scientific reports

Check for updates

OPEN

Individual return patterns of spawning flannelmouth sucker (*Catostomus latipinnis*) to a desert river tributary

Sophia M. Bonjour[1,2 ✉], Keith B. Gido[2], Charles N. Cathcart[3] & Mark C. McKinstry[4]

Tributaries provide temporal and spatial habitat heterogeneity in river networks that can be critical for parts of the life history of a species. Tributary fidelity can benefit individual fish undergoing spawning migrations by reducing time and energy spent exploring new areas and leveraging previous experience, but anthropogenic activities that fragment or degrade these systems can eliminate those benefits. We used multistate models based on passive integrated transponder (PIT) detection data from 2013 to 2023 to estimate the proportion of flannelmouth suckers (*Catostomus latipinnis*) migrating to a tributary, McElmo Creek, from the mainstem San Juan River for spawning. Survival varied among years and among states. The top model for migration probability included sex, with males slightly more likely to migrate (0.93 vs 0.90), and the next model identified interannual variation in migration probability ranging from 0.875 to 0.999 across years, indicating high site fidelity. Individuals showed consistency in relative arrival timing across years, with the highest correlation generally during years with greater spring discharge and extended tributary residence time. Successful tributary spawning may be important for the maintenance of the mainstem San Juan River flannelmouth sucker population, but site fidelity may be maladaptive where tributaries are vulnerable to human alterations.

Repeated spawning migrations of iteroparous fish can shape population dynamics and genetic structure[1], while presenting both potential conservation opportunities and threats. Access to tributary habitat may be essential to support large-river fish populations through portfolio effects, whereby multiple spawning locations stabilize and potentially increase recruitment success[2]. Partial migration, in which only a portion of a population migrates, is widespread in fishes and may allow for competitive release, trade-offs between predation risk and growth, or be a result of within population variation[3]. Fish can use tributaries in a variety of ways depending on how their life history needs match differences in physical, chemical, and biotic factors between tributary and mainstem habitats[4]. Mainstem rivers altered for transportation, sport fisheries, agriculture, hydropower, and water storage may be more difficult to conserve than smaller, less degraded tributaries[5,6]. However, tributaries are often not included in critical habitat designation for large-river fish and are, therefore, vulnerable to human activities that decrease habitat quality[7]. Preservation of tributary habitats may be particularly important for fish that demonstrate site fidelity by returning to the same tributary to spawn.

Riverine fish may express individual tendencies to balance trade-offs among spawning, migration, and survival. Site fidelity benefits individuals by reducing energetic costs of searching for available habitat and increasing local experience and acclimation[8]. Homing ability occurs in a number of species that return to previous spawning locations or natal sites[9], with mechanisms less researched in non-game species such as suckers[10]. Genetic divergence among individuals spawning in different tributaries can result as a product of high site fidelity and reproductive isolation, potentially leading to increased population genetic diversity[11]. However, site fidelity may be maladaptive in systems where these sites are rapidly degraded by human alterations[12]. A single failed year class could have minimal effect on tributary spawning if repeated spawning across the life of the fish compensates for the failed year class. However, several consecutive years of failed recruitment or restricting movement into a tributary could eliminate the fraction of the population with a tributary migration life history strategy.

[1]U.S. Geological Survey, Columbia Environmental Research Center, 4200 E New Haven Rd, Columbia, MO 65201, USA. [2]Division of Biology, Kansas State University, Manhattan, KS 66506, USA. [3]Alaska Department of Fish and Game, Alaska Freshwater Fish Inventory, Anchorage, AK 99518, USA. [4]Upper Colorado Regional Office, U.S. Bureau of Reclamation, Salt Lake City, UT 84138, USA. ✉email: sbonjour@usgs.gov

Populations may use other diversification strategies, in addition to partial migration, to improve chances of a successful spawn. Individual Sakhalin taimen (*Parahucho perryi*) may vary in spawning migration timing, with some individuals consistently moving earlier than others to increase the chance of optimal environmental conditions[13]. Skip spawning in fish might provide more opportunity for growth and recuperation of energetic costs that reduce the risk of mortality before future spawning events[14]. Return pattern of migratory spawners can depend upon sex, as seen with blue sucker (*Cycleptus elongatus*) where males return annually to spawning tributaries while female suckers skip years[15].

Flannelmouth sucker (*Catostomus latipinnis*) is a long-lived species that uses tributaries as a part of its reproductive strategy. Some flannelmouth suckers migrate into tributaries for spring spawning[16,17], exhibiting a partial migration strategy, with probability of tributary use being greatest for fish closer to tributaries[18]. Large spawning aggregations, such as those in tributaries, may increase mate encounter rate and fertilization success, allow for mate selection, or reduce predation rates on adults and offspring[19]. Spawning migrations occur in spring when tributaries warm faster than mainstem rivers. This could be important, as temperature is an important predictor of flannelmouth sucker migration timing[18]. Additionally, tributaries with natural flow regimes and bed material transport dynamics may have a higher prevalence of loose gravel, with aerated interstitial spaces for eggs to develop[20,21] than regulated mainstem rivers with suppressed or regulated flows and, therefore, increased substrate embeddedness[22]. Within-population variation in spawning migrations might benefit the species through bet-hedging against environmental change, habitat loss, and habitat modification. Indeed, flannelmouth sucker have declined less than other native species in the Colorado River that are less likely to spawn in tributaries[23].

Passive integrated transponder (PIT) data have been integral for understanding migration behaviors[24–26]. PIT tags and associated antennas provide a wealth of data that, when interpreted in the context of individual and environmental variability, allows characterization of the life history of a species and consideration of the ecological and evolutionary consequences of movement. Multi-year detection and re-detection of individuals provided by PIT antennas allow for the use of capture-recapture models to estimate spawning site fidelity, or the proportion of the population returning to a specific tributary each year to spawn[27]. Spatially explicit multistate models can be used to estimate survival and transition probabilities from mark–recapture data[28–30]. Survival and transition probabilities each contribute to the return patterns of migratory animals and advance the understanding of the ecology of a population, with tributary migration probability as an indicator of site fidelity. These models can also incorporate individual characteristics (sex, size, etc.) to examine the impact of individual variation on survival and transition probabilities. Although we have previously reported on factors associated with timing of tributary spawning based on multiple years of PIT data from tributaries of the Colorado and San Juan rivers[18], less is known about the return patterns of these migratory fish.

We used PIT antenna data from passive antenna arrays in the San Juan River basin to quantify individual return patterns of flannelmouth suckers to a tributary with large, documented spawning migrations[17,18]. McElmo Creek is the only tributary that consistently flows during the spawning season between the Animas River and Lake Powell (~ 320 km), providing one of few alternatives to mainstem spawning. Our research questions were (1) what were the return patterns of individuals to McElmo Creek for spawning and how are survival and migration probability affected by individual variables (sex, cohort), interannual environmental variability, and handling, (2) where are fish detected in the basin in years when they do not migrate into McElmo Creek for spawning, and (3) was relative arrival timing (ranked arrival order of individuals) consistent across years for individuals?

Site fidelity is prevalent in a variety of species[12], including suckers[16,31,32], so we anticipated relatively high migration probabilities to McElmo Creek for spawning. As tributary migration is more common for fish near the tributary[18], we hypothesized that annual spawning, as opposed to skip spawning, would be the dominant return pattern. We predicted similar patterns in males and females but interannual environmental variation would affect survival and migration probability as different environmental conditions across years, such as greater discharge or earlier warming, impact migration timing[18]. Previous research noted handling effects associated with PIT tagging on exit time, with captured flannelmouth suckers exiting from a spawning tributary within 48 h, while suckers detected only by PIT antenna array remained in the tributary for 10–12 days[26]; so, we tested if handling had even greater impacts than those previously noted and affected immediate apparent survival in our system. For the second question, we predicted that surviving fish not detected returning to McElmo Creek to spawn after previous use of the stream for spawning might be spawning in other tributaries or the mainstem or could have emigrated from the system. Finally, we hypothesized that relative return timing of individuals (i.e., early versus late arrival times) in the population would be consistent across years but more apparent in years with prolonged spawning seasons, as arrival times would be more widely spaced than in years with short spawning seasons[18]. Understanding the individual variation in return patterns of flannelmouth suckers to tributaries provides information about tributary use necessary to inform conservation and management decisions relevant to the maintenance and recovery of this native species and its habitat, including prioritization of stream connectivity restoration projects.

Methods
Study location
McElmo Creek is a tributary to the lower San Juan River with the most consistent flow apart from the Animas River (Fig. 1). Historically, McElmo Creek flowed intermittently, but the creation of McPhee Reservoir on the Dolores River, a tributary to the Colorado River, in 1986 and subsequent return flows from irrigation have resulted in more continuous flow, with only occasional periods of isolated pools during late summer. Flows in McElmo Creek typically decrease in spring after early runoff and peak with late summer monsoons (Supplementary Fig. S1). Discharge from the creek represents approximately two percent of the San Juan River discharge.
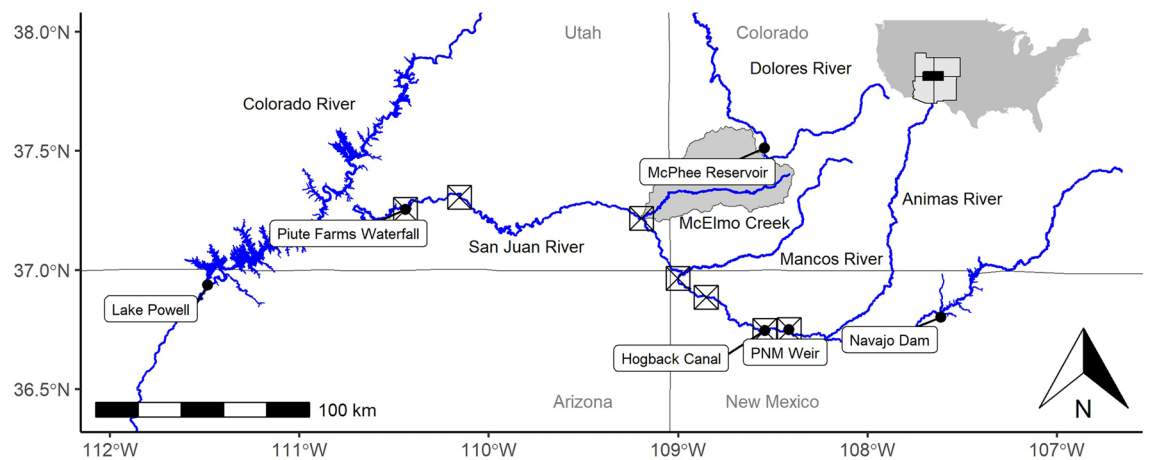
Fig. 1. The Colorado and San Juan rivers along with the focal tributary, McElmo Creek (watershed area in grey). Permanent passive integrated transponder (PIT) tag antenna locations are indicated by squares with an x. Black dots represent barriers.

Fish movement in the San Juan River is restricted to the section between Navajo Dam and Piute Farms Waterfall (Fig. 1), the latter of which prevents upstream movement except under extreme hydrologic conditions[25].

Passive integrated transponder data

Fish were tagged as described in Cathcart et al.[33,34] and Bonjour et al.[18]. Approximately 7000 flannelmouth suckers have been PIT tagged in the San Juan River basin since 2012, mostly in the San Juan River and McElmo Creek, with the primary goal of quantifying movement between the two systems. Two permanent PIT tag antenna systems in a pass-over style (BioMark, Boise, Idaho) were installed in McElmo Creek spanning the width of the creek near the confluence with the San Juan River (Fig. S2). The first, located 150 m upstream of the confluence with the San Juan River, was installed in 2012 and remains active, although seasonal storms and sedimentation have decreased reliability and coverage[34]. The second system was installed 300 m upstream of the confluence at a bridge crossing near Aneth, UT in January 2017. The location of these antennas is such that detections capture movement between the mainstem and tributary. Data from the McElmo Creek array are uploaded as 'Aneth Confluence' and 'Aneth Bridge' into the Species Tagging, Research and Monitoring System (STReaMS[35]) online database, which serves as a centralized repository for fish capture, detection, and stocking data from the Upper Colorado and San Juan River Endangered Fish Recovery programs. Data from other PIT antennas in the San Juan River were used for detections in the mainstem, ranging from Piute Farms Waterfall (186 rkm downstream of McElmo Creek) to Public Service Company of New Mexico (PNM) Weir, 121 km upstream of the confluence of McElmo Creek with the San Juan River (Fig. 1). Deployment and operation of these antennas were variable across the study, with additional information available from the STReaMS database.

Data were retrieved from STReaMS on 07 August 2023 and filtered for flannelmouth suckers that had any records in McElmo Creek. Fish measuring < 300 mm total length (TL) at tagging were excluded to focus on spawning individuals[36]. The work was approved by and carried out in accordance with the Animal Care and Use permit KSU IACUC#4494 for the use of PIT tags and radio transmitters in fish. The study was performed in accordance with ARRIVE guidelines.

Data analysis

Return patterns, survival, and migration probability

We tracked individuals tagged in McElmo Creek during the 2013, 2014, and 2015 spawning events to examine the proportion that returned annually for spawning. Tagging locations ranged from near the confluence of McElmo Creek and the San Juan River to 33 km upstream. We focused on these three tagging cohorts because the McElmo Creek PIT antenna array was not installed until after the spawning season in 2012 and efforts to tag fish spawning in McElmo Creek were reduced after 2015. Encounter histories created for 2013–2023 represent detections of individual flannelmouth suckers in McElmo Creek and the mainstem of the San Juan River. First, we summarized whether a fish was detected or not at the McElmo Creek PIT antenna array during the first 6 months of each year. Although spawning generally occurs in March and April[18], this elongated time allowed us to include early and late spawning movement while excluding movement associated with late-summer monsoons. Detection of an individual during the spawning season was assumed to indicate tributary use for spawning, as very few individuals were detected moving between the tributary and the mainstem during the rest of the year. We then expanded these encounter histories to two time periods per year with detections from the mainstem as a second state. Fish could be detected in the mainstem during the spawning period (January–June) or detected during the rest of the year (July–December). If fish were detected during the spawning season in both McElmo Creek and the mainstem, they were recorded in the McElmo Creek state. All analyses were conducted using Program R version 4.3.2[37].

Multi-state mark-recapture models can be used to estimate survival and movement probabilities between areas while taking into consideration variability in detection by estimating the probability of recapture[28–30].

Specifically, we were interested in the transition probability from mainstem to tributary during the spawning season. We constrained several parameters to reflect the process used to create encounter histories. As the antennas are at the confluence, detections during the non-spawning time period may be reflective of mainstem fish seeking temporary refuge from high flows, but do not reflect the same processes driving movement during the spawning time period[18,34], so we did not allow for detections during the non-spawning time period in the tributary. Transition probabilities from tributary to mainstem were fixed to 1 for all time periods, and transition probabilities from mainstem to tributary were fixed to 0 following the spawning time period, thus the transition probability estimate represents the migration probability. Since fish were not allowed to be detected in the tributary during the second half of the year, survival was fixed at 1 to minimize model estimated parameters, and detection probability was fixed at 0 for the tributary state during that time period.

Candidate models were built to test if survival and migration probability differed by individual covariates sex and tagging cohort (cohort), which served as a proxy for unmeasured factors that could limit fish migrating in a certain year (Table S1). For survival, we considered models that included different sets of covariates: sex, yearly environmental characteristics (time), handling where survival was distinct in the first year after tagging and constant across subsequent years (tag event), and state. For migration probability, we considered models that differed by individual covariates, year, or only state. Although we had 10 years of data, that time frame was insufficient to address all potential environmental factors that vary among years and may contribute to migration, so we used the covariate of time in years to represent unmeasured response to interannual variation in environmental conditions. To examine handling effects, we added the covariate 'tag event' in which survival in the year following tagging (i.e., handling) is estimated separately from survival in the subsequent years when fish were only detected. Probability of detection was estimated using a time:state interaction of all models because the number of antennas in each system differed across years as antennas were added for other projects or lost to extreme flow events. Only individuals with sex and length at tagging data were included in the models. Models were specified and fit using maximum likelihood methods in Program MARK[38] using the package *RMark*[39] and models were compared using AIC and model weights.

Detections of fish not returning to McElmo Creek in a particular year

One limitation of using a tributary PIT antenna array to estimate site fidelity is that we do not have comprehensive data on the location of fish that are not detected in the tributary. Because flannelmouth suckers are irregularly sampled in the San Juan River, additional detections outside of McElmo Creek are biased observations from a few permanent PIT antenna arrays distributed throughout the basin[35]. Regardless, detections at these arrays provide data on annual or seasonal patterns of movement that provided some insight as to factors associated with skipped spawning migrations. For all PIT-tagged flannelmouth suckers that had been detected in McElmo Creek at any point in time, encounter histories were created as in Objective 1 to reflect years they were detected in McElmo Creek during the spawning season. Each year an individual was not detected in McElmo Creek, we interrogated the STReaMS database to identify detections on one of the other PIT antenna arrays that was operational for a majority of our study period. We also used STReaMS data to determine if any flannelmouth sucker had been detected outside the San Juan River basin.

Relative individual arrival timing across years

We ranked individuals based on their arrival time in McElmo Creek each year from 2013 to 2022 to assess individual variation in the migration timing. As mentioned above, we only included detections in the first half of each year, allowing us to include potential outliers in relative arrival timing while excluding any monsoon-driven movement into McElmo Creek. We only included individuals with at least two detections at least 2 days apart because we did not have directional movement for each encounter and assumed the first detection reflected arrival and the last detection indicated departure[18]. Data from the 2016 spawning season were excluded from our analyses because of reduced reliability in arrival timing due to antenna malfunctions (see Fig. 2a in Ref.[18]). For each pair of years, we used Spearman rank correlation to examine the relationship of ranked arrival time for individuals migrating in both years. We first tested if there was a difference between sexes, and if there was not, we pooled these data. To look at timing across years, we z-score transformed[40] the ranked arrival timing for each year and evaluated variance for individuals. Consistent arrival timing across years should result in smaller variance within individuals than expected from random arrival timing. We compared these values to simulated data that were resampled from the observed arrival timing dataset while preserving the distribution of years without detections using a t-test.

Results

Return patterns, survival, and migration probability

We examined detection histories of 756 individuals tagged in 2013, 720 individuals tagged in 2014, and 392 individuals tagged in 2015. There was a steady rate of decline in the number of fish detected each year from tagging through 2022 (Fig. 2), with an average of 78% of fish detected each successive year (Supplementary Fig. S3). Individuals tended to be detected in consecutive years (Fig. 2): only 25% of individuals with detections spanning at least a 3-year period had a non-consecutive detection record, after excluding data from 2016. Six years was the longest period between detections of an individual in McElmo Creek. Seven percent of individuals tagged in 2013, 9% of individuals tagged in 2014, and 16% of individuals tagged in 2015 were detected every year since initial tagging in McElmo Creek through 2022 (Fig. 2).

The top model as determined by AIC ranking included a time and state interaction for survival and detection, and migration probability included the variable sex (Table 1). This model received 64% of the model weight. Migration probability for male fish was 0.93 ± 0.012 and for female fish was $0.90 \pm 0.0.13$ (Fig. 3). Detection
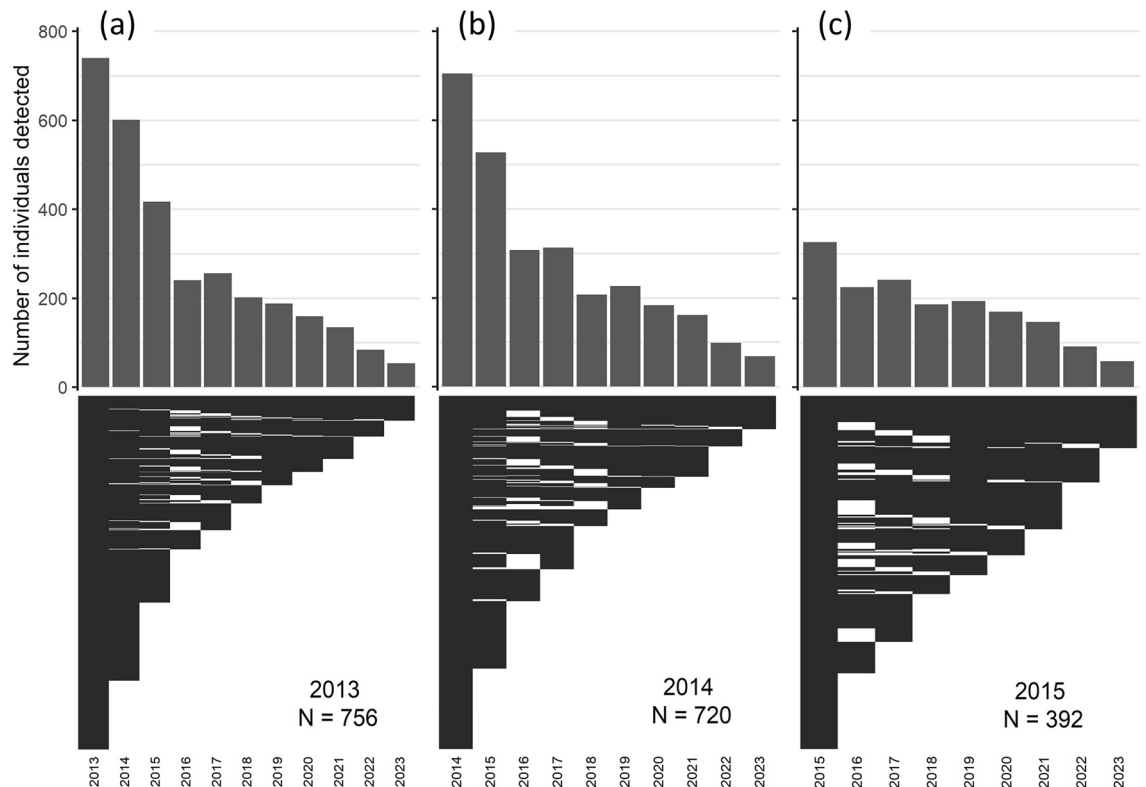
Fig. 2. The top panels depict the number of flannelmouth suckers (*Catostomus latipinnis*) tagged in McElmo Creek during (**a**) 2013, (**b**) 2014, and (**c**) 2015 and subsequently detected on McElmo Creek PIT antenna each year. Bottom panels: Visualization of detection histories of individual flannelmouth suckers migrating to McElmo Creek. Each horizontal line represents the detection history of an individual fish tagged in (**a**) 2013, (**b**) 2014, or (**c**) 2015 (number of individuals/lines indicated in the lower right corner beneath tagging year) with years an individual was detected migrating indicated by black and years without a detection indicated by white. A solid black line represents a fish that returned and was detected each year, whereas a line interrupted by white represents a fish that was intermittently detected across years. Rows are sorted by the final year a fish was detected, with individuals not redetected after their tagging year in the lowest rows.

probability was consistently greater in the tributary than the mainstem until 2022. Variability across time was included in the top 12 models for survival (Table 1). Averaged across years, annual survival for tributary spawning fish was 0.69 for the top model (survival in the tributary state during spawning × survival in the mainstem state during the second half of the year, Fig. 4A). Using the averaged survival probability, 84% of tributary spawners were removed from the population after 5 years (1–0.69[5]). The next ranked model had a delta AICc of 2.13 and included the same variables for survival and detection probability, while migration probability varied across years (Table 1, Fig. S4). Migration probability averaged across years was 0.94, with large confidence intervals in 2016 and 2018 (Fig. 3B).

Even though tag event was not included in our top model, we examined the S(~ tag event)p(~ time:state) Psi(~ time) model (Table 1) to determine if handling impacted survival. Survival probability for fish the year they were tagged was 0.811 ± 0.009 compared to a survival probability during other years of 0.801 ± 0.005, resulting in estimates with overlapping confidence intervals.

Detections of fish not returning to McElmo Creek in a particular year

Of fish previously detected spawning in McElmo Creek that were not detected in the tributary in certain years, 72 of 117 (62%) detections were from the PIT antenna below Piute Farms Waterfall, with 57 of those individual detections occurring during the 2022 spawning season (Figs. 1, 5). In addition to the waterfall, several individuals known to have spawned in McElmo Creek were detected near PNM Weir, 121 km upstream of the confluence of McElmo Creek with the San Juan River, primarily in 2014 and 2015. Detections for all locations mostly occurred during the spawning season when flannelmouth suckers are presumably most mobile (Fig. 5). A single flannelmouth sucker initially tagged in the San Juan River (captured below the waterfall and translocated upstream in 2018) was captured in the Colorado River arm of Lake Powell in 2022 (210 rkm from Piute Farms Waterfall). There were no flannelmouth suckers tagged in McElmo Creek that were also detected in the Colorado River and no other records of flannelmouth sucker moving between the San Juan River Basin and the remainder of the Upper Colorado River Basin.

Equations	npar	AICc	DeltaAICc	weight
S(~ time:state)p(~ time:state)Psi(~ sex)	61	13,701.16	0	0.643
S(~ time:state)p(~ time:state)Psi(~ time)	69	13,703.29	2.13	0.222
S(~ time:state)p(~ time:state)Psi(~ state)	60	13,704.92	3.76	0.098
S(~ time:state)p(~ time:state)Psi(~ year)	62	13,708.16	7.00	0.019
S(~ time:state)p(~ time:state)Psi(~ time × year)	88	13,708.98	7.82	0.013
S(~ time:state)p(~ time:state)Psi(~ time × sex)	80	13,711.16	10.00	0.004
S(~ time:state × sex)p(~ time:state)Psi(~ time)	99	13,742.45	41.29	0.000
S(~ time:state × sex)p(~ time:state)Psi(~ sex)	91	13,747.91	46.75	0.000
S(~ time:state × sex)p(~ time:state)Psi(~ state)	90	13,750.12	48.96	0.000
S(~ time:state × sex)p(~ time:state)Psi(~ time × year)	118	13,750.29	49.13	0.000
S(~ time:state × sex)p(~ time:state)Psi(~ year)	92	13,753.66	52.50	0.000
S(~ time:state × sex)p(~ time:state)Psi(~ time × sex)	110	13,755.85	54.69	0.000
S(~ sex)p(~ time:state)Psi(~ time)	42	13,768.36	67.20	0.000
S(~ tag event × state)p(~ time:state)Psi(~ time)	44	13,769.41	68.25	0.000
S(~ tag event × sex)p(~ time:state)Psi(~ time)	44	13,770.22	69.06	0.000
S(~ sex × state)p(~ time:state)Psi(~ time)	44	13,770.63	69.47	0.000
S(~ state)p(~ time:state)Psi(~ time)	42	13,771.06	69.90	0.000
S(~ tag event)p(~ time:state)Psi(~ time)	42	13,772.04	70.88	0.000
S(~ sex)p(~ time:state)Psi(~ time × year)	61	13,774.56	73.40	0.000
S(~ tag event × sex)p(~ time:state)Psi(~ time × year)	63	13,776.18	75.02	0.000
S(~ sex × state)p(~ time:state)Psi(~ time × year)	63	13,777.37	76.21	0.000
S(~ sex)p(~ time:state)Psi(~ time × sex)	53	13,777.41	76.25	0.000
S(~ state)p(~ time:state)Psi(~ time × year)	61	13,777.87	76.71	0.000
S(~ tag event × state)p(~ time:state)Psi(~ time × year)	63	13,777.97	76.81	0.000
S(~ tag event)p(~ time:state)Psi(~ time × year)	61	13,778.14	76.98	0.000
S(~ tag event × sex)p(~ time:state)Psi(~ time × sex)	55	13,778.66	77.50	0.000
S(~ tag event)p(~ time:state)Psi(~ time × sex)	53	13,779.11	77.95	0.000
S(~ sex × state)p(~ time:state)Psi(~ time × sex)	55	13,780.20	79.04	0.000
S(~ state)p(~ time:state)Psi(~ time × sex)	53	13,780.88	79.72	0.000
S(~ tag event × state)p(~ time:state)Psi(~ time × sex)	55	13,782.51	81.35	0.000
S(~ tag event × sex)p(~ time:state)Psi(~ year)	37	13,786.17	85.01	0.000
S(~ sex)p(~ time:state)Psi(~ sex)	34	13,786.69	85.53	0.000
S(~ sex)p(~ time:state)Psi(~ state)	33	13,786.76	85.60	0.000
S(~ tag event)p(~ time:state)Psi(~ year)	35	13,787.96	86.80	0.000
S(~ sex × state)p(~ time:state)Psi(~ year)	37	13,788.05	86.89	0.000
S(~ state)p(~ time:state)Psi(~ year)	35	13,788.38	87.22	0.000
S(~ tag event × sex)p(~ time:state)Psi(~ state)	35	13,788.49	87.33	0.000
S(~ tag event × sex)p(~ time:state)Psi(~ sex)	36	13,788.57	87.41	0.000
S(~ tag event × state)p(~ time:state)Psi(~ year)	37	13,788.78	87.62	0.000
S(~ tag event)p(~ time:state)Psi(~ sex)	34	13,790.12	88.96	0.000
S(~ sex × state)p(~ time:state)Psi(~ state)	35	13,790.19	89.03	0.000
S(~ tag event)p(~ time:state)Psi(~ state)	33	13,790.34	89.18	0.000
S(~ state)p(~ time:state)Psi(~ state)	33	13,790.51	89.35	0.000
S(~ tag event × state)p(~ time:state)Psi(~ sex)	36	13,790.59	89.43	0.000
S(~ tag event × state)p(~ time:state)Psi(~ state)	35	13,790.97	89.81	0.000
S(~ sex)p(~ time:state)Psi(~ year)	35	13,800.70	99.54	0.000
S(~ state)p(~ time:state)Psi(~ sex)	34	13,843.46	142.30	0.000
S(~ sex × state)p(~ time:state)Psi(~ sex)	36	13,857.29	156.13	0.000

Table 1. Multistate models for survival (S), detection probability (p), migration probability (Psi) for tributary spawning flannelmouth sucker (*Catostomus latipinnis*) in the San Juan River, USA. Variables considered were sex, tagging cohort, tagging event, state, and time. *Npar* number of parameters, *AICc* Akaike's information criteria for small sample sizes, *DeltaAICc* change in AICc, *weight* support for model compared to others in the table.
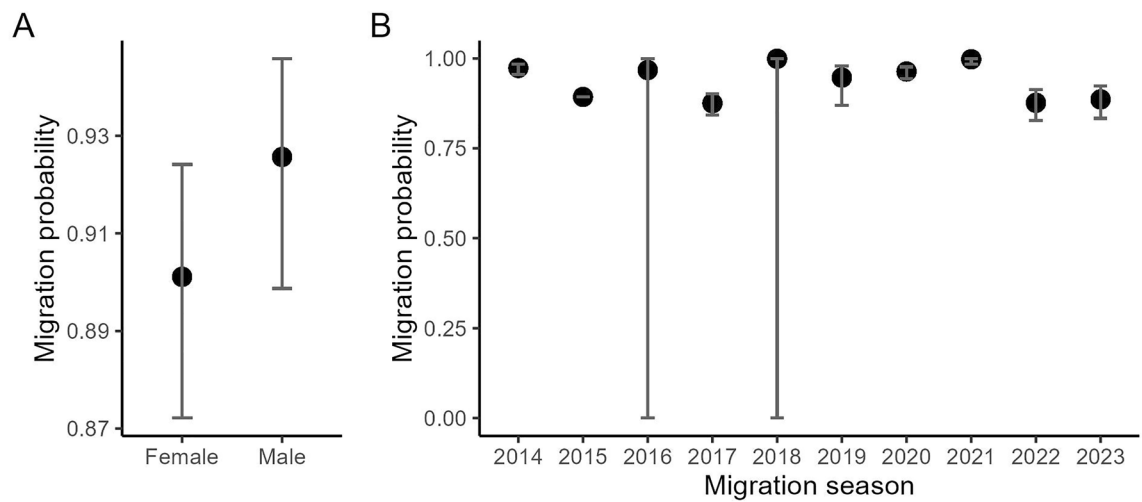
Fig. 3. Migration probability of flannelmouth sucker (*Catostomus latipinnis*) to McElmo Creek for the top two multistate models. Migration probability was dependent upon sex in the top model (**A**) and on time in the next model (**B**, delta AIC = 2.13). Bars represent 95% confidence intervals.
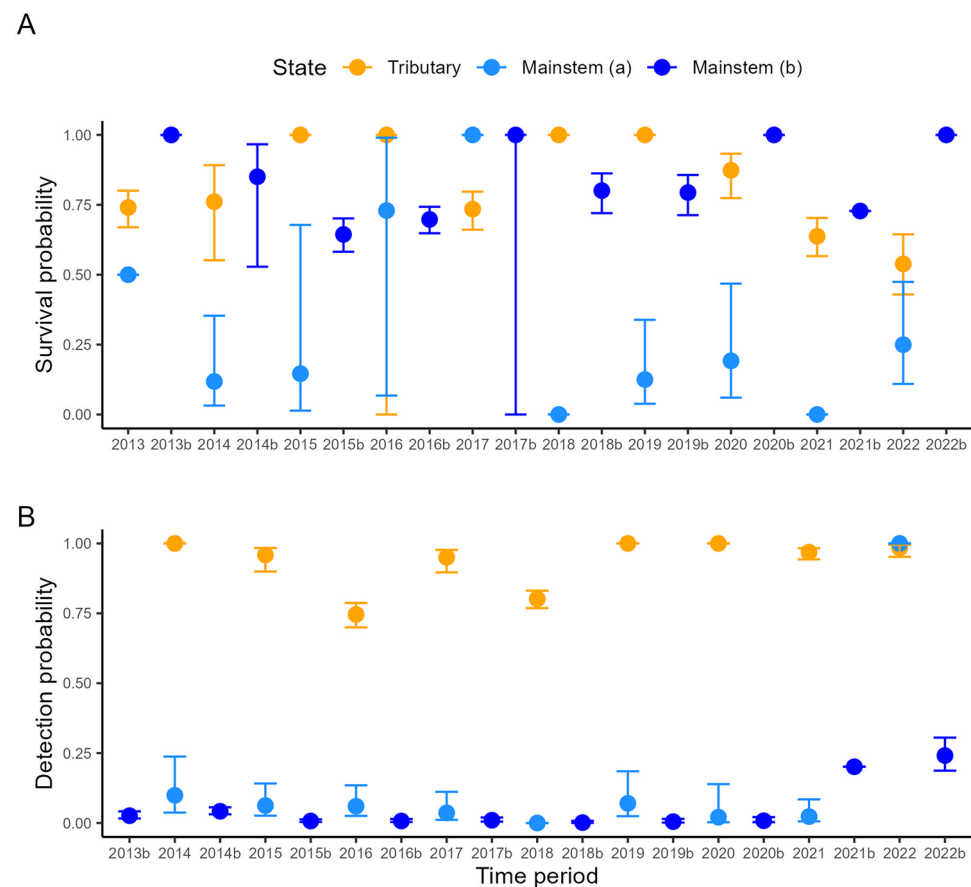

Fig. 4. Survival (**A**) and detection (**B**) probability estimates for flannelmouth sucker (*Catostomus latipinnis*) in the San Juan River, USA from the top multistate model. Years with "b" indicate the time period during the second half of the year when spawning did not take place. Mainstem values are colored by spawning season (light blue, a) and non-spawning season (dark blue, b). Bars represent 95% confidence intervals.

Fig. 5. Detections of flannelmouth sucker (*Catostomus latipinnis*) on the four longest running passive interrogation arrays in the San Juan River during years the individuals were not detected in McElmo Creek after having previously spawned in the tributary. Points are slightly transparent and jittered for visualization purposes. Squares with an x indicate when antennas were installed if not before 2014. Locations are arranged from upstream to downstream. *SJ* San Juna River, *PNM* Public Service Company of New Mexico.

Relative individual arrival timing across years

Relative arrival timing did not differ between males and females (p > 0.05), so data were pooled. As predicted, fish showed consistency in relative arrival timing across years (Fig. 6). All contrasts between years had positive correlation coefficients and were significant (α = 0.05). Moreover, the observed variance within individuals was lower than for resampled data (t = − 14.20, df = 1495.7, p < 0.001, Fig. S5). The median variance value for observed data was 0.40 compared to a median variance of 0.89 for resampled data.

Discussion

McElmo Creek spawning flannelmouth sucker demonstrated a high level of site fidelity, which likely has important consequences for the San Juan River population as a whole. The tributary-migrating fraction of the San Juan River flannelmouth sucker support a population-level risk mitigation strategy made possible by high survival and spawning site fidelity. This individual spawning behavior allows populations to take advantage of successful reproductive years and mitigate the negative impacts of suboptimal years across different habitats (e.g., mainstem and tributary). Some of our fish were detected spawning in McElmo Creek for 10 consecutive years during which mean discharge in the tributary during the spawning season ranged from 0.25 to 1.16 cm. The average migration probability of flannelmouth sucker (0.91) was greater than site fidelity estimates from tributary spawning blue sucker (*Cycleptus elongate*) in Texas (0.83 probability of returning to a tributary, 0.65 of returning to the same tributary[31]). Other suckers, like robust redhorse (*Moxostoma robustum*), have similarly been noted to have a high degree of site fidelity to river spawning locations[41]. However, site fidelity may be inconsistent across populations, as flannelmouth sucker in Coal Creek, Colorado, USA had site fidelity of less than 50%[26]. McElmo Creek spawners appear to be a distinct group of individuals because few fish spawned in McElmo Creek as a one-off event, evidenced by consistent decrease in detections across years (Fig. 2).

The inclusion of time, representing unknown interannual variation, in our models suggests environmental variability as a driver of both survival and migration probability. The average survival of flannelmouth sucker (0.69) was lower than that of Lost River sucker (*Deltistes luxatus*, 0.88) and shortnose sucker (*Chasmistes brevirostris*, 0.76) in Oregon[42] and greater than that of shortnose sucker in California (0.59 for 10 months)[43]. Lower survival estimates may result from the mainstem being a low observability state due to location and number of mainstem PIT antennas. Even with ten years of data, limited inference can be made on the specific features of the water year or other components of environmental variability that may impact survival and migration probability. Interpretation of interannual variation was further complicated by low detection probability in the mainstem (Fig. 4B) resulting in large confidence intervals for survival during some time periods (Fig. 4A). Generally, survival probability was greater for fish in the tributary than in the mainstem, but fish may only migrate if they are in good condition. Spawning and migration are both energetically expensive processes, and, while we would expect survival to be different between the tributary and mainstem, our extended sample periods and low detection probability in the mainstem may make it hard to identify the specific mortality period. However, the use of PIT antennas throughout the basin is increasing[35] and continued data collection could provide additional insights
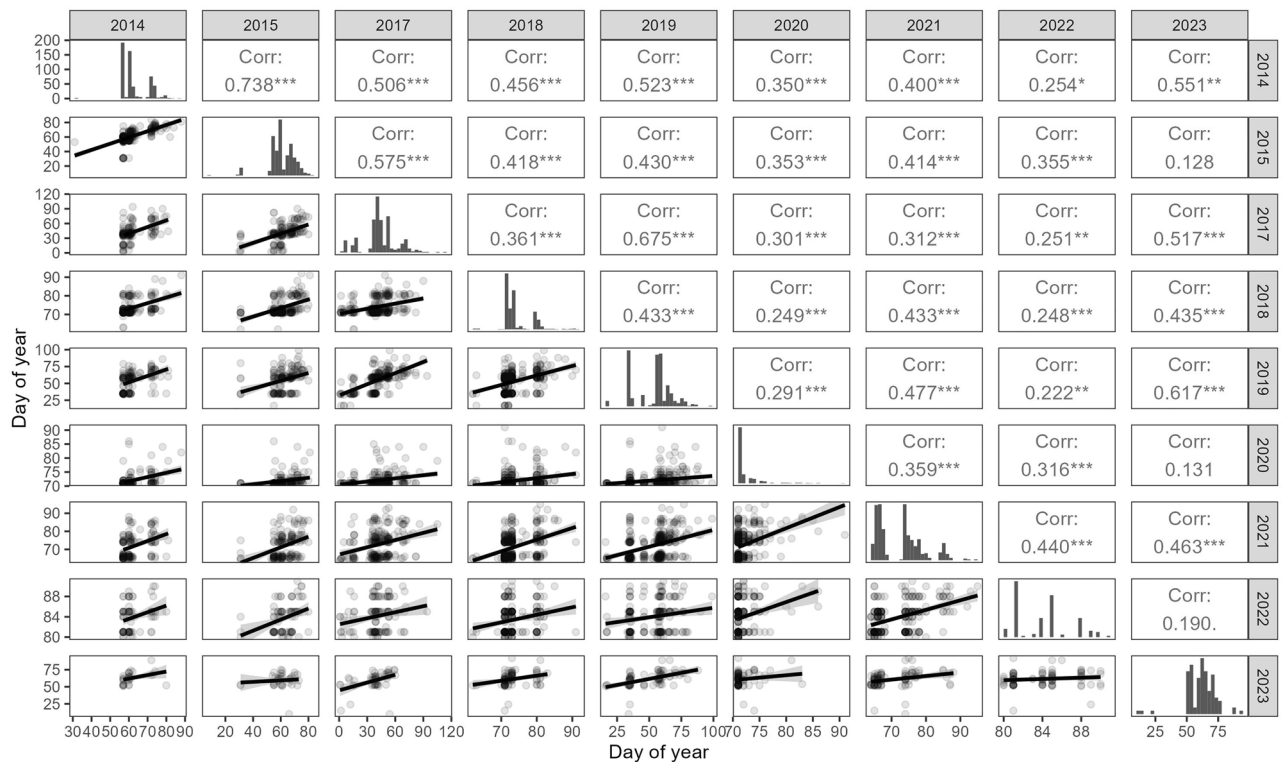
Fig. 6. Spearman correlation for individual flannelmouth sucker (*Catostomus latipinnis*) day of arrival to McElmo Creek across years. Correlation coefficients given in the upper-right half with asterisks indicating significance of *0.05, **0.01 and ***0.001. Bar plots along the diagonal show the distribution of arrival times for each year. Points set to 0.1 transparency so that darker points represent multiple individuals. Lines reflect linear correlation for visualization purposes.

in the future. Several mainstem antennas were installed after the spawning migration in 2021[35] and increases in flannelmouth sucker detection are evident beginning in the second half of 2021 (Fig. 4B).

Specific features of either the water year or other environmental variability may also impact return patterns. Greater correlation coefficients for relative arrival timing occurred in generally wetter years when fish stayed in McElmo Creek for longer periods, including 2014, 2015, 2017, and 2019. The lowest correlation coefficients were in year pairings including 2022, a dry year with a short spawning migration and high overlap in arrival timing among individuals[18]. A monsoon in late July 2021 resulted in observed mortality and emigration of flannelmouth suckers downstream[44] and highlights how acute environmental conditions impact true survival and emigration from a system. However, the general patterns of similar survival and migration probability across years suggested that environmental effects on migration behavior may have been relatively muted among years.

Making generalizations based on averaged individual variations or characteristics, such as sex, size, and experience, can limit the ability to adequately describe and manage a population of individuals[45]. Individual variation within relative return time means individuals may not be interchangeable through individual-specific responsiveness to environmental cues[13], particularly in years with longer spawning periods. This individual variation in arrival timing likely performs an additional risk mitigation strategy to mainstem versus tributary spawning, but more research is needed to understand mechanisms driving the observed variation in individual responses across years. While our top model for migration probability suggested small differences between males and females (Fig. 3A), we did not have information on other covariates like length or age. Larger individuals tend to be more fecund[46] and, while length and age are not perfectly correlated, larger individuals may have more experience in the system. Consideration of population structure and age explicit population models[47] for future management actions could benefit decision making. Age specific survival probabilities paired with recruitment data are necessary to understand population sustainability[48].

We had limited detections outside of the tributary (Fig. 4B), but some individuals moved long distances and returned to McElmo Creek in subsequent years (Fig. 5). A small number of fish were detected on upstream PIT antennas during the spawning season in years they were not detected in McElmo Creek. Some of these individuals may have been in search of better spawning habitat or may have moved upstream during the non-spawning season so the increased migration distance may have reduced the relative value of migrating to McElmo Creek. In a telemetry study in 2021, flannelmouth suckers detected near McElmo Creek at the beginning of the spawning season made large upstream movements (> 100 rkm) during the spawning season[35]. The few other upstream tributaries in this system do not have permanent antenna installations, so we do not know if or how McElmo Creek spawning fish use other tributaries. Other individuals that did not return to McElmo Creek to spawn may have been avoiding adverse environmental conditions such as colder runoff or low water conditions. While

these individuals may return to McElmo Creek after spawning elsewhere, those that moved below the Piute Farms Waterfall, presumably to avoid turbid monsoon flows, were unable to return to McElmo Creek without human intervention. Many of the flannelmouth suckers translocated above the waterfall as part of another study migrated 186 rkm to McElmo Creek for spawning[28]. These observations of individual fish spawning elsewhere or being trapped below a barrier highlight the importance of connectivity throughout the river network to allow for individual variation in movement under different environmental conditions.

The degree to which fish "decide" to return to a spawning area versus natal homing or other "hard-wired" intrinsic factors is critical to determining implications of habitat changes. Species with high site fidelity may be less adaptable to habitat loss or degradation[12,49] because high levels of site fidelity can have different consequences depending upon recruitment from those spawning events. From a bet-hedging or periodic reproductive strategy (sensu[50]), we expect recruitment of tributary spawned fish to be variable across years and asynchronous from recruitment of mainstem spawned fish. If McElmo Creek provides a disproportionately high number of recruits to the entire population, the tributary may be a fragile resource and further water development or modifications to the system could have devastating impacts on the San Juan River population. However, if McElmo Creek produces a disproportionately low number of recruits, the tributary may be acting as an ecological trap in which reproductive efforts are being wasted in a harsh environment. Habitat characteristics of McElmo Creek may be favorable for spawning, but understanding the response of larval and juvenile fish will be necessary to contextualize these findings. Larval and juvenile fish have been detected throughout the tributary, with some drifting to the mainstem within a month of the spawn and others remaining in the tributary throughout the summer[17]. Tracking reproductive output and recruitment, for example through genetic parentage analysis, might be a way to evaluate the value of this tributary.

River connectivity is vital for suckers making spawning migrations, allowing them to access habitat and resources in tributaries. In addition, mainstem and tributary systems are linked through energy and nutrients, process subsidies, and coupled communities[51,52]. Therefore, removing barriers within tributaries, protecting tributary watersheds from further dewatering or degradation, and limiting the introduction and spread of non-native species in tributaries could be important for increasing or maintaining spawning habitat. While fish may be able to identify good spawning habitat characteristics, such as loose substrates, adults return to the mainstem and do not receive direct feedback on their reproductive success. Conservation measures to maintain access to and enhance habitat in this tributary could prevent high tributary fidelity from becoming maladaptive and provide for a portfolio effect in the San Juan River flannelmouth sucker population[2].

Data availability
Data were downloaded from Species Tagging, Research and Monitoring System (https://streamsystem.org/) on 07 August 2023.

References
1. Wilson, C. C., Liskauskas, A. P. & Wozney, K. M. Pronounced genetic structure and site fidelity among native muskellunge populations in Lake Huron and Georgian Bay. *Trans. Am. Fish. Soc.* **145**, 1290–1302 (2016).
2. Bouska, K. L. *et al.* Diverse portfolios: Investing in tributaries for restoration of large river fishes in the Anthropocene. *Front. Environ. Sci.* **11**, 1–18 (2023).
3. Chapman, B. B. *et al.* Partial migration in fishes: Causes and consequences. *J. Fish Biol.* **81**, 456–478 (2012).
4. Fausch, K. D., Torgersen, C. E., Baxter, C. V. & Li, H. W. Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. *BioScience* **52**, 483–498 (2002).
5. Moyle, P. B. & Mount, J. F. Homogenous rivers, homogenous faunas. *Proc. Natl. Acad. Sci. U.S.A.* **104**, 5711–5712 (2007).
6. Pracheil, B. M., McIntyre, P. B. & Lyons, J. D. Enhancing conservation of large-river biodiversity by accounting for tributaries. *Front. Ecol. Environ.* **11**, 124–128 (2013).
7. Bottcher, J. L., Walsworth, T. E., Thiede, G. P., Budy, P. & Speas, D. W. Frequent usage of tributaries by the endangered fishes of the Upper Colorado River basin: Observations from the San Rafael River, Utah. *N. Am. J. Fish. Manag.* **33**, 585–594 (2013).
8. Zhao, Y., Einhouse, D. W. & Macdoughall, T. M. Resolving some of the complexity of a mixed-origin walleye population in the east basin of Lake Erie using a mark–recapture study. *N. Am. J. Fish. Manag.* **31**, 379–389 (2011).
9. Harris, P. M., Hubbard, G. & Sandel, M. In *Freshwater Fishes of North America* (eds Warren, M. L. & Burr, B. M.) 451–501 (Johns Hopkins University Press, 2014).
10. Cathcart, C. N. Olfactory activation: Imprinting as an emerging frontier in the conservation of non-salmonid migratory fishes. *Fisheries* **1**, 1–6. https://doi.org/10.1002/fsh.10646 (2021).
11. Meffe, G. K. & Vrijenhoek, R. C. Conservation genetics in the management of desert fishes. *Conserv. Biol.* **2**, 157–169 (1988).
12. Merkle, J. A. *et al.* Site fidelity as a maladaptive behavior in the Anthropocene. *Front. Ecol. Environ.* **20**, 187–194 (2022).
13. Fukushima, M. & Rand, P. S. Individual variation in spawning migration timing in a salmonid—Exploring roles of environmental and social cues. *Ecol. Evol.* **1**, 1–12. https://doi.org/10.1002/ece3.10101 (2023).
14. Copeland, T., Bowersox, B. J., Ackerman, M. W. & Camacho, C. Patterns of iteroparity in wild snake River Steelhead. *Trans. Am. Fish. Soc.* **148**, 926–937 (2019).
15. Lyons, J., Walchak, D., Haglund, J., Kanehl, P. & Pracheil, B. Habitat use and population characteristics of potentially spawning shovelnose sturgeon *Scaphirhynchus platorynchus* (Rafinesque, 1820), blue sucker *Cycleptus elongatus* (Lesueur, 1817), and associated species in the lower Wisconsin River, USA. *J. Appl. Ichthyol.* **32**, 1003–1015 (2016).
16. Hooley-Underwood, Z. E., Stevens, S. B., Salinas, N. R. & Thompson, K. G. An intermittent stream supports extensive spawning of large-river native fishes. *Trans. Am. Fish. Soc.* **148**, 426–441 (2019).
17. Cathcart, C. N., Gido, K. B. & Brandenburg, W. H. Spawning locations within and among tributaries influence flannelmouth sucker offspring experience. *Trans. Am. Fish. Soc.* **148**, 963–977 (2019).
18. Bonjour, S. M. *et al.* Migration timing and tributary use of spawning flannelmouth sucker (*Catostomus latipinnis*). *J. Fish Biol.* **103**, 1144 (2023).

19. Molloy, P. P., Cote, I. M. & Reynolds, J. D. In *Reef Fish Spawning Aggregations: Biology, Research and Management* (eds de Mitcheson, Y. S. & Colin, P. L.) 57–83 (Springer, 2020).
20. Sigler, W. F. & Sigler, J. W. *Fishes of Utah; a Natural History* (University of Utah Press, 1996).
21. Weiss, S. J., Otis, E. O. & Maughan, O. E. Spawning ecology of flannelmouth sucker, *Catostomus latipinnis* (Catostomidae), in two small tributaries of the lower Colorado river. *Environ. Biol. Fish.* **52**, 419–433. https://doi.org/10.1023/A:1007497513762 (1998).
22. Osmundson, D. B., Ryel, R. J., Lamarra, V. & Pitlick, J. Flow-sediment-biota relations: Implications for river regulation effects on native fish abundance. *Ecol. Appl.* **12**, 1719–1739 (2002).
23. Bezzerides, N. & Bestgen, K. *Status Review of Roundtail Chub, Flannelmouth Sucker, and Bluehead Sucker in the Colorado River Basin* (Colorado State University, 2002).
24. Cathcart, C. N. *et al.* Waterfall formation at a desert river–reservoir delta isolates endangered fishes. *River Res. Appl.* **34**, 948–956 (2018).
25. Pennock, C. A. *et al.* Movement ecology of imperiled fish in a novel ecosystem: River-reservoir movements by razorback sucker and translocations to aid conservation. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **30**, 1540–1551 (2020).
26. Fraser, G. S., Winkelman, D. L., Bestgen, K. R. & Thompson, K. G. Tributary use by imperiled flannelmouth and bluehead suckers in the upper Colorado River basin. *Trans. Am. Fish. Soc.* **146**, 858–870 (2017).
27. Hayden, T. A. *et al.* Spawning site fidelity and apparent annual survival of walleye (*Sander vitreus*) differ between a Lake Huron and Lake Erie tributary. *Ecol. Freshw. Fish* **27**, 339–349 (2018).
28. Pennock, C. A. *et al.* Translocation in a fragmented river provides demographic benefits for imperiled fishes. *Ecosphere* **1**, e4874 (2024).
29. Arnason, A. N. The estimation of population size, migration rates and survival in a stratified population. *Popul. Ecol.* **15**, 1–8 (1973).
30. Schwarz, C. J. & Arnason, A. N. A general methodology for the analysis of capture–recapture experiments in open populations. *Biometrics* **52**, 860–873 (1996).
31. Dyer, J. J. & Brewer, S. K. Seasonal movements and tributary-specific fidelity of blue sucker *Cycleptus elongatus* in a Southern Plains riverscape. *J. Fish Biol.* **97**, 279–292 (2020).
32. Tornabene, B. J. *et al.* Trends in river discharge and water temperature cue spawning movements of Blue Sucker, *Cycleptus elongatus*, in an impounded Great Plains river. *Copeia* **108**, 151–162 (2020).
33. Cathcart, C. N., Gido, K. B. & McKinstry, M. C. Fish community distributions and movements in two tributaries of the San Juan River, USA. *Trans. Am. Fish. Soc.* **144**, 1013–1028 (2015).
34. Cathcart, C. N., Gido, K. B., McKinstry, M. C. & MacKinnon, P. D. Patterns of fish movement at a desert river confluence. *Ecol. Freshw. Fish* **27**, 492–505 (2018).
35. STReaMS. *Species Tagging, Research and Monitoring System*. www.streamsystem.org
36. Compton, R. *Population Fragmentation and White Sucker Introduction Affect Populations of Bluehead Suckers, Flannelmouth Suckers, and Roundtail Chubs in a Headwater Stream System, Wyoming*. https://www.proquest.com/openview/c9958ece6f1101ccd6da7450e0d35b30/1?pq-origsite=gscholar&cbl=18750 (Univ of Wyoming, 2007).
37. R Core Team. *R: A Language and Environment for Statistical Computing*. https://www.R-project.org/ (2023).
38. White, G. C. & Burnham, K. P. Program MARK: Survival estimation from populations of marked animals. *Bird Study* **46**, 120–139 (1999).
39. Laake, J. L. *RMark: An R Interface for Analysis of Capture–Recapture Data with MARK*. https://repository.library.noaa.gov/view/noaa/4372 (2013).
40. Mac Nally, R. Multiple regression and inference in ecology and conservation biology: Further comments on identifying important predictor variables. *Biodivers. Conserv.* **11**, 1397–1401 (2002).
41. Grabowski, T. B. & Isely, J. J. Seasonal and diel movements and habitat use of robust redhorses in the lower Savannah River, Georgia and South Carolina. *Trans. Am. Fish. Soc.* **135**, 1145–1155 (2006).
42. Janney, E. C., Shively, R. S., Hayes, B. S., Barry, P. M. & Perkins, D. Demographic analysis of Lost River Sucker and Shortnose sucker populations in Upper Klamath Lake, Oregon. *Trans. Am. Fish. Soc.* **137**, 1812–1825 (2008).
43. Pope, A. C., Skalski, J. R., Lockhart, T. & Buchanan, R. A. Generation of multistate release–recapture models using a graphic user interface (GUI). *Anim. Biotelem.* **4**, 23 (2016).
44. Whitney, J. E., Hansen, B. G., Bonjour, S. M., Bell, A. M. & Fishback, M. G. Fish behavior, mortality, diet, and movement following a monsoonal spate in the San Juan River, UT, USA. *West. N. Am. Nat.* **84**, 233–242 (2024).
45. Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E. & Spiegel, O. Trends and missing parts in the study of movement ecology. *PNAS* **105**, 19060–19065 (2008).
46. Dowling, T. E. *et al.* Time-series analysis reveals genetic responses to intensive management of razorback sucker (*Xyrauchen texanus*). *Evol. Appl.* **7**, 339–354 (2014).
47. Dzul, M. C. *et al.* Partial migration and spawning movements of humpback chub in the Little Colorado River are better understood using data from autonomous PIT tag antennas. *Can. J. Fish. Aquat. Sci.* **78**, 1057–1072 (2021).
48. Belk, M. C. & Tuckfield, R. C. Demography of an endangered, long-lived fish: Informing management options in the face of cyclic and stochastic climate variation. *Popul. Ecol.* **61**, 349–360 (2019).
49. Warkentin, I. G. & Hernández, D. The conservation implications of site fidelity: A case study involving nearctic-neotropical migrant songbirds wintering in a Costa Rican mangrove. *Biol. Conserv.* **77**, 143–150 (1996).
50. Winemiller, K. O. & Rose, K. A. Patterns of life-history diversification in North American fishes: Implications for population regulation. *Can. J. Fish. Aquat. Sci.* **49**, 2196–2218 (1992).
51. Childress, E. S., Allan, J. D. & McIntyre, P. B. Nutrient subsidies from iteroparous fish migrations can enhance stream productivity. *Ecosystems* **17**, 522–534 (2014).
52. Bauer, S. & Hoye, B. J. Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science* **344**, 1242552 (2014).

Acknowledgements

Author contributions

S.M.B., K.B.G., C.N.C, and M.C.M. designed the study and collected the data. K.B.G. and M.C.M. procured funding. S.M.B. performed the analyses and drafted the manuscript with input from K.B.G., C.N.C, and M.C.M.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-024-72273-7.

Correspondence and requests for materials should be addressed to S.M.B.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.