations often consist of individuals displaying heterogeneous movement strategies whereby most individuals move relatively short distances and a smaller contingent make longer distance movements (Fraser, Gilliam, Daley, Le, & Skalski, 2001; Radinger & Wolter, 2014; Rodríguez, 2010). Fish make movements to gain access to patchily distributed resources, critical habitats (e.g. spawning habitat), and capitalize on favourable environmental conditions (Lucas & Baras, 2001). These movements influence demographic processes such as immigration and emigration, possible genetic exchange, and functionally connect habitats through transfer of materials and subsidies (Childress, Allan, & McIntyre, 2014; Cooke et al., 2016; Flecker et al., 2010). Conservation of mobile fish species is challenged by continued habitat degradation and blocked migration routes (McIntyre et al., 2016), and a lack of data on the spatial ecology of species in river–reservoir systems hinders management efforts (Clarke, Telmer, & Shrimpton, 2007; Cooke et al., 2016).

The Colorado River basin, USA, epitomizes the novel ecosystem. Water storage reservoirs, and associated dams, have transformed and fragmented rivers, causing habitat loss and restricting access to potentially important native fish habitat (Minckley & Deacon, 1991). Colorado River basin fishes may have evolved to use spatially and temporally disjunct habitats including the Colorado River Delta (Glenn, Lee, Felger, & Zengel, 1996; Sykes, 1937), volcanically impounded reaches (Dalrymple & Hamblin, 1998), and other lentic environments created by high water events (i.e. Salton Sea; Minckley, 1983). These fish must now cope with an abundance of lacustrine environments, created by artificial barriers, that are habitat for introduced fishes (Clarkson, Marsh, Stefferud, & Stefferud, 2005). Because native fishes no longer have access to a large, diverse network of connected habitats, they are restricted to fragmented populations in highly altered habitats and there is a need to understand habitat use and how fish are moving through these novel ecosystems.

Razorback sucker (*Xyrauchen texanus*) is one of the imperilled, endemic species in the Colorado River Basin and understanding its movement ecology has been complicated by habitat alterations. Razorback sucker make movements for spawning, rearing, and refuge, and they use a variety of habitats including mainstem rivers, smaller tributaries, floodplain wetlands, and reservoirs (Albrecht et al., 2018; Bottcher, Walsworth, Thiede, Budy, & Speas, 2013; Cathcart, McKinstry, MacKinnon, & Ruffing, 2019). Early studies in the Colorado River basin suggested that razorback sucker were sedentary outside the spawning season, but could move long-distances (> 100 km) to spawn (Modde & Irving, 1998; Tyus & Karp, 1990). The presumed sedentary nature of razorback suckers is cited in recovery documents (USFWS, 1998) and recent studies (Durst & Francis, 2016). Studies of stocked fish over broader spatial extents (>1,000 km) have focused mainly on post-stocking dispersal using physical recapture data, and indicate that a few individuals move long distances (514–684 km; Durst & Francis, 2016; Zelasko, Bestgen, & White, 2010). For example, Zelasko et al. (2010) showed that the longest movements made were those initially following stocking events and movements were mostly in downstream directions. Despite knowledge of how fragmentation and study design influence interpretations of fish movement (Gowan, Young, Fausch, & Riley, 1994), razorback sucker movement studies are typically limited in spatial extent because of the remoteness of study areas and the resources needed to tag and recapture sufficient numbers of fish to adequately describe movement patterns. However, by combining passive integrated transponder (PIT) tagging technology across the basin and developing data-sharing programmes by multiple agencies, data can begin to be synthesized across a broader geographical extent to discern the scales at which individuals in the Colorado River basin are moving among novel reservoir and river habitats, which may lead to a better understanding of population connectivity and further the conservation of the species.

Assessing movement is critical to evaluate connectivity within a novel ecosystem featuring large river corridors connected to a large reservoir. Extensive tagging and stocking efforts across the Colorado River basin can provide a better understanding of the spatial ecology of imperilled fishes. Movements were characterized of razorback sucker collected in Lake Powell into its two main tributary inflows that have contrasting access to upstream river habitats. Specifically, Lake Powell is fed by the Colorado River that offers fish unimpeded access to the upper Colorado River and associated tributaries. In contrast, the San Juan River is blocked by a 6 m tall waterfall approximately 30 km upstream of the current river–reservoir transition zone (Cathcart, Pennock, et al., 2018). By linking PIT-tags to encounter records compiled in a multi-agency database and tracking acoustic-tagged fish, basin-wide dispersal capability was assessed, the proportion of fish moving between the reservoir and rivers, and movement of razorback sucker translocated upstream of the waterfall barrier. Specifically three questions were addressed: 1. Where do razorback sucker captured in the Colorado River arm of Lake Powell redistribute?, 2. What is the proportion of fish moving upstream from the San Juan River arm of Lake Powell to the waterfall?, and 3. Where do fish move after translocation and what proportion of fish return below the waterfall? Given that fish populations consist of individuals displaying heterogeneous movement behaviours (Radinger & Wolter, 2014), it was expected that the majority of individuals would remain in the river–reservoir inflow and some fish would move into rivers upstream of Lake Powell. Although movement into the San Juan River is impeded by a waterfall, it was still expected that fish would make annual movements between the reservoir and river below the waterfall. For translocated fish, it was expected that individuals would move relatively long distances into upstream river habitat deemed suitable for spawning and most fish would remain resident in the San Juan River (Cathcart, Pennock, et al., 2018).

2 | METHODS

2.1 | Study area

The upper Colorado River basin drains parts of Colorado, New Mexico, Utah, and Wyoming before entering Lake Powell, an impoundment that has inundated the historical confluence of the Colorado and San Juan rivers since Glen Canyon Dam was closed in 1963 (Figure 1). At full pool, Lake Powell inundates the Colorado River arm 299 km upstream approximately 30 km downstream from

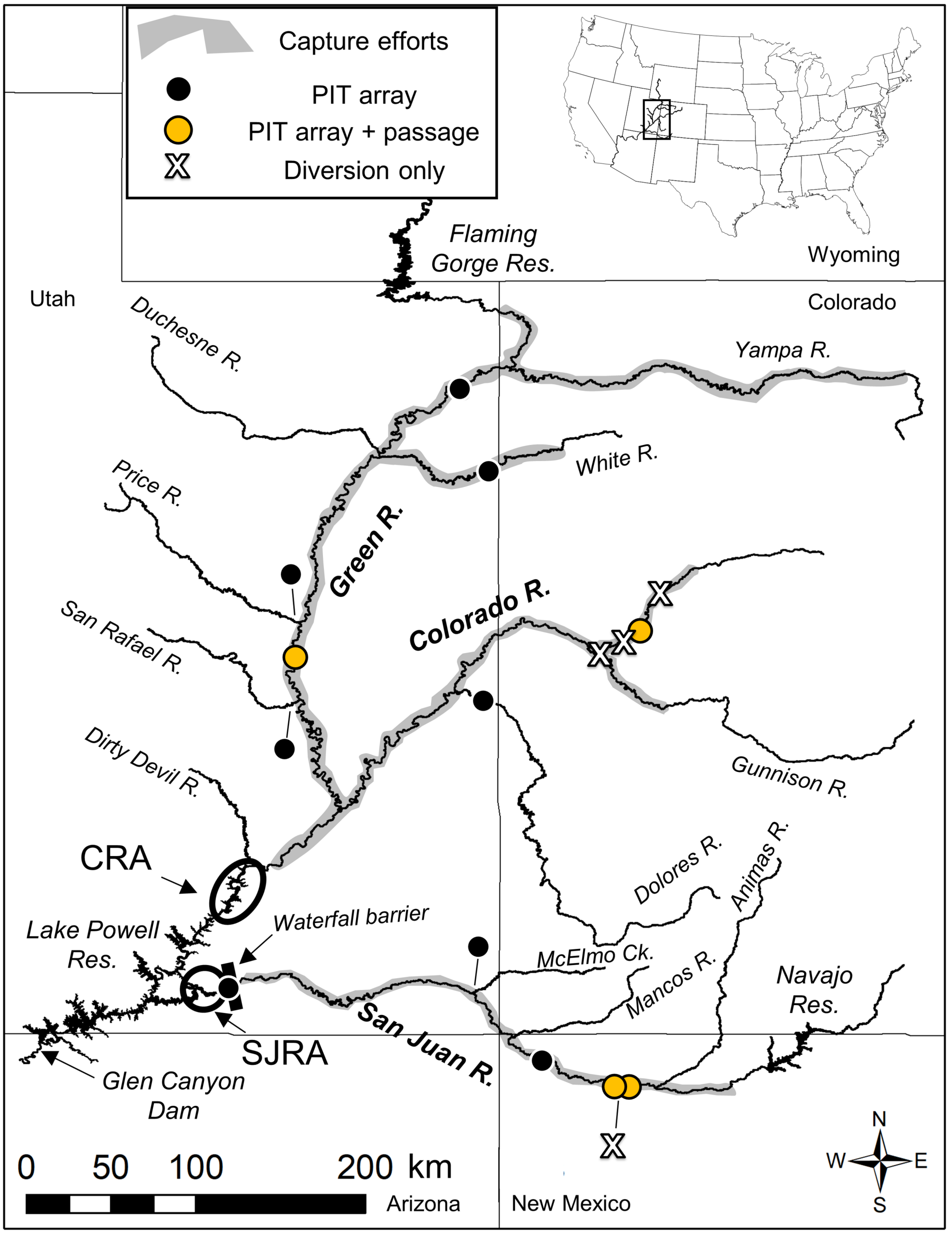

FIGURE 1 Major rivers and reservoirs of the upper Colorado River basin. Sampling for the occurrence of razorback sucker in Lake Powell reservoir inflow areas occurred in the Colorado River arm (CRA) and San Juan River arm (SJRA). Sampling efforts occur throughout the basin for various projects (grey shading), and various PIT-tag antenna arrays have been installed or are maintained seasonally (filled dots). Antenna arrays are installed at several diversion weirs with associated fish passages (yellow filled dots). The Piute Farms Waterfall (Waterfall barrier) is located at the upper end of the San Juan River arm of Lake Powell

the confluence with the Green River. The San Juan River arm is inundated for approximately 110 km upstream of its historical confluence with the Colorado River.

Management for imperilled fishes consistently occurs in three major river systems (Green, Colorado, and San Juan rivers) of the upper Colorado River basin. These rivers differ in mean annual discharge and the degree to which small diversion structures impede movement in upstream reaches (Figure 1). For instance, from 2014 to 2018 mean annual discharge from the Colorado and Green rivers combined was about eight times that of the San Juan River (USGS gauge data). Fishes in Lake Powell have access to upstream river habitat on the Colorado River arm of the reservoir. On the San Juan River arm, upstream access is limited by the Piute Farms Waterfall (hereafter referred to as the 'waterfall'). The waterfall recently emerged in the inflow area after reservoir elevations dropped following the reservoir initially filling to capacity in the 1980s and the river cutting a new channel through deposited sediments (see Cathcart, Pennock, et al., 2018 for more details). With the exception of a 2-week inundation event in late July and early August of 2011, the waterfall has presented a complete barrier to upstream fish movement since 2001 and periodically formed in two different places between 1992 and 2001 (Durst & Francis, 2016; Ryden & Ahlm, 1996). In addition to variable access to river habitat directly upstream of Lake Powell inflow areas, fishes must also contend with problems of fragmentation further upstream, where eight relatively large diversion structures are located on the Green, Colorado, Gunnison, and San Juan rivers. These structures have varying degrees of fish passage capability, including no passage structure, non-selective passages, or selective passages (Figure 1). Although fish passages can increase the functional connectivity of fish populations (Birnie-Gauvin, Franklin, Wilkes, & Aarestrup, 2019; McLaughlin et al., 2013; Pennock, Bender, et al., 2018), no quantitative evaluation (e.g. passage efficiency; Noonan, Grant, & Jackson, 2012; Roscoe & Hinch, 2010) of passage structures has been completed in the upper Colorado River basin apart from documenting the presence and relative abundance of fish species captured or detected within, upstream, or downstream of passages.

Recovery and maintenance of razorback sucker relies on intense management efforts administered through two federal recovery programmes. These programmes include a multidisciplinary group of researchers representing state, federal, tribal and private stakeholders. Accordingly, joint activities include education and outreach, operating hatchery facilities, and the formation of a centralized tagging database. As part of coordinated stocking efforts, most razorback sucker have been PIT-tagged prior to being stocked into upper Colorado and San Juan river systems (Cathcart, Pennock, et al., 2018), and all research and monitoring efforts associated with the programmes scan captured fishes for PIT-tags and tag previously untagged individuals. The programmes maintain a centralized database, in which all fish stocking, capture, tagging, and tag detection records are compiled from efforts across the entire upper Colorado River basin, including the San Juan River and Lake Powell (STReaMS, 2018).

2.2 | Data summary and analysis

All razorback sucker occurring in Lake Powell were stocked in upstream rivers and have moved downstream into the reservoir since being stocked. Although untagged fish are captured in the reservoir, the proportion of untagged fish either matches that from upstream rivers (e.g. tag loss in fishes from the Green, Colorado, and Gunnison rivers; Zelasko et al., 2010), or age estimates of untagged fish overlap with year classes of hatchery fish being stocked without PIT-tags in 2006 and 2007 (e.g. San Juan River arm; Furr, 2016). The lacustrine-transition zones (Thornton, Kimmel, & Payne, 1990) of the Colorado River arm of Lake Powell (CRA in Figure 1 & 2) were sampled in April, May, and June from 2014 to 2016 to assess the occurrence and number of razorback sucker (Albrecht et al., 2018). Fish were sampled with a combination of trammel nets and boat electrofishing. Any captured but previously untagged razorback sucker were PIT-tagged (Biomark, Boise, Idaho, 12-mm full-duplex, 134.2 kHz) before release. Concomitant with sampling events, a total of 44 razorback sucker were tagged with acoustic telemetry tags (Sonotronics, Inc., Tuscon, AZ, CT-05-48). Acoustic-tagged fish were either stocked from a hatchery (n = 13) or captured in the reservoir (n = 31) and released. To assess the redistribution of fish tagged in the reservoir, records were identified in the STReaMS database of razorback sucker physically captured in 2014–2016 in the Colorado River arm of Lake Powell. Then, the STReaMS database was queried for all post-capture re-encounters (physical captures, PIT-tag detections, telemetry detections) of these fish across the entire upper Colorado River basin. The distance was calculated between fish capture location in Lake Powell and their most upstream encounter. For this objective, re-encounters could have taken place any time between the capture of a fish in Lake Powell and December 13, 2018, when the database was queried. A standard set of river kilometres was provided with the STReaMS database to calculate movement distances for all objectives. From these data, frequency histograms (bin width = 25 km) were plotted of absolute movement distances (i.e. all values were considered positive). Kurtosis of this distribution was tested using an Anscombe-Glynn's test of kurtosis (Anscombe & Glynn, 1983) using the 'anscombe.test' function in the moments package in Program R version 3.5.1 (Komsta & Novomestky, 2015; R Core Team, 2018). Logistic regression was performed using the 'glm' function to assess whether days at large and fish total length were significant (α = 0.05) predictors of whether a fish was encountered outside of the capture area. Likelihood ratio tests were used to assess significance using the 'Anova' function in the car package (Fox & Weisberg, 2011). For fish that moved outside of the capture area, correlations were tested between movement distances and days at large and fish total length, two common predictors of fish movement (Radinger & Wolter, 2014).

Fish sampling efforts occurred throughout the upper Colorado River basin but varied in spatial and temporal distribution and sampling methods depending on the goals of individual projects, including sampling for non-native fish removal, Colorado pikeminnow (*Ptychocheilus lucius*) and humpback chub (*Gila cypha*) population estimates, adult native fish monitoring, and various other research projects across

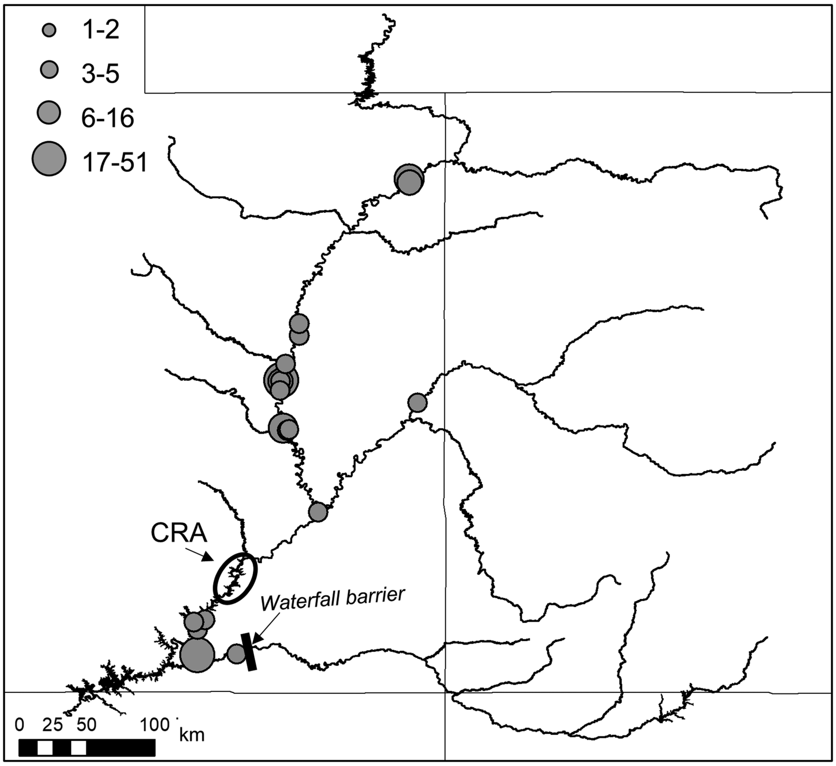

FIGURE 2 Most upstream encounter locations (physical captures, PIT-tag detections, and telemetry detections) of individual razorback sucker (*n* = 107; STReaMS, 2018) following physical capture in the Colorado River Arm (CRA) of Lake Powell reservoir in 2014–2016. The size of dots corresponds to the number of individuals encountered at a location

>1,800 km of river (Figure 1; Cathcart, Pennock, et al., 2018; Franssen, Davis, Ryden, & Gido, 2014; Zelasko et al., 2010). In addition to efforts that physically capture fish, the use of PIT-tag antennas to re-encounter PIT-tagged fishes has increased throughout the basin at mainstem and tributary stream locations (Bottcher et al., 2013; Cathcart, Gido, McKinstry, & MacKinnon, 2018; Cathcart, Pennock, et al., 2018). In addition, acoustic receivers were opportunistically maintained and deployed in both arms of Lake Powell. Thus, analysis was limited to quantifying the broad dispersal capability of razorback sucker outside the Colorado River arm of the reservoir because sampling was not standardized, and representative PIT-tag antenna and acoustic receiver locations were not placed systematically throughout the basin.

To quantify the proportion of razorback sucker moving between reservoir and river habitats, capture data were used from 2017 and 2018 in the San Juan River arm of Lake Powell (SJRA in Figure 1) and PIT-tag detection data from 2017 and 2018 at the waterfall upstream on the San Juan River. Fish sampling was conducted in the lacustrine-transition zones of the San Juan River arm of Lake Powell with trammel netting and electrofishing, as previously described for the Colorado River arm. PIT-tag detections were compiled by a submersible antenna (Biomark, Inc., Boise, Idaho) located directly downstream of the waterfall. Estimates of exchange between reservoir and river habitat were considered to be more robust in the San Juan River arm, because migrating fish aggregate below the waterfall, creating high tag detection probabilities for PIT-tag antennas there (0.6–0.9; Cathcart, Pennock, et al., 2018). The proportion of fish captured in the reservoir and then detected at the PIT-tag antenna below the waterfall within a calendar year (365 days post-capture) was calculated and non-parametric confidence intervals for the proportion of fish moving were estimated using 10,000 bootstrap iterations.

To mimic historical access to river habitats in the San Juan River upstream of the waterfall, razorback sucker were translocated upstream of the waterfall in late winter – early spring of 2016 and 2017. Fish were translocated during this period because detections and captures indicated abundant sexually mature, ripe fish directly below the waterfall during periods when temperatures and flows were approaching or at observed spawning conditions (Cathcart, Pennock, et al., 2018). Razorback sucker were captured below the waterfall with raft-mounted electrofishing, scanned for the presence of a PIT-tag, injected with one if one was not present, and translocated by motorized raft up to 3.5 km upstream depending on flow conditions. Although fallback of translocated fish is possible (Hagelin, Calles, Greenberg, Nyqvist, & Bergman, 2016), it was assumed that fish were motivated to move upstream based on the number of fish in spawning condition (Cathcart, Pennock, et al., 2018). Fish could not be transported further upstream because of a rapid and cobble bar (~1 km long) that were not passable by boat. A subset of fish was also tagged either with acoustic tags in 2016 (*n* = 10) or dual acoustic-radio telemetry tags in 2017 (*n* = 32; ART-01-80). Fish could be re-encountered via a combination of physical re-captures, passive detections (PIT), and active detections in 2017 only (telemetry). 'Minimum distance moved' was used to describe the river distance between the waterfall and the most upstream encounter location. This term is described as a 'minimum', because only data on the first and last encounter locations was used, not any movement between or outside these two points. Similarly, 'minimum river residence time' was calculated as the number of days between the translocation of a fish and when it was last encountered in the river. This metric is a conservative estimate as it is not known if a fish left the river after re-encounter. Whether any of these fish returned downstream of the waterfall was assessed using

TABLE 1 Number of razorback suckers originally stocked into rivers of the upper Colorado River system (n = 627 out of 722) that were subsequently captured in the Colorado River arm of Lake Powell in 2014–2016

Stocking river (rkm[a]; range)	Year 2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
Colorado River (244–385)	3	1	4	4	3	7	3	2	3	2	2	2	1	
Green River (192–511)		5	18	13	14	42	35	82	106	113	91	46	9	1
Gunnison River (91)						2				1		7	5	
Total	3	6	22	17	17	51	38	84	109	116	93	55	15	1
Total stocked across upper basin	11,941	17,437	25,260	22,643	45,521	46,547	39,165	47,061	59,970	51,945	47,438	34,698	16,422	13,592

Note: The total number stocked per year across the upper basin is also presented.
[a]river kilometre (rkm).

physical re-captures, passive detections (PIT and acoustic telemetry in the reservoir), and active detections (radio telemetry in the river).

3 | RESULTS

3.1 | Where do razorback sucker captured in the Colorado River arm of the reservoir redistribute?

Between 2014 and 2016, 722 individual razorback suckers (mean ± SD; 485 ± 57 mm TL) were captured in the Colorado River arm of Lake Powell. Most (87%) of these fish had stocking records in upper basin rivers (Table 1). The majority, 427 fish (59%), were never re-encountered, so are not reported on further. In total, 295 fish were re-encountered after capture. Sixty-four per cent (n = 188 of 295) were only re-encountered within the original capture area, and 108 of those individuals were recaptured in multiple years. Thirty-six per cent (n = 107 of 295) were either recaptured (n = 8) or detected (n = 99) outside the capture area including in the Green and Colorado river systems as well as across the reservoir in the San Juan River arm of Lake Powell (Figure 2). Of these 107 fish, 33 were originally captured in 2014, 40 in 2015, and 35 in 2016. The distribution of movement distances (n = 295) showed significant kurtosis (kurtosis = 3.86, P = 0.01; Figure 3). Fish that were at large for longer periods of time were more likely to be encountered outside the capture area (GLM: likelihood ratio = 57.8, $P < 0.001$), but fish total length was not a significant predictor (likelihood ratio = 3.2, P = 0.08). Of fish that left the capture area, distance moved was not correlated with days at large (r = –0.08, df = 105, P = 0.39) or fish total length (r = 0.04, df = 105, P = 0.67). Passive detections on PIT-tag antennas comprised the majority of re-encounters. Fifty-six fish were encountered in the Green River at permanent PIT-tag antenna arrays near the Tusher Diversion weir, approximately 300 km upstream of the reservoir (Figure 3). After this antenna system was installed in May 2016, cumulative tag detections sharply increased. Fish from all capture cohorts were detected – specifically, 13 fish originally captured in 2014, 22 in 2015, and 21 in 2016. Opportunistically placed PIT-tag antennas in the upper Green River detected 14 individuals approximately 600 km upstream of the Lake Powell capture area. All re-encounters of fish in the San Juan River arm of Lake Powell were passive detections of either PIT-tags (n = 2) or acoustic telemetry tags (n = 17). Of these 17 acoustically tagged fish, 16 were fish captured from the reservoir and one was stocked into the reservoir in 2015.

3.2 | What is the proportion of fish moving upstream from the San Juan River arm of Lake Powell to the waterfall?

Fish moved annually among reservoir and river habitats in the San Juan River arm of Lake Powell, and proportions were relatively consistent across years. In 2017, 147 razorback sucker (496 ± 39 mm TL) were captured in the lacustrine transition zones of the San Juan River

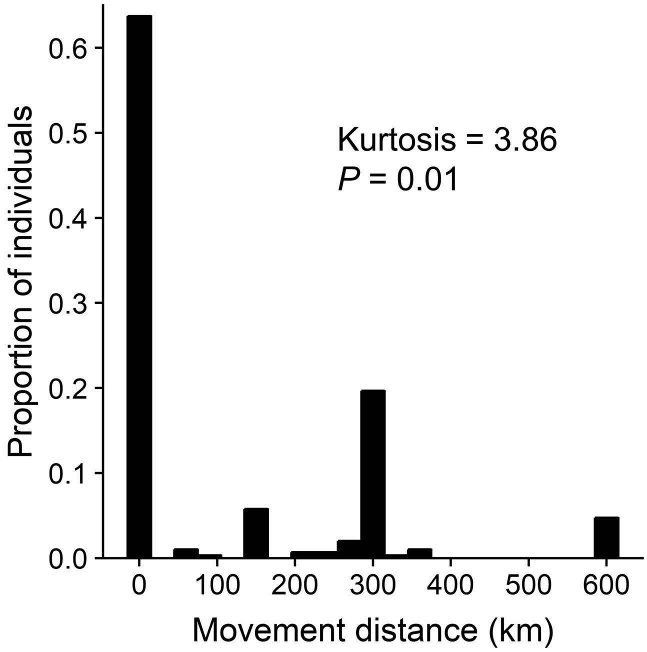

FIGURE 3 Absolute distances moved by razorback sucker (n = 295) that were initially captured in the Colorado River arm of Lake Powell and encountered throughout the upper Colorado River basin. Sixty-four per cent were only re-encountered within the original capture area, and 36% were re-encountered outside the original capture area. The distribution showed significant leptokurtosis

arm of Lake Powell, ~30–40 km downstream of the waterfall. After being captured in the reservoir, 29% (95% CI [21–36%]) moved upstream towards river habitat and were later detected at the waterfall within a year of being captured in the reservoir. In 2018, 20% (95% CI [12–30%]) of 74 reservoir-captured fish were detected at the waterfall within a year.

3.3 | Where do fish move after translocation and what proportion of fish return below the waterfall?

One hundred and fifty-two razorback suckers were captured and translocated in 2016 and 151 in 2017 (492 ± 39 mm TL; Table 2). In 2016, nine of 152 fish were re-encountered in the river (Figure 4). Six of those nine fish were physically recaptured, and three fish were detected on PIT-tag antennas. Eight fish moved at least 99 km upstream, including one fish that moved upstream 307 km to the Public Service Company of New Mexico (PNM) diversion, which has a selective fish passage structure. The minimum distance moved upstream averaged 218 km, and minimum residence time ranged from 17 to 536 days. In 2017, 20 of 151 fish were re-encountered in the river by physical recapture (n = 2), PIT-tag antenna detection (n = 4), or telemetry detection (n = 14) with a range of minimum distances travelled between 17 and 186 km and a minimum residence time between 13 and 132 days. In general, fish were not detected as far upstream in 2017 compared with 2016 (Figure 4). By July, active

TABLE 2 Summary of encounters (physical captures, PIT-tag detections, telemetry detections) of razorback sucker captured immediately downstream of the Piute Farms Waterfall in 2016–2017 and subsequently translocated 0.2–3.5 km upstream into the San Juan River

Year	Number translocated	Number encountered in river	Minimum distance moved (km; mean, range)	Minimum residence time (days; mean, range)	Number never re-encountered	Number encountered back in Lake Powell
2016	152	9 (6%)	218, 99–307	182, 17–536	27 (18%)	123 (81%)
2017	151	20 (13%)	90, 17–186	39, 13–132	27 (18%)	119 (79%)

Note: Percentages following numbers are relative to the number translocated in each year. Encounters were assessed via records in the STReaMS database from the date of translocation until December 2018.

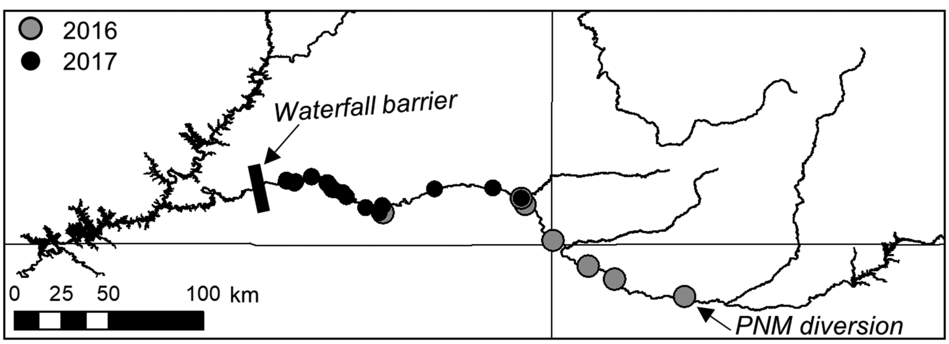

FIGURE 4 Encounter locations (physical captures, PIT-tag detections, or telemetry detections) of razorback sucker that were translocated upstream of the Piute Farms Waterfall and into the San Juan River in 2016–2017. The most upstream encounter occurred at the Public Service Company of New Mexico (PNM) Diversion (2016). Records accessed from the STReaMS database included any encounters after the date of translocation until December 13, 2018

telemetry trips covering 290 km of river detected none of the 32 telemetry-tagged fish upstream of the waterfall. The same number of fish (*n* = 27) in both years were not re-encountered after translocation. Eighty per cent and 79% of translocated fish from 2016 and 2017, respectively, were re-encountered back downstream of the waterfall within a year (Table 2).

4 | DISCUSSION

Razorback sucker movement was quantified across an entire river basin relative to novel habitat types, including movements through a large reservoir and upstream into river networks. By quantifying movement potential across a broad spatial extent, these data build on previous evidence of trans-basin movements (Durst & Francis, 2016), and suggest that there is connectivity between populations of razorback sucker in major tributary arms of the upper Colorado River basin that is maintained by movement of more than a few individuals. The distribution of movement distances displayed significant kurtosis as has been reported from other studies on fish movement (Fraser et al., 2001; Radinger & Wolter, 2014; Wells et al., 2017), and about one-third of fish made long-distance movements in this study. Also, because of limitations on where PIT antennas were located, the number of fish making shorter movement distances was likely to have been underestimated. Notably, 17 of 44 acoustic-tagged razorback sucker moved from the Colorado River arm through lacustrine habitat to the San Juan River arm, a distance of at least 170 km. These results suggest that razorback sucker have high dispersal capability through both lacustrine and river habitats and can move upstream distances of more than 600 km where unimpeded in the current riverscape. The results also suggest that about one-third of the individuals dwelling in the reservoir are moving upstream to river habitat and this was consistent among years. This is the minimum proportion of individuals making annual movements from the reservoir to rivers upstream, given our assumption that all fish migrating to the waterfall would be detected. Although reservoirs have been considered movement barriers for riverine species (Hudman & Gido, 2013; Pelicice et al., 2015), the data suggest that razorback sucker in Lake Powell and its adjoining tributary networks function as metapopulations where there is notable exchange of individuals among major habitats.

Movement among spatiotemporally dynamic habitats is likely to be important for long-lived, periodic strategists such as razorback sucker, which are thought to have evolved bet-hedging strategies to capitalize on environmental variation (e.g. water temperatures, flows) that plays out over broad spatial and temporal extents (Schindler, Armstrong, & Reed, 2015; Winemiller & Rose, 1992). Razorback sucker are hypothesized to experience a recruitment bottleneck in early life stages (Pennock, Farrington, & Gido, 2019; Schooley & Marsh, 2007) and this obviously must be remedied to establish genetic flow from migrating individuals. If recruitment conditions vary across large spatial and temporal scales, however, it is important that spawning adults can reach as many places as possible to increase the chances of successful recruitment (Cathcart, Gido, & Brandenburg, 2019; Lopes et al., 2019). Where fish have the most access to river habitat in the upper Colorado River basin, recruitment to adulthood by razorback sucker is still rarely documented (Bestgen et al., 2017), suggesting that connectivity is not the only management action required to ensure recovery of this species. Although increasing or maintaining connectivity may not override other limiting factors, such as temperature or rearing habitat necessary for successful recruitment of early life stages (Bestgen, 2008; Bestgen, Beyers, Haines, & Rice, 2006), it might increase the long-term viability of the entire metapopulation by ensuring immigration–emigration pathways are maintained and by allowing access to favourable habitats (Fagan, 2002; Fullerton et al., 2010; Gido, Whitney, Perkin, & Turner, 2016).

Although this study focused on the movement of razorback sucker, the occurrence of riverine species in reservoirs, and movement between reservoir arms and their associated river tributaries, is by no means unique to the Colorado River basin. Substantial exchanges of migrant fishes have been documented in other river–reservoir systems (Hladík & Kubečka, 2003; Říha et al., 2013), illustrating that mobile fish functionally connect rivers and reservoirs. For instance, Hladík and Kubečka (2003) found that 26 species and more than 11% of all fish biomass in Římov Reservoir, Czech Republic, migrated between the reservoir and the Malše River inflow. These movements were mainly associated with spawning runs into the river by cyprinids such as bleak (*Alburnus alburnus*), roach (*Rutilus rutilus*), and bream (*Abramis brama*) (among others), but also included Eurasian perch (*Perca fluviatilis*). Thus, reservoir-dwelling fishes will readily move between lacustrine and riverine habitats, particularly rheophilic species that might be searching for spawning or feeding habitat. Together with movements for spawning (Graeb, Willis, & Spindler, 2009), fishes might move among rivers and reservoirs to exploit spatiotemporally dynamic habitats near inflow areas offering abundant food, such as phytoplankton and zooplankton (Thornton et al., 1990), cover in turbid water from high sedimentation rates (Miranda et al., 2010), and complex habitat structure (deltas, submerged vegetation, higher water temperatures) no longer found or limited in upstream portions of regulated rivers (Bestgen, Haines, & Hill, 2011; Buckmeier et al., 2014; Volke, Scott, Johnson, & Dixon, 2015). Fisheries managers in reservoirs and rivers often have varying objectives (i.e. maximizing sport fish production versus conservation of native species), and these habitats have traditionally been managed as independent systems (Buckmeier et al., 2014). Identifying mechanistic drivers of fish movements within and among river and reservoir habitats could inform managers of ecological costs and benefits (e.g. growth, diet, survival, and spawning productivity) experienced by individuals exhibiting these movements, which would ultimately help to manage these systems more holistically (Buckmeier et al., 2014).

The majority of fish translocated upstream of the waterfall barrier on the San Juan River returned to the reservoir within a year. It is not immediately clear why so many fish returned back downstream of the waterfall. One possibility is that translocated fish were searching for suitable habitat (Carpenter-Bundhoo et al., 2020) but happened to move too far downstream, similar to how fish might have entered the reservoir after being stocked in the river. Alternatively, fish might have encountered spawning habitat, contributed to spawning, and actively moved back downstream to the inflow area where low-velocity habitat and trophic resources are presumed to be high. In the San Juan River upstream of the waterfall, spawning habitat might occur only 30–40 km upstream where translocated fish were found to aggregate immediately downstream of rapids and cobble bars in spawning condition (i.e. expressing eggs or milt; B. Hines and C. Pennock, pers. obs.). Translocation of fish is a means to mitigate river fragmentation for native species at places such as the waterfall, where preventing access to upstream river habitat by non-native fishes (e.g. striped bass *Morone saxatilis*) is an objective for managers (McLaughlin et al., 2013; Pennock, Durst, et al., 2018; Rahel & McLaughlin, 2018). Downstream movements by most fish in this study suggest that annual pre-spawn translocations of razorback sucker would be necessary for fish to gain access to spawning habitat upstream of the waterfall.

We acknowledge that the variable efforts used to re-encounter fish across the basin might limit the interpretation of razorback sucker dispersal patterns. For instance, although more translocated fish were encountered in the San Juan River in 2017 than in 2016, efforts to re-encounter fish were greater because of active telemetry tracking. In addition, the different detection probabilities among various methods used to re-encounter fish in this study (e.g., acoustic telemetry versus PIT-tag antennas) prevented a more rigorous quantification of the relative proportion of razorback sucker that moved among habitats. Even differences in detection probability using the same method but at different locations (e.g. PIT-tag antennas at Tusher Diversion versus the waterfall) probably exist and complicate quantitative efforts to assess fish movements at the population level. For these reasons, relative differences in the number of encounters among specific locations were not analysed, such as the number of fish detected at Tusher Diversion versus the waterfall, but instead the analyses focused on broad dispersal capabilities of razorback sucker throughout the upper Colorado River basin.

Conservation managers must acknowledge the effect of novel ecosystems on population dynamics of imperilled species. Novel aquatic ecosystems are now ubiquitous across the globe (Havel et al., 2005; Reidy Liermann et al., 2012), and many freshwater fishes contend with altered habitats and species assemblages. Although conservation efforts are challenged by increasing imperillment of species without a full understanding of the mechanisms driving their declines (Closs, Krkosek, & Olden, 2016), management might be more effective if efforts account for diverse life-history strategies (e.g. movements) that increase population resilience to environmental change (Allen & Singh, 2016; Hilborn, Quinn, Schindler, & Rogers, 2003; Schindler et al., 2015). A more complete understanding of how species use variable movement syndromes (Comte & Olden, 2018) among habitats in contemporary riverscapes, such as between rivers and reservoirs, could allow these habitats to be managed more completely for the benefit of imperilled species – especially if management promotes and maintains connectivity.

ACKNOWLEDGEMENTS

We thank the various researchers from multiple tribal, state and federal agencies, and other entities who contributed to data collection throughout the upper Colorado River basin and made their data available in STReaMS. Specifically, we thank D. Ryden (U.S. Fish and Wildlife Service; USFWS), N. Franssen (USFWS), S. Durst (USFWS), L. Bruckerhoff (Kansas State University; KSU), C. Hedden (KSU), B. Albrecht (BioWest), R. Keggeries (BioWest), M. Farringtion (American Southwest Ichthyological Researchers; ASIR), H. Brandenburg (ASIR), and S. Platania (ASIR) for assistance in recent field efforts in Lake Powell and the San Juan River. We also thank M. Trammell, S. Ross, M. Tobler, N. Franssen, W. Dodds, L. Bruckerhoff, J. Perkin, and two anonymous reviewers for comments and discussion that improved the manuscript. Permitting for data collection was provided by the Navajo Nation, National Park Service, and U.S. Fish and Wildlife Service. Funding for this study was provided by the U.S. Bureau of Reclamation (USBR) through various contracts, grants, and cooperative agreements to the Upper Colorado and San Juan River recovery programmes, and additional funding for translocation efforts was provided by a grant from the Salt River Project (administered by W. Stewart, USBR). Reference to trade names does not imply endorsement by the U.S. Government. The authors declare no conflict of interest.

ORCID

Casey A. Pennock https://orcid.org/0000-0002-3547-6477
Keith B. Gido https://orcid.org/0000-0002-4342-161X
Skyler C. Hedden https://orcid.org/0000-0003-3214-6752

REFERENCES

Albrecht, B. A., Mohn, H. E., Kegerries, R., McKinstry, M. C., Rogers, R., Francis, T., … Senger, B. (2018). Use of inflow areas in two Colorado River Basin reservoirs by the endangered razorback sucker (*Xyrauchen texanus*). *Western North American Naturalist*, *77*, 500–515. https://doi.org/10.3398/064.077.0410

Allen, A. M., & Singh, N. J. (2016). Linking movement ecology with wildlife management and conservation. *Frontiers in Ecology and Evolution*, *3*, 155. https://doi.org/10.3389/fevo.2015.00155

Anscombe, F. J., & Glynn, W. W. (1983). Distribution of the kurtosis statistic b_2 for normal statistics. *Biometrika*, *70*, 227–234. https://doi.org/10.2307/2335960

Bestgen, K. R. (2008). Effects of water temperature on growth of razorback sucker larvae. *Western North American Naturalist*, *68*, 15–20. https://doi.org/10.3398/1527-0904(2008)68[15:EOWTOG]2.0.CO;2

Bestgen, K. R., Beyers, D. W., Haines, G. B., & Rice, J. A. (2006). Factors affecting recruitment of young Colorado Pikemninnow: Synthesis of predation experiments, field studies, and individual-based modeling. *Transactions of the American Fisheries Society*, *135*, 1722–1742. https://doi.org/10.1577/T05-171.1

Bestgen, K. R., Haines, G. B., & Hill, A. A. (2011). Synthesis of flood plain wetland information: Timing of razorback sucker reproduction in the Green River, Utah, related to stream flow, water temperature, and flood plain wetland availability. Final Report. Larval Fish Laboratory Contribution 163, Upper Colorado River Endangered Fish Recovery Program, Denver, Colorado.

Bestgen, K. R., Shelly, R. C., Staffeldt, R. R., Breen, M. J., Snyder, D. E., & Jones, M. T. (2017). First reproduction by stocked Bonytail in the upper Colorado River basin. *North American Journal of Fisheries*

Management, *37*, 445–455. https://doi.org/10.1080/02755947.2017.1280571

Birnie-Gauvin, K., Franklin, P., Wilkes, M., & Aarestrup, K. (2019). Moving beyond fitting fish into equations: Progressing the fish passage debate in the Anthropocene. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *29*, 1095–1105. https://doi.org/10.1002/aqc.2946

Bottcher, J. L., Walsworth, T. E., Thiede, G. P., Budy, P., & Speas, D. W. (2013). Frequent usage of tributaries by the endangered fishes of the upper Colorado River basin: Observations from the San Rafael River, Utah. *North American Journal of Fisheries Management*, *33*, 585–594. https://doi.org/10.1080/02755947.2013.785993

Buckmeier, D. L., Smith, N. G., Fleming, B. P., & Bodine, K. A. (2014). Intra-annualvariation in river–reservoir interface fish assemblages: Implications for fish conservation and management in regulated rivers. *River Research and Applications*, *30*, 780–790. https://doi.org/10.1002/rra.2667

Carpenter-Bundhoo, L., Butler, G. L., Espinoza, T., Bond, N. R., Bunn, S. E., & Kennard, M. J. (2020). Reservoir to river: Quantifying fine-scale fish movements after translocation. *Ecology of Freshwater Fish*, *29*, 89–102. https://doi.org/10.1111/eff.12490

Cathcart, C. N., Gido, K. B., & Brandenburg, W. H. (2019). Spawning locations within and among tributaries influence flannelmouth sucker offspring experience. *Transactions of the American Fisheries Society*, *148*, 963–977. https://doi.org/10.1002/tafs.10191

Cathcart, C. N., Gido, K. B., McKinstry, M. C., & MacKinnon, P. D. (2018). Patterns of fish movement at a desert river confluence. *Ecology of Freshwater Fish*, *27*, 492–505. https://doi.org/10.1111/eff.12364

Cathcart, C. N., McKinstry, M. C., MacKinnon, P. D., & Ruffing, C. M. (2019). A tribute to tributaries: Endangered fish distributions within critical habitat of the San Juan River, U.S.A. *North American Journal of Fisheries Management*, *38*, 1015–1025. https://doi.org/10.1002/nafm.10335

Cathcart, C. N., Pennock, C. A., Cheek, C. A., McKinstry, M. C., MacKinnon, P. D., Conner, M. M., & Gido, K. B. (2018). Waterfall formation at a desert river–reservoir delta isolates endangered fishes. *River Research and Applications*, *34*, 948–956. https://doi.org/10.1002/rra.3341

Childress, E. S., Allan, J. D., & McIntyre, P. B. (2014). Nutrient subsidies from iteroparous fish migrations can enhance stream productivity. *Ecosystems*, *17*, 522–534. https://doi.org/10.1007/s10021-013-9739-z

Clarke, A. D., Telmer, K. H., & Shrimpton, J. M. (2007). Habitat use and movement patterns for a fluvial species, the Arctic grayling, in a watershed impacted by a large reservoir: Evidence from otolith microchemistry. *Journal of Applied Ecology*, *44*, 1156–1165. https://doi.org/10.1111/j.1365-2664.2007.01350.x

Clarkson, R. W., Marsh, P. C., Stefferud, S. E., & Stefferud, J. A. (2005). Conflicts between native fish and nonnative sport fish management in the southwestern United States. *Fisheries*, *30*, 20–27. https://doi.org/10.1577/1548-8446(2005)30[20:CBNFAN]2.0.CO;2

Closs, G. P., Krkosek, M., & Olden, J. D. (2016). *Conservation of freshwater fishes*. Cambridge: Cambridge University Press. https://doi.org/10.1017/CBO9781139627085

Comte, L., & Olden, J. D. (2018). Evidence for dispersal syndromes in freshwater fishes. *Proceedings of the Royal Society B*, *285*, 20172214. https://doi.org/10.1098/rspb.2017.2214

Cooke, S. J., Martins, E. G., Struthers, D. P., Gutowsky, L. F. G., Power, M., Doka, S. E., … Krueger, C. C. (2016). A moving target—Incorporating knowledge of the spatial ecology of fish into the assessment and management of freshwater fish populations. *Environmental Monitoring and Assessment*, *188*, 239. https://doi.org/10.1007/s10661-016-5228-0

Cooke, S. J., Paukert, C., & Hogan, Z. (2012). Endangered river fish: Factors hindering conservation and restoration. *Endangered Species Research*, *17*, 179–191. https://doi.org/10.3354/esr00426

Dalrymple, G. B., & Hamblin, W. K. (1998). K-Ar of Pleistocene lava dams in the Grand Canyon in Arizona. *Proceedings of the National Academy of Sciences*, *95*, 9744–9749. https://doi.org/10.1073/pnas.95.17.9744

Dunham, J. B., Young, M. K., Gresswell, R. E., & Rieman, B. E. (2004). Effects of fire on fish populations: Landscape perspectives on persistence of native fishes and nonnative fish invasions. *Forest Ecology and Management*, *178*, 183–196. https://doi.org/10.1016/S0378-1127(03)00061-6

Durst, S. L., & Francis, T. A. (2016). Razorback sucker transbasin movement through Lake Powell, Utah. *The Southwestern Naturalist*, *61*, 60–63. https://doi.org/10.1894/0038-4909-61.1.60

Fagan, W. F. (2002). Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology*, *83*, 3243–3249. https://doi.org/10.1890/0012-9658(2002)083[3243:CFAERI]2.0.CO;2

Fausch, K. D., Torgersen, C. E., Baxter, C. V., & Li, H. W. (2002). Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. *Bioscience*, *52*, 483–498. https://doi.org/10.1641/0006-3568(2002)052[0483:LTRBTG]2.0.CO;2

Flecker, A. S., McIntyre, P. B., Moore, J., Anderson, J. T., Taylor, B. W., & Hall, R. O. (2010). Migratory fishes as material and process subsidies in riverine ecosystems. In K. B. Gido & D. Jackson (Eds.), *Community ecology of stream fishes: Concepts, approaches, and techniques* (pp. 559–592). Bethesda: American Fisheries Society Symposium.

Fox, J., & Weisberg, S. (2011). *An {R} companion to applied regression* (second ed.). Thousand Oaks, CA: Sage. Retrieved from http://socserv.socsci.mcmaster.ca/jfox/Books/Companion

Franssen, N. R., Davis, J. E., Ryden, D. W., & Gido, K. B. (2014). Fish community responses to mechanical removal of nonnative fishes in a large southwestern river. *Fisheries*, *39*, 352–363. https://doi.org/10.1080/03632415.2014.924409

Fraser, D. F., Gilliam, J. F., Daley, M. J., Le, A. N., & Skalski, G. T. (2001). Explaining leptokurtic movement distributions: Intrapopulation variation in boldness and exploration. *The American Naturalist*, *158*, 124–135. https://doi.org/10.1086/321307

Fullerton, A. H., Burnett, K. M., Steel, E. A., Flitcroft, R. L., Pess, G. R., Feist, B. E., … Sanderson, B. L. (2010). Hydrological connectivity for riverine fish: Management challenges and research opportunities. *Freshwater Biology*, *55*, 2215–2237. https://doi.org/10.1111/j.1365-2427.2010.02448.x

Furr, W. (2016). San Juan River razorback sucker *Xyrauchen texanus* & Colorado pikeminnow *Ptychocheilus lucius* population augmentation: 2015. Final report to San Juan River Basin Recovery Implementation Program, US Fish & Wildlife Service.

Gido, K. B., Whitney, J. E., Perkin, J. S., & Turner, T. F. (2016). Fragmentation, connectivity and fish species persistence in freshwater ecosystems. In G. P. Closs, M. Krkosek, & J. D. Olden (Eds.), *Conservation of freshwater fishes* (pp. 292–323). Cambridge: Cambridge University Press. https://doi.org/10.1017/CBO9781139627085.011

Glenn, E. P., Lee, C., Felger, R., & Zengel, S. (1996). Effects of water management on the wetlands of the Colorado River Delta, Mexico. *Conservation Biology*, *10*, 1175–1186. https://doi.org/10.1046/j.1523-1739.1996.10041175.x

Gowan, C., Young, M. K., Fausch, K. D., & Riley, S. C. (1994). Restricted movement in resident stream salmonids: A paradigm lost? *Canadian Journal of Fisheries and Aquatic Sciences*, *51*, 2626–2637. https://doi.org/10.1139/f94-262

Graeb, B. D. S., Willis, D. W., & Spindler, B. D. (2009). Shifts in sauger spawning locations after 40 years of reservoir ageing: Influence of a novel delta ecosystem in the Missouri River, USA. *River Research and Applications*, *25*, 153–159. https://doi.org/10.1002/rra.1107

Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., … Zarfl, C. (2019). Mapping the world's free-flowing rivers. *Nature*, *569*, 215–221. https://doi.org/10.1038/s41586-019-1111-9

Hagelin, A., Calles, O., Greenberg, L., Nyqvist, D., & Bergman, E. (2016). The migratory behaviour and fallback rate of landlocked Atlantic salmon (*Salmo salar*) in a regulated river: Does timing matter? *River Research and Applications*, *32*, 1402–1409. https://doi.org/10.1002/rra.3007

Havel, J. E., Lee, C. E., & Vander Zanden, J. M. (2005). Do reservoirs facilitate invasions into landscapes? *Bioscience*, *55*, 518–525. https://doi.org/10.1641/0006-3568(2005)055[0518:DRFIIL]2.0.CO;2

Hilborn, R., Quinn, T. P., Schindler, D. E., & Rogers, D. E. (2003). Biocomplexity and fisheries sustainability. *Proceedings of the National Academy of Sciences*, *100*, 6564–6568. https://doi.org/10.1073/pnas.1037274100

Hladík, M., & Kubečka, J. (2003). Fish migration between a temperate reservoir and its main tributary. *Hydrobiologia*, *504*, 251–266. https://doi.org/10.1023/B:HYDR.0000008525.46939.42

Hobbs, R. J., Arico, S., Aronson, J., Baron, J. S., Bridgewater, P., Cramer, V. A., … Zobel, M. (2006). Novel ecosystems: Theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, *15*, 1–7. https://doi.org/10.1111/j.1466-822X.2006.00212.x

Hudman, S. P., & Gido, K. B. (2013). Multi-scale effects of impoundments on genetic structure of creek chub (*Semotilus atromaculatus*) in the Kansas River basin. *Freshwater Biology*, *58*, 441–453. https://doi.org/10.1111/fwb.12079

Junge, J., Museth, J., Hindar, K., Kraabol, M., & Vollestad, L. A. (2014). Assessing the consequences of habitat fragmentation for two migratory salmonid fishes. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *24*, 297–311. https://doi.org/10.1002/aqc.2391

Komsta, L., & Novomestky, F. 2015. moments: Moments, cumulants, skewness, kurtosis and related tests. R package version 0.14. Retrieved from https://CRAN.R-project.org/package=moments

Lopes, J. M., Pompeu, P. S., Alves, C. B. M., Peressin, A., Prado, I. G., Suzuki, F. M., … Kalapothakis, E. (2019). The critical importance of an undammed river segment to the reproductive cycle of a migratory Neotropical fish. *Ecology of Freshwater Fish*, *28*, 302–316. https://doi.org/10.1111/eff.12454

Lucas, M. C., & Baras, E. (2001). *Migration of freshwater fishes*. Oxford, UK: Blackwell Science Ltd. https://doi.org/10.1002/9780470999653

McIntyre, P. B., Reidy Liermann, C., Childress, E., Hamann, E. J., Hogan, J. D., Januchowski-Hartley, S. R., … Pracheil, B. M. (2016). Conservation of migratory fishes in freshwater ecosystems. In G. P. Closs, M. Krkosek, & J. D. Olden (Eds.), *Conservation of freshwater fishes* (pp. 324–360). Cambridge: Cambridge University Press. https://doi.org/10.1017/CBO9781139627085.012

McLaughlin, R. L., Smyth, E. R. B., Castro-Santos, T., Jones, M. L., Koops, M. A., Pratt, T. C., & Vélez-Espino, L.-A. (2013). Unintended consequences and trade-offs of fish passage. *Fish and Fisheries*, *14*, 580–604. https://doi.org/10.1111/faf.12003

Minckley, W. L. (1983). Status of the razorback sucker, *Xyrauchen texanus* (Abbott), in the Lower Colorado River Basin. *The Southwestern Naturalist*, *28*, 165–187. https://doi.org/10.2307/3671385

Minckley, W. L., & Deacon, J. E. (1991). *Battle against extinction. Native fish management in the American West*. Tucson: The University of Arizona Press.

Miranda, L. E., Spickard, M., Dunn, T., Webb, K. M., Avcock, J. N., & Hunt, K. (2010). Fish habitat degradation in U. S. Reservoirs. *Fisheries*, *35*, 175–184. https://doi.org/10.1577/1548-8446-35.4.175

Modde, T., & Irving, D. B. (1998). Use of multiple spawning sites and seasonal movement by razorback suckers in the middle Green River, Utah. *North American Journal of Fisheries Management*, *18*, 318–326. https://doi.org/10.1577/1548-8675(1998)018<0318:UOMSSA>2.0.CO;2

Noonan, M. J., Grant, J. W. A., & Jackson, C. D. (2012). A quantitative assessment of fish passage efficiency. *Fish and Fisheries*, *13*, 450–464. https://doi.org/10.1111/j.1467-2979.2011.00445.x

Pelicice, F. M., Pompeu, P. S., & Agostinho, A. A. (2015). Large reservoirs as ecological barriers to downstream movements of Neotropical migratory fish. *Fish and Fisheries*, *16*, 697–715. https://doi.org/10.1111/faf.12089

Pennock, C. A., Bender, D., Hofmeier, J., Mounts, J. A., Waters, R., Weaver, V. D., & Gido, K. B. (2018). Can fishways mitigate fragmentation effects on Great Plains fish communities? *Canadian Journal of Fisheries and Aquatic Sciences*, *75*, 121–130. https://doi.org/10.1139/cjfas-2016-0466

Pennock, C. A., Durst, S. L., Duran, B. R., Hines, B. A., Cathcart, C. N., Davis, J. E., … Franssen, N. R. (2018). Predicted and observed responses of a nonnative Channel Catfish population following managed removal to aid the recovery of endangered fishes. *North American Journal of Fisheries Management*, *38*, 565–578. https://doi.org/10.1002/nafm.10056

Pennock, C. A., Farrington, M. A., & Gido, K. B. (2019). Feeding ecology of early life stage razorback sucker relative to other sucker species in the San Juan River, Utah. *Transactions of the American Fisheries Society*, *148*, 938–951. https://doi.org/10.1002/tafs.10188

Perkin, J. S., Gido, K. B., Costigan, K. H., Daniels, M. D., & Johnson, E. R. (2015). Fragmentation and drying ratchet down Great Plains stream fish diversity. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *25*, 639–655. https://doi.org/10.1002/aqc.2501

Perkin, J. S., Starks, T. A., Pennock, C. A., Gido, K. B., Hopper, G. W., & Hedden, S. C. (2019). Extreme drought causes fish recruitment failure in a fragmented Great Plains riverscape. *Ecohydrology*, *12*, e2120. https://doi.org/10.1002/eco.2120

R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for statistical computing. Retrieved from https://www.R-project.org/

Radinger, J., & Wolter, C. (2014). Patterns and predictors of fish dispersal in rivers. *Fish and Fisheries*, *15*, 456–473. https://doi.org/10.1111/faf.12028

Rahel, F. J., & McLaughlin, R. L. (2018). Selective fragmentation and the management of fish movement across anthropogenic barriers. *Ecological Applications*, *28*, 2066–2081. https://doi.org/10.1002/eap.1795

Reidy Liermann, C., Nilsson, C., Robertson, J., & Ng, R. Y. (2012). Implications of dam obstruction for global freshwater fish diversity. *Bioscience*, *62*, 539–548. https://doi.org/10.1525/bio.2012.62.6.5

Říha, M., Hladík, M., Mrkvička, T., Prchalová, M., Čech, M., Draštík, V., … Kubečka, J. (2013). Post-spawning dispersal of tributary spawning fish species to a reservoir system. *Folia Zoologica*, *62*, 1–13. https://doi.org/10.25225/fozo.v62.i1.a1.2013

Rodríguez, M. A. (2010). A modeling framework for assessing long-distance dispersal and loss of connectivity in stream fish. In K. B. Gido & D. Jackson (Eds.), *Community ecology of stream fishes: Concepts, approaches, and techniques* (pp. 559–592). Bethesda: American Fisheries Society Symposium.

Rolls, R. J., Ellison, T., Faggotter, S., & Roberts, D. T. (2013). Consequences of connectivity alteration on riverine fish assemblages: Potential opportunities to overcome constraints in applying conventional monitoring designs. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *23*, 624–640. https://doi.org/10.1002/aqc.2330

Roscoe, D. W., & Hinch, S. G. (2010). Effectiveness monitoring of fish passage facilities: Historical trends, geographical patterns and future directions. *Fish and Fisheries*, *11*, 12–33. https://doi.org/10.1111/j.1467-2979.2009.00333.x

Ryden, D. W., & Ahlm, L. A. (1996). Observations on the distribution and movements of Colorado squawfish, *Ptychocheilus lucius*, in the San Juan River, New Mexico, Colorado, and Utah. *The Southwestern Naturalist*, *41*, 161–168. https://www.jstor.org/stable/30055101

Sabater, S. (2008). Alterations of the global water cycle and their effects on river structure, function and services. *Freshwater Reviews*, *1*, 75–88. https://doi.org/10.1608/FRJ-1.1.5

Schindler, D. E., Armstrong, J. B., & Reed, T. E. (2015). The portfolio concept in ecology and evolution. *Frontiers in Ecology and Evolution*, *13*, 257–263. https://doi.org/10.1890/140275

Schlosser, I. J. (1991). Stream fish ecology: A landscape perspective. *Bioscience*, *41*, 704–712. https://doi.org/10.2307/1311765

Schooley, J. D., & Marsh, P. C. (2007). Stocking of endangered razorback suckers in the lower Colorado River basin over three decades: 1974-2004. *North American Journal of Fisheries Management*, *27*, 43–51. https://doi.org/10.1577/M05-088.1

Species Tagging, Research and Monitoring System (STReaMS). 2018. Accessed via the internet at https://streamsystem.org/ on 12/18/2018.

Sykes, G. (1937). The Colorado Delta. Publication no. 460. Carnegie Institution of Washington, D.C.

Thornton, K. W., Kimmel, B. L., & Payne, F. E. (1990). *Reservoir limnology: Ecological perspectives*. New York: John Wiley & Sons.

Tyus, H. M., & Karp, C. A. (1990). Spawning and movement of razorback sucker, *Xyrauchen texanus*, in the Green River basin of Colorado and Utah. *The Southwestern Naturalist*, *35*, 427–433. https://doi.org/10.2307/3672041

U.S. Fish and Wildlife Service (USFWS). (1998). Razorback sucker (*Xyrauchen texanus*) recovery plan. Denver, Colorado.

Volke, M. A., Scott, M. L., Johnson, W. C., & Dixon, M. D. (2015). The ecological significance of emerging deltas in regulated rivers. *Bioscience*, *65*, 598–611. https://doi.org/10.1093/biosci/biv040

Wells, W. G., Johnson, T. C., Gebhard, A. E., Paine, R. T. R., Hix, L. A., Ferrell, H. N., … Perkin, J. S. (2017). March of the sculpin: Measuring and predicting short-term movement of banded sculpin *Cottus carolinae*. *Ecology of Freshwater Fish*, *26*, 280–291. https://doi.org/10.1111/eff.12274

Winemiller, K. O., & Rose, K. A. (1992). Patterns of life-history diversification in North American fishes: Implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences*, *49*, 2196–2218. https://doi.org/10.1139/f92-242

Zelasko, K. A., Bestgen, K. R., & White, G. C. (2010). Survival rates and movement of hatchery-reared razorback suckers in the Upper Colorado River Basin, Utah and Colorado. *Transactions of the American Fisheries Society*, *139*, 1478–1499. https://doi.org/10.1577/T09-107.1

How to cite this article: Pennock CA, McKinstry MC, Cathcart CN, et al. Movement ecology of imperilled fish in a novel ecosystem: River-reservoir movements by razorback sucker and translocations to aid conservation. *Aquatic Conserv: Mar Freshw Ecosyst*. 2020;30:1540–1551. https://doi.org/10.1002/aqc.3399