Transactions of the American Fisheries Society

ISSN: 0002-8487 print / 1548-8659 online
DOI: 10.1002/tafs.10141

ARTICLE

An Intermittent Stream Supports Extensive Spawning of Large-River Native Fishes

Zachary E. Hooley-Underwood, Summer B. Stevens, Nicholas R. Salinas, and Kevin G. Thompson*
Colorado Parks and Wildlife, Aquatic Research Section, 2300 South Townsend Avenue, Montrose, Colorado 81401, USA

Abstract
Intermittent or ephemeral streams make up a large percentage of all stream habitats and may have significant roles in spawning, foraging, refugia, and early life history habitat for many fishes. From 2015 to 2017 we examined the use of Cottonwood Creek, an intermittent tributary in the Gunnison River basin, Colorado, by spawning Flannelmouth Sucker *Catostomus latipinnis*, Bluehead Sucker *C. discobolus*, and Roundtail Chub *Gila robusta*. We used combinations of a stream-spanning picket weir and PIT-tag antennae near the mouth of the creek to determine fish movement in and out of the stream, which was more effective for the suckers than for Roundtail Chub. Large numbers of suckers used the stream each year despite very different flow regimes. The timing of initial fish entry varied by 6 weeks across 3 years of study from March 17 to May 6. Immigration was only loosely and inconsistently correlated to abiotic factors (various stream temperature metrics and discharge) among years and was most heavily dependent on the presence of sufficient water in the stream to permit fish passage. Average residency times of suckers ranged from 26 to 37 d depending on year and species, and spawning fish lost 10–18% of their body weight depending on species and sex. Both sucker species displayed a high level of annual site fidelity—61–71% of fish returned the year after being tagged. Larval drift was sporadic and many larvae failed to evacuate the stream before flow ceased each year. While further research is needed to assess the overall recruitment contribution from Cottonwood Creek to the regional population, this study revealed use of an intermittent tributary by thousands of native Colorado River fishes, highlighting the importance of nonperennial waters for the completion of the life histories of some large-river fish species.

The biological and physical benefits of intermittent and ephemeral streams are not given nearly the consideration of perennial streams due to their short wetted periods. In fact, these streams are often not even afforded the protections of regulatory laws such as the Clean Water Act in the United States (Downing et al. 2003). Intermittent streams are those that flow continuously only at certain times of year, while ephemeral streams are those that flow only briefly in direct response to local precipitation (Levick et al. 2008). Both are often overlooked with respect to aquatic organisms, and much of the work that has been done in these habitats examines how resident invertebrates and small-bodied fishes survive in relation to drying patterns and cycles (Closs and Lake 1994; Miller and Golladay 1996; Labbe and Fausch 2000; Falke et al. 2011; Datry et al. 2014). However, intermittent and ephemeral streams may also provide useful habitat for migratory and large-bodied, large-river fishes when adequate connections to main-stem rivers exist (Erman and Hawthorne 1976; Wigington et al. 2006). These fishes may use intermittent and ephemeral streams not only for spawning and foraging, but as refugia from high main-

*Corresponding author: kevin.thompson@state.co.us
Received August 22, 2018; accepted December 3, 2018

stem flows and early life history habitat for the offspring of main-stem fishes (Rice et al. 2008).

In arid regions in particular, intermittent or ephemeral streams may be prevalent among relatively scarce options for fish seeking tributary habitats. In the southwestern United States, intermittent and ephemeral habitats make up 81% of all stream habitats (Levick et al. 2008). The Colorado River basin is 632,000 km^2 in size and is composed of several large rivers, many smaller perennial tributaries, and countless intermittent and ephemeral tributaries. These waters collectively support a depauperate assemblage of native species that are highly threatened, often endemic, and specifically adapted to the harsh and variable conditions of the arid region (Minckley and Deacon 1968). Physical and biological anthropogenic alterations to the basin have led to regional extirpations and reduced populations of many of these specialized fishes (Minckley and Deacon 1968; Bezzerides and Bestgen 2002; Olden et al. 2006; Budy et al. 2015). As a result, substantial research has focused on distributions, population trends, biological and ecological needs, and potential threats to these species (Bezzerides and Bestgen 2002; Clarkson et al. 2005; Bower et al. 2008; Dauwalter et al. 2011). The majority of this research has occurred on main-stem rivers and perennial streams, leaving relationships between these fishes and nonperennial streams poorly understood and rarely documented.

Included in the at-risk species of the Colorado River basin are Flannelmouth Sucker *Catostomus latipinnis*, Bluehead Sucker *C. discobolus*, and Roundtail Chub *Gila robusta*. A review of the status of these three species in the upper Colorado River basin (Bezzerides and Bestgen 2002) and an occupancy analysis in Utah based on long-term records (Budy et al. 2015) suggest these native fishes presently occupy 50% or less of their respective historical ranges, and extant populations are declining in many localities. State, federal, and tribal agencies concerned with the recent decline of these native fishes have signed a range-wide conservation agreement to work toward ensuring the persistence of populations throughout their native ranges (Three Species Conservation Agreement and Strategy [TSCAS]: UDNR 2006). These and other Colorado River basin fishes are known to use a diversity of habitat types and move extensively among connected tributary and main-stem systems (Weiss et al. 1998; Modde and Irving 2011; Bottcher et al. 2013; Cathcart et al. 2015), which were more abundant and available before the development of water resources for irrigation, hydroelectric, and municipal purposes. Detailed information concerning the distribution, life history, population trends, and community ecology of native suckers of the upper Colorado River basin and its subbasins is relatively limited, but the migration of these fishes from main-stem waters to tributaries for spawning is common and increasingly well documented (Bezzerides and Bestgen 2002; Cathcart et al. 2017; Fraser et al. 2017). Determining conservation needs associated with the biology and ecology of these fishes is a major goal of the TSCAS.

The Gunnison River, a major tributary to the Colorado River in western Colorado, supports robust populations of these three species (Anderson and Stewart 2007). Construction of the Aspinall Unit dams (Blue Mesa, Morrow Point, and Crystal) resulted in their extirpation from the uppermost reaches of the Gunnison River, and diversion structures have greatly limited access to some of its tributaries, but robust populations remain throughout most of the lower main stem itself (Bezzerides and Bestgen 2002). Because of the health and apparent stability of these populations, the Gunnison River is an ideal system for studying the ecology of these fishes and their biological and habitat requirements. In spring 2014, random-site sampling of an intermittent tributary in the Gunnison River basin, Cottonwood Creek, revealed large numbers of spawning Bluehead Sucker, Flannelmouth Sucker, and Roundtail Chub (up to 70 fish/100 m for all species combined). Because of the surprising number of fish present, and the intermittent nature of the stream, we characterized the use of the stream by these fishes in an effort to elevate the possible importance of a habitat that was potentially undervalued within the scientific and fisheries management communities. Understanding conditions associated with the use of this stream by these fishes is an important step towards identifying other intermittent habitats that may have been overlooked and would expand knowledge on the general ecology and landscape use of these species. Our objectives were to (1) relate stream use by Bluehead and Flannelmouth suckers (primarily) and Roundtail Chub (secondarily) to day of year, stream temperature, and stream flow metrics; (2) estimate length of stay of spawning fish in the stream; (3) determine the energetic cost of reproduction in terms of weight loss of individual fish; (4) determine annual tributary fidelity of adult fish that use Cottonwood Creek; and (5) record observations on the timing of spawning and larval drift.

STUDY SITE

Our study site was located on Cottonwood Creek approximately 7.6 km southwest of Delta, Colorado (Figure 1). Cottonwood Creek is an intermittent tributary of Roubideau Creek, which is a perennial tributary of the Gunnison River. The confluence of the two creeks is approximately 5 km upstream from the confluence of Roubideau Creek with the Gunnison River. The hydrograph of Cottonwood Creek is driven primarily by snowmelt, flowing between March and the end of June in most years. Discharge during this run-off period varies annually; during our study snowpack was 17, 102, and 106%

of long-term median on April 1 of 2015, 2016, and 2017 respectively. The highest discharge we measured in any year was 3.4 m^3/s (2017), but it averages much less (e.g., 0.59 m^3/s in 2017; described in Results). Low snowpack years may result in no flow at the mouth, while monsoonal rain events may result in brief wetted periods later in the summer. During dry periods, wetted, isolated pools are rare or nonexistent in the lower several kilometers of the creek. Cottonwood Creek has a relatively steep gradient (11.44 m/km) over the lower 11 km, resulting in high water velocities and substrates consisting of gravel, cobble, and boulders. This is in contrast to Roubideau Creek and the Gunnison River, which have lower gradients (2.99 m/km and 1.48 m/km, respectively) and substrates dominated by sand and silt near the confluences of the three waters. Cottonwood Creek is devoid of aquatic vegetation, though it does carry a heavy load of terrestrial detritus during the run-off period. The Cottonwood Creek drainage is dominated by undeveloped, public lands with some private hay production higher upstream in the drainage supported by at least three small diversion ditches. The intermittent nature of the creek is believed to predate these diversions, as both the creek and diversions are dry for the majority of the year.

At least the lower 23 km of Cottonwood Creek experience intermittency in years with typical snowpack. In this portion of the creek, our three subject species predominate, but native Speckled Dace *Rhinichthys osculus* also use the creek when it is flowing, as do the following nonnative fishes: White Sucker *C. commersonii*, Longnose Sucker *C. catostomus*, hybridized suckers (hybridization occurs among all species present, but native sucker × White Sucker hybrids are most common), Brown Trout *Salmo trutta*, Fathead Minnow *Pimephales promelas*, and Red Shiner *Cyprinella lutrensis*. Historical Colorado Parks and Wildlife sampling records indicate that Colorado River Cutthroat Trout *Oncorhynchus clarkii pleuriticus* inhabit the headwaters of the stream over 35 km upstream from the mouth, suggesting that perennial flows exist in these headwater reaches.

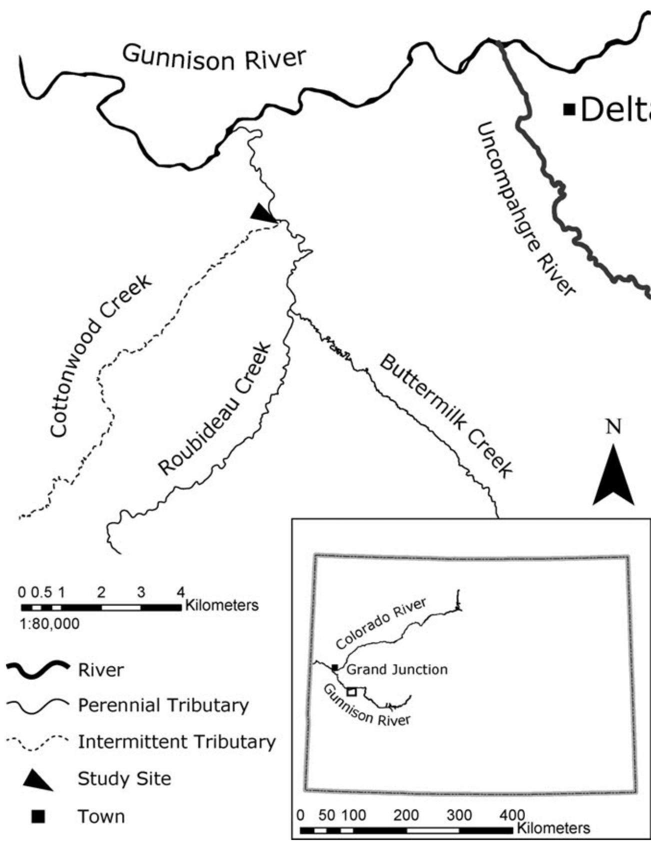

FIGURE 1. Cottonwood Creek in relation to Roubideau Creek, other tributaries, and the Gunnison River. Our weir, water temperature, and flow-monitoring sites were located just upstream from the confluence of Cottonwood Creek with Roubideau Creek (study site). The rectangle on the reference map shows the extent of the map in relation to the state of Colorado.

METHODS

Temperature and Discharge

Stream temperature data were collected near our weir site using a HOBO U22 Water Temp Pro v2 logger (Onset, Bourne, Massachusetts) that recorded data hourly, from which we calculated daily and weekly mean temperatures for Cottonwood Creek. An additional logger was located in Roubideau Creek approximately 4.1 km downstream from the mouth of Cottonwood Creek. We also deployed two pressure sensors (U20L-04, Onset) to collect barometric and water pressure data every half hour at the same location. Data from these sensors were used to estimate water depth (via water pressure corrected for barometric pressure). Discharge measurements were taken over a range of flows using a portable velocity meter (FH950, Hach Company, Loveland, Colorado). These measurements were later matched with closest-in-time water depth estimates to create a depth–discharge relationship, from which discharge was estimated semi-hourly for the duration of the active flow season.

Adult Fish Usage of Cottonwood Creek

Sampling.— We installed a picket weir and trap boxes designed to separately capture and hold upstream- and downstream-bound fish (as described in Hooley-Underwood et al. 2017) in Cottonwood Creek 130 m above its mouth. The 22-mm spacing of weir pickets was selected to prevent the passage of suckers (our primary target) longer than 210 mm in 2015 and 2016, but after experiencing difficulties associated with debris accumulation in 2016, we expanded the spaces to 28.6 mm to limit only suckers greater than 250 mm in 2017. We could not target Roundtail Chub (which mature at smaller sizes than the suckers and are more laterally compressed) over their entire mature size range because picket spacing would have been too narrow to withstand discharge conditions during the runoff period in Cottonwood Creek. The weir was installed before or near the beginning of stream flow that permitted fish access each year, and we monitored fish captures regularly throughout each day but more frequently when movement rates were high. We grouped fish capture data by day, though we did retain time stamps from PIT tag scans for residency time calculations. Each fish captured was identified to species using morphological characteristics (Baxter and Stone 1995; Snyder et al. 2004), measured (TL, mm), weighed (g), and scanned for a PIT tag using a hand-held portable reader (Biomark model 601 or Biomark model HPR Plus, Boise, Idaho). We implanted a 12.5-mm, 134.2-kHz, full-duplex PIT tag abdominally in every native sucker (our primary species of interest) and some Roundtail Chub ≥150 mm TL not previously tagged and in apparent good health, as described in Hooley-Underwood et al. (2017), until available tags were depleted for each year. Hooley-Underwood et al. (2017) observed ≥98% retention rates of newly implanted PIT tags during the spawning season and potential short-term tagging mortality of just 0.3% using this method for spawning suckers in this stream. In 2015 we had an excess of tags and were able to tag all healthy suckers and many chub (651 tags deployed in total), but in 2016 and 2017 we deployed all available tags (2,644 and 1,646, respectively). Fish that passed upstream without a PIT tag in 2016 and 2017 received a batch mark consisting of a hole punch in the ventral lobe of the caudal fin. Late in the 2016 and 2017 spawning seasons, the rate of emigration frequently greatly out-paced our ability to handle fish, resulting in densities of fish in the trap box and even on the upstream side of the picket weir that were damaging to both the fish and the weir. During these periods, data for only previously tagged or batch-marked fish were collected in full; other fish were simply tallied by species.

We grouped fish into four reproductive categories in order to evaluate sex-related demographics. For suckers, we designated fish expressing milt as males, fish expressing eggs as females, fish possessing nuptial tubercles but not expressing milt as "probable males," and fish not possessing nuptial tubercles nor expressing milt or eggs as "probable females." Roundtail Chub males and females were identified by the expression of milt or eggs, respectively. All chub not expressing gametes were considered to be of unknown sex. After processing, fish moving upstream were released 50 m above the weir and fish moving downstream were released directly below the weir.

Before the installation of the weir in 2016 and 2017, we placed one (2016) or two (2017) 1-m-diameter circular submersible PIT-tag antennae (Biomark, Boise, Idaho) in Cottonwood Creek between the weir site and the mouth of the stream to passively detect tagged fish using the stream. The antennae were 65 m upstream from the mouth of the creek and anchored to the substrate in the thalweg, in a narrow portion of channel, in order to maximize the odds that fish would pass directly over the antenna. In 2017, the second antenna was deployed approximately 5 m downstream from the first.

Analysis.— We calculated total weir-capture and individual fish numbers, as well as size metrics (mean, minimum, and maximum) broken down by species and sex assignment for 2015–2017. We also calculated daily entry and exit numbers for all Bluehead and Flannelmouth suckers handled at the weir. We supplemented these data with daily detection data from the submersible antennae to bracket the main immigration and emigration periods.

We used submersible antenna detections to identify conditions associated with immigration of fish into Cottonwood Creek. Knowing that fish occasionally linger near antennae and trigger multiple detections, we included only the first detection per day of any individual tag to avoid inflating immigration rates. We compared submersible antenna PIT tag detection data, stream temperature and discharge metrics, and daylight duration to identify the effects on immigration into Cottonwood Creek during 2016 and 2017 (we did not capture the full immigration period or employ a submersible antenna in 2015; see Results). We selected these variables based on our observations of fish movement into other tributaries in the region and the results of similar spawning-movement-oriented studies on these species by Cathcart et al. (2017) and Fraser et al. (2017). Our objective was to identify variables with the greatest correlation to entry timing, but not to construct a predictive model as we were only able to model 2 years of entry data. We hypothesized that fish were cued to enter the stream relative to the following variables: mean daily temperature ($\hat{t}$), maximum daily temperature (t_{max}), change in mean daily temperature (previous day's mean temperature subtracted from current day's mean temperature; $\Delta\hat{t}$), mean weekly temperature ($\hat{t}_w$), the mean daily temperature of Roubideau Creek below the confluence ($\hat{t}_R$), mean daily stream discharge ($\hat{Q}$), photoperiod (total daylight hours; DL), or a combination of these variables. We created a "both years" model set from 2016 and 2017 data grouped, excluding $\hat{Q}$ as a variable (we were unable to use discharge data for 2016, see Results) and including DL (for Delta, Colorado: 38°44′32″N, 108°4′8″W) as a measure of seasonality. We also created a "2017 only" model set for 2017 data only, including $\hat{Q}$ but excluding DL, as the latter is uninformative without multiseason comparison. Using Program R

(R Core Team 2013), we $\log_{10}$ transformed numbers of fish detected daily by submersible antennae and checked for collinear variables in each model set ("both years" and "2017 only") using the function "ggpairs" in R package GGally (Schloerke et al. 2018). We considered variable pairs with $r \geq 0.7$ to be collinear (Dormann et al. 2013) and built our candidate models using all variables, but without collinear pairs. To achieve this, we built multiple global model subsets for the "both years" and "2017 only" model sets so that all variables were present, but no collinear variables were paired in a given global model. Then we used the function "glmulti" in R package glmulti (Calcagno 2013) to run all main-effect combinations of each global model in each subset and obtained the Akaike information criterion (Akaike 1987) corrected for small sample size (AIC_c; Burnham and Anderson 2002) for each model. All unique variable combinations and the null model from each subset global model within the "both years" and "2017 only" sets were compared based on AIC_c differences (ΔAIC_c), model likelihood (ℓ), model weight (w), and evidence ratio (Burnham et al. 2011). Relative variable importance was inferred based on presence in top-ranked models and the information lost or gained by the inclusion of other variables, but we did not calculate variable importance (Burnham and Anderson 2002) because models were not balanced due to our collinear variable exclusion method. Finally, we calculated the fit (adjusted R^2) of the top-performing models in each set to determine how well the best model explained the data overall.

We calculated length of stay (days) for PIT-tagged Bluehead and Flannelmouth suckers using weir data from individuals that we handled both entering and exiting the creek. We also calculated the mean length of stay by species. We compared these estimates between species within years, and within species between years using two-tailed t-tests (assuming unequal variance, $\alpha = 0.05$). Using this same set of fish, we also estimated mean change in weight between immigration and emigration to evaluate the energetic cost of reproduction. We calculated the mean and 95% CI for initial and final weights by species and sex. We grouped confirmed and probable sexes for this analysis, and if sex determinations disagreed between handlings, we counted fish based on the confirmed designation or, if determined to be of probable sex on both occasions, the presence of tubercles on either handling. We also tested for significant differences in percentage weight change between males and females of each species within years with two-tailed t-tests (assuming unequal variance, $\alpha = 0.05$). For these analyses, we grouped known and probable sex designations.

Finally, we estimated spawning tributary fidelity of Cottonwood Creek PIT-tagged fish as the percentage of tagged fish (by species) that returned from one year to the next based on original tag numbers implanted and subsequent year recaptures and redetections. These estimates of tributary fidelity were considered conservative because some mortality of tagged fish was expected between years, which would have deflated the rate of return of tagged fish. All analyses and figures for this paper were produced in Program R, ArcMap (ESRI 2011), and Microsoft Excel.

Egg and Larval Drift

Eggs and larval fish were collected in Cottonwood Creek using drift nets with 0.3 × 0.5-m rectangular mouths and 3.6-m-long, 560-μm-mesh nets terminating in a PVC collection canister. Two nets were generally set near the trap site for 1–2-h periods from 2100 hours to 0900 hours; however, we set nets for longer periods of up to 7.5 h on several occasions when water flow and debris load allowed. We identified larvae to genus, but made no attempts to identify eggs nor to differentiate among sucker species for either eggs or larvae (some were likely the progeny of nonnative suckers, which we attempted to exclude from Cottonwood Creek by culling or releasing in Roubideau Creek all such weir-captured fish). We calculated catch per net-hour for each net and then averaged the catch rates for all nets used in each netting session. We used egg catch to infer spawning duration and larval catch to infer the hatch-out period, which we compared with mean daily temperature and growing degree-days (GDD). Temperature is a cue for spawning in these fishes and affects maturation of eggs and larvae, and thermal time such as GDD is a physiologically relevant measure of temperature (Bezzerides and Bestgen 2002; Neuheimer and Taggart 2007). The lowest temperatures cited for spawning-related activities of these three species are near 6°C (minimum of spawning temperature range for Flannelmouth Sucker; Bezzerides and Bestgen 2002; Snyder et al. 2004; Barkalow et al. 2016), so we considered 6°C as the minimum temperature for our GDD calculations using the following formula:

$$\mathrm{GDD} = \sum_{i=1}^{n} (T_{mean})_i - T_{min},$$

where i is the number of days since fish were first detected or handled in Cottonwood Creek, T_{mean} is the mean daily temperature of day i, and T_{min} is the minimum temperature of physiological relevance (6°C).

RESULTS

Cottonwood Creek began flowing on May 6, 2015, was flowing by March 12, 2016, and began flowing between February 17 and February 24, 2017. Snowpack in the Cottonwood Creek drainage was minimal in 2015, and spring runoff was entirely rain driven. Peak flow occurred shortly after the creek began flowing, and completely ceased around June 15, though there was little or no flow between June 4 and 7. Snowmelt drove spring runoff in 2016 and 2017. In 2016, discharge was very low and clear until April 8, and flowing water remained until June 3. In 2017, discharge was very low ($\leq$0.057 m^3/s) until March 14 and completely ceased by June 7. The weir was in place from May 11 to 22, 2015; from April 5 to May 6 and from May 22 to 25, 2016; and from March 31 to May 19, 2017. In 2015 and 2017 we were unable to deploy the weir and traps before fish began to enter the stream (in 2015 it was initially set up in another location as Cottonwood Creek was not expected to deliver any water to its mouth, and in 2017 fish began entering the creek 3 weeks earlier than expected). In 2016 and 2017 there were occurrences of high flows accompanied by substantial debris that necessitated removal of pickets or the entire apparatus (2016), which resulted in the loss of control of fish movement to and from the creek. The submersible antenna deployed in 2016 was in place from April 19 to June 3, and two deployed in 2017 were in place from March 6 to June 7 and from March 20 to June 7.

Adult Fish Usage of Cottonwood Creek

Timing.— In 2015, fish began using the creek before the weir was installed, and the majority of fish captured were leaving Cottonwood Creek, which prevented us from estimating the main entry and exit periods. Immigrating Bluehead Suckers (n = 93) and Roundtail Chub (n = 40) were caught between May 12 and May 15, and again between May 19 and May 21. Emigrating Bluehead Suckers (n = 544) and Roundtail Chub (n = 272) were caught daily between May 13 and May 22. During this same period, all five Flannelmouth Suckers caught in 2015 were captured exiting the stream. We did not conduct further analyses on 2015 adult fish usage of the creek due to the abbreviated spawning season in Cottonwood Creek that year.

In 2016, we documented the earliest immigrants, which included both Flannelmouth and Bluehead suckers, with the weir (tagged and untagged immigrants) on April 8, 3 d after deployment. Based on 2016 weir and submersible antenna data, the majority of the immigration of both suckers occurred between April 8 and May 7 (Figure 2). The earliest weir captures of immigrating Roundtail Chub were on April 12, but were rare throughout the season. Roundtail Chub were detected in low but consistent numbers on the submersible antenna between April 21 and May 14, which was likely their main immigration period. Based on submersible antenna data, our redeployment of the weir from May 23 to 26 serendipitously encompassed three of the four peak days of emigrating fish movement (Figure 2), though relatively large numbers of Roundtail Chub were detected through June 1.

In 2017, early immigrants of both sucker species were detected with the submersible antenna on March 17. We do not believe untagged fish immigrated earlier than March 17, 2017, because shallow water depths prohibited entry before that date. Immigrating suckers (both species) were captured at the weir beginning with its installation on March 31 through May 7; however, based on the combined weir and antenna data, the primary sucker immigration occurred between March 17 and April 25, with several later immigration events. Roundtail Chub were not captured or detected until April 14, and immigration likely ceased on April 25. All species began emigrating on May 4 and 5. Peak emigration based on weir captures occurred between May 8 and May 17, but antenna detections suggest additional substantial emigration of suckers through May 27 and of chub through June 1. Flow ceased by June 7.

Demographics.— Overall, we handled 609 (in 2015), 8,118 (in 2016), and 10,726 (in 2017) individual target fish in Cottonwood Creek during the three spawning seasons (though many Roundtail Chub in 2015 were not counted as unique individuals because no batch marks were used that year and few were PIT-tagged). We captured mature Bluehead Sucker, Flannelmouth Sucker, and Roundtail Chub all 3 years. Total catch of both sucker species was highest in 2017 and lowest in 2015, while the inverse was true for Roundtail Chub (Table 1). Bluehead Sucker (66.8–80.3% of total yearly catch) were consistently the most abundant species, while Roundtail Chub (0.5–32.7% of total yearly catch) were more abundant than Flannelmouth Sucker (0.5–25.6% of total yearly catch) only in 2015.

Female suckers (including probable females) made up 39% to 57% of each species' population, with both species exhibiting an increase in female abundance in each year (excluding Flannelmouth Sucker in 2015 when only five individuals were handled; Table 1). Bluehead Sucker females made up 46, 51, and 55% of the total Bluehead Sucker Population in 2015, 2016, and 2017, respectively, and Flannelmouth Sucker females made up 39% and 50% of the population in 2016 and 2017, respectively. Sex of Roundtail Chub was largely undetermined because few individuals expressed gametes, but those for which we made sex determinations were largely male in 2015 and 2017. In 2016 we only identified female Roundtail Chub.

Mean observed lengths (mm TL) appeared to increase for both Bluehead Sucker (2015: 347.9 mm, SE = 0.45; 2016: 361.2 mm, SE = 0.35; 2017: 371.9 mm, SE = 0.34) and Flannelmouth Sucker (2016: 450.5 mm, SE = 0.39; 2017: 463.9 mm, SE = 0.38) over the 3 years of study (Figure 3). Roundtail Chub observed mean TLs (mm) also appeared to be different among years, but were largest in 2016 (279.7 mm, SE = 0.388) and smallest in 2017 (236.4 mm, SE = 0.462).

Temperature, stream discharge, and fish use.— We missed the main immigration period in 2015 and were

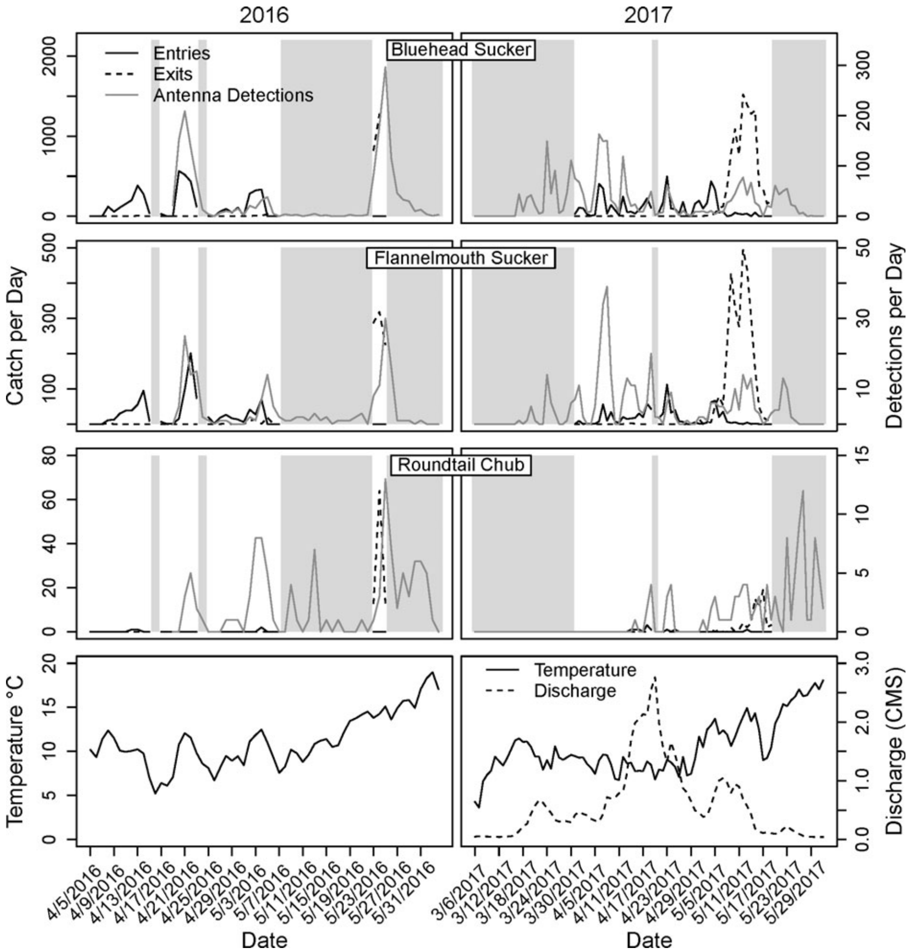

FIGURE 2. Daily catch numbers of Bluehead Sucker, Flannelmouth Sucker, and Roundtail Chub at the Cottonwood Creek fish weir, and all unique daily detections of PIT-tagged fish on submersible PIT-tag antennas during 2016 and 2017 sampling. "Entries" and "Exits" are catch of fish in the upstream and downstream movement traps, respectively. Gray-shaded portions of the panels indicate periods in which the weir was not functional. "Antenna Detections" display unique PIT tags detected per day from one (2016) or two (2017) 1-m-diameter submersible antennae located below the weir. The bottom two panels show daily average temperature and stream discharge measured just upstream from the weir. Dates on *x*-axis are given as month/day/year. Note differing *y*-axis scales to aid visualization of the data.

unable to compare temperature and discharge with immigration numbers. In 2016, higher-than-expected flows dislodged our water pressure sensor and resulted in erroneous depth estimates, precluding the development of a reliable depth–discharge equation or a hydrograph. However, we were able to relate immigration numbers to temperature data for 2016 and 2017 and to discharge data for 2017. We obtained 16 discharge measurements in 2017 and were able to produce a depth–discharge curve [Discharge = $52.807(\text{Depth})^2 - 102.87(\text{Depth}) + 51.792$; R^2 = 0.9918], which we used to build a hydrograph for 2017 (Figure 2).

During both years, apparent changes in daily immigration rates of all species, observed via weir data and antenna detections, generally mirrored major changes in temperature (Figure 2). Even relatively small temperature changes paralleled changes in immigrant numbers, and increases or decreases in temperature typically matched increases or decreases in immigration numbers, respectively. Immigration of all three species in both years roughly corresponded to temperatures between 6°C and 12°C, while emigration occurred with rising temperatures, ranging from approximately 13°C to 18°C (Figure 2). Alternatively, changes in flow (in 2017) did not consistently align with changes in immigration numbers. For instance, in late March, an increase in discharge from 0.44 to 0.67 m^3/s occurred as immigration rates of the sucker species dropped to zero. In contrast, 1 week into April, an eightfold increase in Flannelmouth Sucker detections and a substantial increase in weir captures occurred during an increase in discharge from 0.35 to 0.72 m^3/s. In general, increases in discharge were accompanied by decreases in

TABLE 1. Bluehead Sucker, Flannelmouth Sucker, and Roundtail Chub were encountered at the Cottonwood Creek fish weir in large numbers in 2016 and 2017, but delayed and reduced spring runoff in 2015 limited use of the creek by these species. Fish were captured moving either upstream (US) or downstream (DS). Displayed are counts of total catch (US and DS) and individual fish (Ind. fish) by species and sex (♂, male; ♀, female). Sexes are denoted as confirmed (subscript c) and probable (subscript p), or unsexed (?) as defined in the methods (only confirmed sex determinations for Roundtail Chub). Individual fish are counted as those with unique PIT tag numbers and first-capture, batch-marked fish. We were unable to count individual Roundtail Chub in 2015 as few were tagged or marked. Sex percentages (% Sex) are based on both confirmed and probable designated individual fish.

	2015				2016				2017			
Sex	US	DS	Ind. fish	% Sex	US	DS	Ind. fish	% Sex	US	DS	Ind. fish	% Sex
					Bluehead Sucker							
♂$_c$	49	236	327	54	1,984	212	2,201	49	1,482	1,396	2,047	45
♂$_p$	2	62			84	649			4	184		
♀$_c$	15	68	274	46	174	65	2,249	51	156	154	2,533	55
♀$_p$	27	178			2,032	743			1,775	2,062		
?	0	3	3		5	1,743	1,739		5	2,960	2,960	
Total	93	547	604		4,279	3,412	6,349		3,422	6,756	7,540	
					Flannelmouth Sucker							
♂$_c$	0	1	3	60	548	96	652	61	443	463	613	50
♂$_p$	0	2			9	70			0	61		
♀$_c$	0	0	2	40	84	23	416	39	72	72	615	50
♀$_p$	0	2			278	75			280	482		
?	0	0	0		0	611	610		7	1,884	1,884	
Total	0	5	5		919	875	1,678		802	2,962	3,112	
					Roundtail Chub							
♂$_c$	14	141			0	0	0		1	20	21	
♀$_c$	1	14			1	7	6		0	1	1	
?	25	118			3	83	85		9	44	52	
Total	40	273			4	90	91		10	65	74	

temperature, and the two were weakly negatively correlated ($r = -0.35$).

For our immigration models, we limited our data to periods when fish were able to access the stream preceding and during the main immigration periods (April 8–May 7 in 2016 and March 17–April 25 in 2017). Based on 2017 discharge data and our daily observations, flows under 0.14 m^3/s provided insufficient depth for fish to enter the stream. In 2016, such flows existed until April 7 when we measured 0.06 m^3/s. Discharge visibly increased the following day. In 2017, flows were prohibitive through March 16 (Figure 2). We were only able to use daily mean discharge as an immigration model variable in 2017. We further limited our analyses to the suckers, as detections of Roundtail Chub were low in both 2016 and 2017.

For the "both years" model set, $\hat{t}$, t_{max}, and $\hat{t}_R$ were all collinear ($r > 0.7$), and the resulting global subset models were (1) $\hat{t} + \Delta\hat{t} + DL + \hat{t}_w$, (2) $\Delta\hat{t} + t_{max} + DL + \hat{t}_w$, and (3) $\Delta\hat{t} + \hat{t}_R + DL + \hat{t}_w$. These three subsets resulted in a total of 32 unique models for each sucker species. For both species, the best-performing model was more than 2.00 ΔAIC_c from the null model (Table 2). The best-performing "both years" model for Bluehead Sucker immigration included t_{max}, DL, and $\hat{t}_w$ and was 781.6 times more probable than the null model. The variable t_{max} was the most informative single variable, and DL and $\hat{t}_w$ contributed little information to the best model and were independently the two lowest-ranked variables. The $\Delta\hat{t}$ variable may also offer some information as it was included in several high-ranked models. Of the collinear variables, t_{max} consistently outperformed the others. For Flannelmouth Sucker immigration models, all six variables occurred in models with $\Delta AIC_c < 3$ and the best-performing model was only 6.24 times more probable than the null model (Table 2; Table S.1 found online in the Supporting Information section at the end of the article). The top-ranked model included $\hat{t}_R$ and $\hat{t}_w$, and $\hat{t}_R$ was the most informative single variable, while $\hat{t}_w$ and DL were again ranked as the least-informative variables independently or combined. There was little evidence that $\hat{t}_R$ outperformed the other two collinear variables. In the "2017 only" model set, collinear pairs were $\hat{t}$ and t_{max}, $\hat{t}$ and $\hat{t}_R$, and $\hat{t}_w$ and $\hat{Q}$ ($r > 0.7$). Our global model subsets were (1) $\hat{t} + \hat{Q} + \Delta\hat{t}$, (2) $\hat{t} + \Delta\hat{t} + \hat{t}_w$, (3) $\hat{Q} + \Delta\hat{t} + t_{max} + \hat{t}_R$, and (4) $\Delta\hat{t} + t_{max} + \hat{t}_R + \hat{t}_w$. These four subsets produced 30 unique variable combinations for each sucker species. For Bluehead Suckers, the top "2017 only" model included only

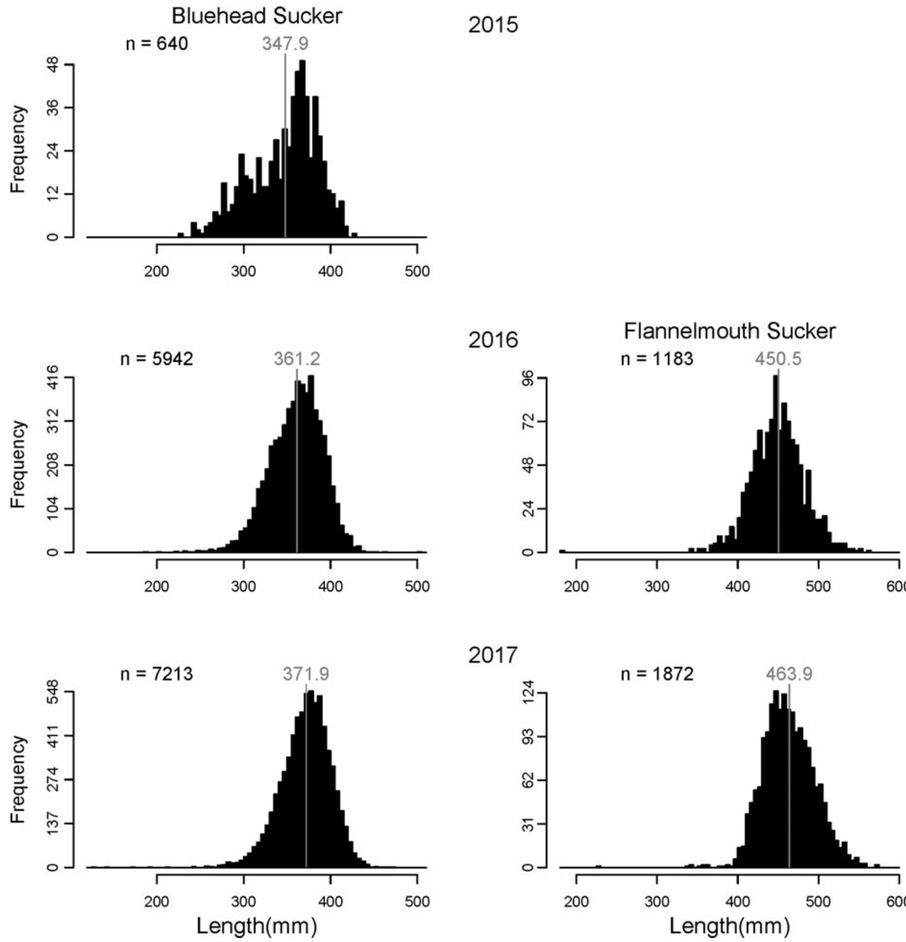

FIGURE 3. Bluehead and Flannelmouth suckers captured at the Cottonwood Creek weir were primarily large, adult fish. Presented here are the numbers of individuals within each 5-mm length bin handled in 2015, 2016, and 2017. The gray lines (width = SE) and numbering indicate the mean length of all fish. Only five Flannelmouth Sucker were handled in 2015, so we do not present a plot for the species captured in 2015.

$\Delta\hat{t}$ and was 136.81 times more probable than the null model and 3.05 times more probable than the second-best model, which also included t_{max} (Table 3). Replacing t_{max} with any of the collinear variables resulted in minimal decreased model performance. Models with three or more terms and those that excluded $\Delta\hat{t}$ had the greatest ΔAIC_c values (Table S.2). The top "2017 only" model for Flannelmouth Sucker immigration was $\hat{t} + \hat{t}_w$ and was 128.52 times more probable than the null model. Of collinear $\hat{t}$, t_{max}, and $\hat{t}_R$, the most informative was $\hat{t}$. The $\Delta\hat{t}$ term may provide some information as it did in the Bluehead "both years" model. Discharge ($\hat{Q}$) was in low-ranked models only ($w < 0.019$; Table S.2). All top-performing models in each subset explained the variation in the data relatively weakly ($0.13 < R^2 < 0.35$; Tables 2, 3).

Length of stay.— There were 691 and 937 individual, PIT-tagged Bluehead Suckers and 54 and 255 Flannelmouth Suckers in 2016 and 2017, respectively, that we handled as they both entered and exited Cottonwood Creek. We did not catch any PIT-tagged Roundtail Chub entering and exiting the creek in 2016, and we only caught one in 2017. We did not catch any individuals of any species on both their entry and exit in 2015.

In 2016, Cottonwood Creek residency times were similar for Bluehead Suckers (mean, 36.7 d; SE = 0.277) and Flannelmouth Suckers (mean, 35.5 d; SE = 0.239; t = 1.17, df = 743, P = 0.244), but in 2017 Bluehead Suckers used the stream longer on average (mean, 30.4 d; SE = 0.239) than did Flannelmouth Suckers (mean, 25.7 d; SE = 0.484; t = 8.87, df = 1190, P < 0.001). Residency times were significantly shorter for both Bluehead Suckers (t = 17.47, df = 1626, P < 0.001) and Flannelmouth Suckers (t = 8.15, df = 307, P < 0.001) in 2017 than they were in 2016. The single Roundtail Chub for which we were able to determine residency time was in the creek for 21.0 d.

Energetic cost of reproduction.— Of the fish handled going in both directions, our sex determinations (male

TABLE 2. Top models ($w \geq 0.05$) relating $\log_{10}$ transformed antenna detections of PIT-tagged native suckers to environmental variables during the immigration period on Cottonwood Creek for combined 2016 and 2017 data. Models are ranked by Akaike information criterion corrected for small sample sizes (AIC_c; smallest to largest), and ΔAIC_c, model likelihood (ℓ), model probability (w), evidence ratio (w_1/w_i), and adjusted R^2 are shown for model comparison. The variables are: mean daily temperature ($\hat{t}$), the change in mean daily temperature ($\Delta\hat{t}$), the maximum daily recorded temperature (t_{max}), and the weekly mean temperature of Cottonwood Creek ($\hat{t}_w$), the mean daily temperature of Roubideau Creek ($\hat{t}_R$), and the daily daylight length for Delta, Colorado (DL).

Model	AIC_c	ΔAIC_c	ℓ	w	Evidence ratio	Adjusted R^2
			Bluehead Sucker			
$\beta_0 + t_{max} + DL + \hat{t}_w$	137.824	0.000	1.000	0.223	1.000	0.31
$\beta_0 + t_{max}$	138.611	0.787	0.675	0.150	1.482	0.26
$\beta_0 + t_{max} + DL$	139.210	1.386	0.500	0.111	1.999	0.27
$\beta_0 + \Delta\hat{t} + t_{max} + DL$	139.680	1.855	0.395	0.088	2.529	0.29
$\beta_0 + \Delta\hat{t} + t_{max} + DL + \hat{t}_w$	139.734	1.910	0.385	0.086	2.598	0.31
$\beta_0 + \Delta\hat{t} + t_{max}$	139.838	2.014	0.365	0.081	2.737	0.26
$\beta_0 + t_{max} + \hat{t}_w$	140.822	2.998	0.223	0.050	4.477	0.25
β_0	151.147	13.323	0.001	0.000	781.605	
			Flannelmouth Sucker			
$\beta_0 + \hat{t}_R + \hat{t}_w$	144.842	0.000	1.000	0.149	1.000	0.13
$\beta_0 + \hat{t} + \hat{t}_w$	145.069	0.227	0.893	0.133	1.120	0.12
$\beta_0 + \hat{t}_R + DL + \hat{t}_w$	146.404	1.562	0.458	0.068	2.184	0.13
$\beta_0 + \hat{t}_R$	146.544	1.702	0.427	0.064	2.342	0.07
$\beta_0 + \hat{t} + DL + \hat{t}_w$	146.642	1.800	0.407	0.061	2.459	0.12
$\beta_0 + \hat{t}$	146.985	2.143	0.342	0.051	2.920	0.06
β_0	148.503	3.661	0.160	0.024	6.236	

TABLE 3. Top models ($w \geq 0.05$) relating $\log_{10}$ transformed antenna detections of PIT-tagged native suckers to environmental variables during the 2017 immigration period on Cottonwood Creek. Model ranking criteria and model variables are as in Table 2, with the exception that DL is replaced by mean daily discharge ($\hat{Q}$).

Model	AIC_c	ΔAIC_c	ℓ	w	Evidence ratio	Adjusted R^2
			Bluehead Sucker			
$\beta_0 + \Delta\hat{t}$	80.576	0.000	1.000	0.293	1.000	0.31
$\beta_0 + \Delta\hat{t} + t_{max}$	82.805	2.229	0.328	0.096	3.047	0.30
$\beta_0 + \Delta\hat{t} + \hat{t}_w$	82.811	2.235	0.327	0.096	3.057	0.30
$\beta + \hat{Q} + \Delta\hat{t}$	83.235	2.659	0.265	0.078	3.780	0.29
$\beta_0 + \hat{t} + \Delta\hat{t}$	83.245	2.668	0.263	0.077	3.797	0.29
$\beta_0 + \Delta\hat{t} + \hat{t}_R$	83.253	2.677	0.262	0.077	3.812	0.29
$\beta_0 + \Delta\hat{t} + t_{max} + \hat{t}_w$	84.169	3.593	0.166	0.049	6.027	0.31
β_0	90.413	9.837	0.007	0.002	136.813	
			Flannelmouth Sucker			
$\beta_0 + \hat{t} + \hat{t}_w$	90.409	0.000	1.000	0.399	1.000	0.35
$\beta_0 + \hat{t}_R + \hat{t}_w$	93.146	2.737	0.254	0.101	3.929	0.28
$\beta_0 + \hat{t} + \Delta\hat{t} + \hat{t}_w$	93.195	2.786	0.248	0.099	4.027	0.32
$\beta_0 + t_{max} + \hat{t}_w$	93.340	2.931	0.231	0.092	4.329	0.28
$\beta_0 + \Delta\hat{t} + \hat{t}_w$	94.175	3.766	0.152	0.061	6.572	0.26
$\beta_0 + \Delta\hat{t} + \hat{t}_R + \hat{t}_w$	94.430	4.021	0.134	0.053	7.466	0.29
$\beta_0 + \hat{t}_w$	94.589	4.180	0.124	0.049	8.083	0.21
β_0	100.121	9.712	0.008	0.003	128.524	

versus female whether confirmed or probable) agreed between handlings 97.5% of the time for all fish in both years. There were disagreements wherein sex was confirmed on one occasion, but was determined to be probable and of the opposite sex in 1.7% of the fish, but all were counted as the confirmed sex for the length of stay and energetic cost of reproduction analyses. In 0.8% of all fish, sex was determined to be probable on both occasions but of the opposite sex; these fish were counted as male as tubercles were present on one of the handling occasions. Disagreements stemmed from either late development or early reabsorption of tubercles, or from observational or data recording errors.

The PIT-tagged Bluehead and Flannelmouth suckers we handled as they both entered and exited Cottonwood Creek displayed clear weight loss over their stay in the creek in both 2016 and 2017 (Figure S.3), though weight loss was likely underestimated for spawning fish as we had no way to verify that fish actually spawned while at large in Cottonwood Creek. In both 2016 and 2017, Bluehead Sucker female weight loss (2016: mean, 17.9%; SE = 0.004; 2017: mean, 17.8%; SE = 0.002) was significantly larger (2016: $t = 5.51$, df = 351, $P < 0.001$; 2017: $t = 24.12$, df = 1,305, $P < 0.001$) than weight loss for males (2016: mean, 13.0%; SE = 0.008; 2017: mean, 11.9%, SE = 0.002). In 2016, Flannelmouth Sucker sample sizes were small, and there was no significant difference ($t = 1.49$, df = 30, $P = 0.147$) between the weight loss of females (mean, 15.4%; SE = 0.008) and males (mean, 7.8%; SE = 0.050). However, in 2017 the weight loss of Flannelmouth Sucker females (mean, 15.5%; SE = 0.003) was significantly larger ($t = 14.32$, df = 253, $P < 0.001$) than that of males (mean, 9.7%; SE = 0.002).

Tributary fidelity.— Based on antenna detections and weir captures, returns of Bluehead (70%) and Flannelmouth (71%) suckers PIT-tagged in Cottonwood Creek were highest for those tagged in 2016 and returning in 2017 (Table 4). Returns of Bluehead Suckers tagged in 2015 were also relatively high (61%) in 2016. Despite low numbers of Flannelmouth Suckers tagged in 2015, two out of the four were detected in 2016. Many Bluehead Suckers (49%) and one Flannelmouth Sucker tagged in 2015 also returned in 2017. Roundtail Chub exhibited much lower fidelity. Only 18% of those tagged in 2015 returned and were handled or detected in 2016. However, 42% of the 2015 Roundtail Chub were encountered in 2017. No Roundtail Chub were tagged in 2016.

Egg and Larval Drift

We conducted seven, four, and six drift netting sessions in 2015, 2016, and 2017, respectively, and collected both eggs and larval fish on multiple occasions in all 3 years (Figure S.4). We were able to identify nearly all larvae that we collected as Catostomidae, and therefore limited our results to that family only. Likewise, based on size, the majority of eggs we collected seemed to be Catostomidae, and several fertilized eggs hatched in the lab and the larvae were confirmed to be catostomids. This, along with the known composition of large-bodied fish in the stream, supported our assumption that all but a few noticeably small eggs (which we did not count in our data) were catostomid eggs, and we treated our data as such. The eggs of both catostomid species are demersal and adhesive (Snyder et al. 2004), so eggs that we captured were most likely deposited in relatively close proximity to our sampling location and thus representative of temporally recent spawning. We collected eggs on our first netting occasion every year, indicating that spawning was already ongoing. Fish were therefore spawning by May 18, 2015, May 16, 2016, and May 2, 2017. These dates correspond to 195.4, 138.0, and 135.0 GDD (°C; $T_{min} = 6°C$), respectively, since fish began entering the stream, and the mean daily temperatures at the time were 16.1, 10.5, and 10.5°C, respectively. In 2015, the first larval sucker was also collected on the first drift-netting occasion (May 18; 195.4 GDD; mean daily temperature, 16.1°C), but drift was high only on the June 9 sampling when GDD was 593.5 and the mean daily temperature was 20.4°C. In 2016, larvae were not sampled until May 24 (196.9 GDD, 14.3°C) and were most abundant on May 30 (251.0 GDD, 14.9°C). Similarly, in 2017 we sampled the first larvae on May 16 (230.6 GDD, 12.4°C), but they were most abundant on May 26 (306.0 GDD, 17.0°C). Catch rates of drifting larvae were typically low (10.4 larvae or fewer per net-hour), but were much higher on the June 9, 2015, occasion when the rate was 117.1 larvae per net-hour.

TABLE 4. Between-year numbers of individual PIT-tagged and recaptured (both physically and via antenna detections) study species in Cottonwood Creek near Delta, Colorado. The sucker species showed a high propensity to return to Cottonwood Creek in years following their initial tagging. Total tagged are numbers of tags deployed by year, followed by the total number and the percentage (%) of those tags recaptured in subsequent years.

	Total tagged		2016 recaptures		2017 recaptures			
Species	2015	2016	2015 fish	Percent of total	2015 fish	Percent of total	2016 fish	Percent of total
Bluehead Sucker	570	2,243	347	61	279	49	1,572	70
Flannelmouth Sucker	4	399	2	50	1	25	282	71
Roundtail Chub	77	2	14	18	32	42	0	0

DISCUSSION

Adult Usage of Cottonwood Creek

Cottonwood Creek is an intermittent stream, yet still supports extensive spawning use by Bluehead and Flannelmouth suckers. Overall numbers of suckers encountered in this relatively small stream were surprisingly large. Studies on the use of tributaries by Bluehead and Flannelmouth suckers are scarce. However, in studies on Flannelmouth Sucker tributary spawning on the Paria River (perennial tributary to the Colorado River, Arizona) and Coal Creek (perennial tributary of the White River, Colorado) far fewer fish were documented using the tributaries than were observed in our study (Weiss 1993; Fraser et al. 2017). Additionally, Fraser et al. (2017) evaluated Bluehead Sucker tributary spawning in Coal Creek and encountered fewer fish by an order of magnitude. While these studies used different methods (i.e., fyke nets, hoop nets, and seining) and the source populations are likely demographically different, we still documented an unprecedented number of spawning suckers in Cottonwood Creek compared with estimates available in the literature. Cathcart et al. (2017) detected PIT-tagged Flannelmouth Suckers entering McElmo Creek (tributary of the San Juan River, New Mexico) numbering in the thousands, suggesting heavy usage of the system, but in this case the tributary was perennial with one additional perennial and several intermittent tributaries upstream from the detection point. While we know that Cottonwood Creek does support extensive sucker spawning, we do not know the relative importance of this tributary compared with other Gunnison River tributaries in terms of total spawning use or the resulting recruitment. We have documented spawning suckers in nearby small perennial tributaries (e.g., Buttermilk Creek; Figure 1), but not to the same extent as in Cottonwood Creek. Future study should aim to determine the relative population level importance of Cottonwood Creek, as well as habitat or water quality factors that may drive the high level of spawning use despite its intermittency. While we did document use of Cottonwood Creek by Roundtail Chub, our weir was designed specifically to exclude suckers and was not fully effective for the smaller bodied, laterally compressed chub. Therefore, our data on Roundtail Chub usage are limited, and more research is needed to characterize the spawning usage of the creek by this species.

Despite substantial differences in the timing and duration of the wetted season of Cottonwood Creek, we documented use of the stream and successful spawning in all 3 years of study. While relationships between stream use and environmental variables such as temperature and discharge were supported by the data, they were generally weak and varied greatly between species and years. For these fish, it appeared that when adequate water was available, fish would enter the stream independent of other variables that we measured. The relationships we did observe were more strongly related to Cottonwood Creek temperature variables than to discharge or seasonality. In perennial systems, spawning and immigration into spawning tributaries is typically related to specific environmental variables such as water temperature (Bezzerides and Bestgen 2002). For instance, Cathcart et al. (2017) found that Flannelmouth Suckers entered a tributary of the San Juan River in New Mexico in relation to main-stem temperature. Likewise, Fraser et al. (2017) found that immigration of Bluehead and Flannelmouth suckers into a spawning tributary of the White River in Colorado was related to the difference in temperature between the main-stem and tributary. Weiss et al. (1998) observed spawning synchrony among multiple Colorado River tributaries throughout Grand Canyon despite temperature and flow differences and suggested spawning was cued by main-stem conditions or other nontributary-specific variables. In this study, main-stem (Roubideau Creek) temperatures were associated with only the immigration of Flannelmouth Sucker, though a high correlation between temperatures in Cottonwood and Roubideau creeks precluded determination of the more influential factor. In other systems and with different species, migrations and spawning-related activities typically occur in relation to very specific environmental variables such as daily temperature, temperature changes, and stream discharge (Ovidio et al. 1998; Dahl et al. 2005; Nunn et al. 2010). We found limited support for temperature cues (including mean daily temperature change, maximum daily temperature, and mean weekly temperature) influencing immigration, but these cues varied between species and depended on whether both years of data were analyzed independently or jointly. We did not find convincing support in our models for discharge as a cue, nor did we see a seasonality effect between years. This aligns with our observations that fish used the stream as long as discharge was above a physically limiting threshold, which occurred approximately 3 weeks earlier in 2017 than 2016. There are other variables such as turbidity that we did not measure that may have further explained the timing of immigration, but the variability and weak relationships we observed may reflect behavioral and physiological plasticity in these sucker populations that is a result of the highly stochastic nature of Cottonwood Creek and the desert Southwest in general.

We observed apparent shifts in fish length among our sampling years for all three species as well as a changing sex ratio. Flannelmouth Sucker sample size was small in 2015, but large in 2016 and 2017, and Bluehead Sucker sample sizes were large for all 3 years. Therefore, the size shift (an approximate 30-mm increase between 2015 and 2017 for Bluehead Sucker, and an approximate 13-mm increase for Flannelmouth Sucker between 2016 and 2017; Figure 3) we observed is probably representative of a true demographic shift. While we also saw a shift from male- to female-dominated sex ratios for both sucker species, the shift towards larger individuals is observable for each sex of each species, so we do not believe the change in sex ratio explains the size shift. This directional shift in the suckers could be explained by stochastic variation, annual variability in growth rates, annual behavioral differences (such as skipped spawning, as has been observed for another Colorado River large-bodied fish: Pearson et al. 2015), or recent decreased recruitment of smaller mature fish. With only 3 years of data to compare (two for Flannelmouth Sucker), it is impossible determine the true cause of the size shift, but the most concerning possibility is that of decreased recruitment of mature suckers. Weiss et al. (1998) observed a 50-mm increase in the mean length of Flannelmouth Suckers spawning in the Paria River between 1981 and 1993 and concluded that despite the persistence of spawning fish, there was limited spawning success. Shifting size structures towards larger individuals may indicate recruitment failure and that sucker spawning success has been limited in recent years in Cottonwood Creek; for that reason, the population should be monitored closely in future years should this trend continue. Our data for Roundtail Chub are sparse, but primarily we found that reproductive members of this species that use Cottonwood Creek are somewhat small compared with what may be found in the Gunnison River (K. G. Thompson, unpublished). We also saw variability in the size structure and sex ratios of Roundtail Chub between years, but because we incompletely sampled the population with our weir design, there is no strong evidence that these differences were biologically relevant.

We found that both Bluehead and Flannelmouth suckers use Cottonwood Creek for lengthy periods of time (25–37 d on average) if the stream is flowing sufficiently. Due to the sudden rainfall-induced inundation of Cottonwood Creek before the installation of the weir in 2015, we did not capture early immigrating fish and were unable to calculate length of stay that year, but the greatly reduced wetted season (over a month shorter than in 2016 and 2017) forced fish to use the creek for less time than they did in the following years. We also saw differences between 2016 and 2017, with length of stay being, on average, longer for both sucker species in 2016. However, average residency time estimated for 2016 is likely inflated because the weir was ineffective or completely disabled from May 5 through mid-day on May 23. Emigrating fish during that period were not available as part of our paired data set. Detections of PIT-tagged fish on the submersible antenna indicate that May 23–25 captured most of a 4-d period of intense emigration, but also that we missed handling fish represented by 111 unique tags detected by the antenna during the period that the weir was in operation, some of which presumably represented emigrants. Of those tags, at least 79 (57 Bluehead Sucker, 22 Flannelmouth Sucker) probably represented emigrations because the tags were soon after detected downstream in Roubideau Creek at a fixed antenna site. Assuming true emigrations and recalculating 2016 residency duration with these data included, Bluehead Sucker residency was reduced to 35.7 d and Flannelmouth Sucker residency to 32.0 d, still considerably longer than the values observed in 2017. Despite any inflation of the 2016 estimate, we still observed longer length of stay in Cottonwood Creek than these species have displayed in other tributaries such as perennial Coal Creek, where Fraser et al. (2017) observed average residency times of 10–12 d with a maximum 32 d for both Bluehead and Flannelmouth suckers. We observed small differences in residency time between the two sucker species with Bluehead Suckers using the stream longer on average.

Reproduction took an energetic toll on both sucker species as evidenced by weight loss. We could not verify that the individual fish we used in our estimations had spawned. If nonbreeding fish (displaying no sexual signs and losing no weight via spawning) were captured both immigrating and emigrating, it would decrease mean female weight loss because such fish would have been deemed probable females on both occasions based on lack of tubercles. Therefore, estimates of weight loss are representative for males, while potentially underestimating that for females. Weight loss or decreased condition after spawning is common in fish (Pope and Willis 1996) and has been documented for catostomids and Flannelmouth Suckers specifically (Raney and Webster 1942; Brown and Graham 1954; Paukert and Rogers 2004). Raney and Webster (1942) found that tributary-spawning White Sucker females lost 20–25% of their prespawn weight, while weight loss in males was not detectable. Spawning in intermittent tributaries like Cottonwood Creek may impose energetic costs to both sexes, as the short wetted-season inhibits the production of food resources.

All of the fish we used for estimating length of stay and spawning-season weight loss were physically handled. Although Fraser et al. (2017) observed an overwhelming flight response of physically handled native suckers in each of 2 years, we observed no such phenomenon in Cottonwood Creek. Our newly handled fish were released upstream from our picket weir and would not have been able to flee the creek without being caught in our downstream-oriented trap box or being impinged on the picket weir. We also had our picket weir deployed at a location in Roubideau Creek in 2015, before Cottonwood Creek began to flow, and failed to observe a flight response on the part of handled suckers there (Thompson, unpublished). Explanations for the response observed by Fraser et al. (2017) remain elusive. We have noted that Cottonwood Creek has a steeper gradient and less-sedimented channel substrate characteristics than much of Roubideau Creek in its lower reaches. Cleaner spawning habitats may be more abundant in upper Roubideau Creek or its other tributaries as well, motivating spawning fish to be persistent in seeking those habitats.

We captured or detected numerous individuals of both sucker species during multiple sampling years in Cottonwood Creek, suggesting some degree of spawning tributary fidelity. In fact, at least 71% of Flannelmouth Suckers and 70% of Bluehead Suckers tagged in 2016 returned to Cottonwood Creek in 2017. In 2016, we saw lower returns of Bluehead Suckers (61%) tagged in 2015, but were only able to tag four Flannelmouth Suckers in 2015. We saw much lower fidelity in Roundtail Chub (42% at most), but because we designed our weir to target suckers and numbers of chub captured were low, we do not believe that these estimates are reflective of the entire spawning population and are, at best, conservative estimates for only the largest Roundtail Chub that used Cottonwood Creek. We assume that some mortality of all species occurred between the time of tagging and the following spawning seasons, either within Cottonwood Creek as a result of terrestrial predation and spawning-related stresses, or within the rest of the river system as a result of terrestrial and aquatic predation, disease, and senescence. Therefore, our estimates of tagged-fish tributary fidelity probably underestimated true fidelity. Spawning-site fidelity has been documented previously for members of Catostomidae and for these two species specifically. Larval development of olfactory anatomy in some White Sucker populations suggests they may possess the ability to imprint and home on their natal origin (Werner and Lannoo 1994). Razorback Suckers *Xyrauchen texanus* in the Green River in Utah and Colorado can repeatedly return to the same river section to spawn (Modde and Irving 2011). For a tributary of the San Juan River, Cathcart et al. (2017) found some tributary fidelity for Flannelmouth Suckers, and for a tributary of the White River, Fraser et al. (2017) found spawning-site fidelity of 13–45% for Flannelmouth and Bluehead suckers. In these examples, spawning occurred within perennial tributaries. Because Cottonwood Creek fidelity rates (50–71%) are comparable or higher suggests that despite its intermittent nature, the creek is at least as suitable if not preferable for spawning compared with the perennial habitats discussed in the other studies.

Egg and Larval Drift

Numerous sucker eggs and larvae in Cottonwood Creek in all 3 years of study confirmed that the fish accessed the stream to spawn, which resulted in large numbers of viable offspring. We caught eggs and larvae during the month of May in all 3 years, but only larvae in June. In 2016 and 2017, spawning likely began before the end of April, as numerous immigrant females expressed eggs during April. In the geographically close San Juan River, Flannelmouth Suckers spawn primarily in May and June and Bluehead Suckers in April and May (Barkalow et al. 2016). In contrast, there was little temporal separation in Cottonwood Creek, as we saw a shorter spawning window and little difference in the entry and exit timing of the two species. Spawning appeared to occur regardless of accumulated GDD or mean daily temperature, but in the San Juan River basin, spawn date was correlated to GDD (Barkalow et al. 2016). The shortened, nontemperature-driven spawning period reflects the window of available water in Cottonwood Creek and suggests physiological plasticity in these fishes, which allows them to make use of the variable conditions associated with intermittent tributary spawning.

We documented catostomid larval drift near the mouth of Cottonwood Creek indicating that some larvae evacuate the creek, which may result in some recruitment. In all 3 years, high densities of larvae remained in wetted pools of Cottonwood Creek from its mouth to over 5 km upstream after active flow ceased. Stranded larvae represent a large amount of doomed reproduction, though monsoonal rains may reconnect these pools with Roubideau Creek allowing additional escapement. We do not know the overall reproductive success of the Bluehead and Flannelmouth suckers that spawned in Cottonwood Creek, but this remains an important topic for future study to reveal the population level importance of this spawning tributary.

CONCLUSIONS

We observed considerable annual variability in the spawning-related behavior and biology of Bluehead and Flannelmouth suckers in Cottonwood Creek and found further deviance when we compared our results to those of other studies. This highlights the ability of these species to cope with the fluctuating conditions of the arid Colorado River basin, but also cautions against range-wide blanket management and conservation approaches as regional adaptations could be ignored with potential detriment to localized populations. In general, there is a dearth of literature on these species. Flannelmouth Suckers are more widely represented in the literature than Bluehead Suckers and Roundtail Chub, and further research on the localized and general physical, ecological, and biological needs of these species may improve conservation effectiveness.

Perhaps the most significant finding of our study is the highlighted need to expand our conservation paradigm for these three species to consider intermittent tributaries. Others have recently called for increased attention to Colorado River basin tributary habitats, whether on behalf of endangered fishes (Bottcher et al. 2013), less-imperiled fishes (UDNR 2006; Fraser et al. 2017), or both (Cathcart et al. 2015; Laub et al. 2018). While these studies focused primarily on perennial tributaries, in some instances with enhanced flows resulting from irrigation projects, our study focused on a stream that is dry for a majority of the year. We know of no other investigation establishing the level of spawning activity for Bluehead and Flannelmouth suckers in a snowmelt-driven intermittent stream that we observed. Intermittent streams generally receive little attention; even in the arid Southwest there are many perennially wetted streams demanding the attention of managers. However, their likely importance with respect to the future persistence of the endemic fishes of the Colorado River basin suggests that their status, and the protections extended to them, be elevated to reflect the role such streams may play in the completion of critical life-history phases.

ACKNOWLEDGMENTS

We thank R. Keith for initial input on the design and construction of the picket weir and trap boxes. Crew members instrumental in the completion of the project were C. Brittain, E. Guy, K. Seto, L. Simmons, J. Whitton, T. O'Dell, K. Meisberger, and K. Shollenberger. Fellow Colorado Parks and Wildlife employees D. Kowalski, E. Gardunio, P. Jones, and J. Logan repeatedly offered their personal assistance or that of their technicians during some critical times. R. Japuntich (Bureau of Land Management) and M. Woody (U.S. Forest Service) also offered personal and technician assistance. This study was funded by Colorado Parks and Wildlife. We thank K. Bestgen, two anonymous reviewers, and an associate editor of the journal for providing helpful reviews of our manuscript. There is no conflict of interest declared in this article.

REFERENCES

Akaike, H. 1987. Factor analysis and AIC. Psychometrika 52:317–332.

Anderson, R. M., and G. Stewart. 2007. Impacts of stream flow alterations on the native fish assemblage and their habitat availability as determined by 2D modeling and the use of fish population data to support instream flow recommendations for the sections of the Yampa, Colorado, Gunnison, and Dolores rivers in Colorado. Colorado Division of Wildlife, Special Report, Number 80, Part II, Fort Collins.

Barkalow, S. L. C., M. A. Brandenburg, S. P. Platania, and J. L. Kennedy. 2016. Reproductive ecology and early life history of Bluehead Sucker and Flannelmouth Sucker in the San Juan River. Share with Wildlife, New Mexico Department of Game and Fish, Santa Fe.

Baxter, G. T., and M. D. Stone. 1995. Fishes of Wyoming. Wyoming Game and Fish Department, Cheyenne.

Bezzerides, N., and K. R. Bestgen. 2002. Status review of Roundtail Chub *Gila robusta*, Flannelmouth Sucker *Catostomus latipinnis*, and Bluehead Sucker *Catostomus discobolus* in the Colorado River basin. Colorado State University, Larval Fish Laboratory Contribution 118, Final Report, Fort Collins.

Bottcher, J. L., T. E. Walsworth, G. P. Thiede, P. Budy, and D. W. Speas. 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.

Bower, M. R., W. A. Hubert, and F. J. Rahel. 2008. Habitat features affect Bluehead Sucker, Flannelmouth Sucker, and Roundtail Chub across a headwater tributary system in the Colorado River basin. Journal of Freshwater Ecology 23:234–357.

Brown, C. J. D., and R. J. Graham. 1954. Observations on the Longnose Sucker in Yellowstone Lake. Transactions of the American Fisheries Society 83:38–46.

Budy, P., M. M. Conner, N. L. Salant, and W. W. Macfarlane. 2015. An occupancy-based quantification of the highly imperiled status of desert fishes of the southwestern United States. Conservation Biology 29:1142–1152.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information theoretic approach, 2nd edition. Springer-Verlag, New York.

Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Biology and Sociobiology 65:23–35.

Calcagno, V. 2013. glmulti: model selection and multimodel inference made easy. R package version 1.0.7. Available: https://CRAN.R-project.org/package=glmulti. (January 2019).

Cathcart, C. N., K. B. Gido, and M. C. McKinstry. 2015. Fish community distributions and movements in two tributaries of the San Juan River, USA. Transactions of the American Fisheries Society 144:1013–1028.

Cathcart, C. N., K. B. Gido, M. C. McKinstry, and P. D. MacKinnon. 2017. Patterns of fish movement at a desert river confluence. Ecology of Freshwater Fish 2017:1–14.

Clarkson, R. W., P. C. Marsh, L. E. Stefferud, and J. A. Stefferud. 2005. Conflicts between native fish and nonnative sport fish management in the southwestern United States. Fisheries 30(9):20–27.

Closs, G. P., and P. S. Lake. 1994. Spatial and temporal variation in the structure of an intermittent-stream food web. Ecological Monographs 64:1–21.

Dahl, J., J. Dannewitz, L. Karlsson, E. Petersson, A. Löf, and B. Ragnarsson. 2005. The timing of spawning migration: implications of environmental variation, life history, and sex. Canadian Journal of Zoology 82:1864–1870.

Datry, T., S. T. Larned, and K. Tockner. 2014. Intermittent rivers: a challenge for freshwater ecology. BioScience 64:229–235.

Dauwalter, D. C., S. J. Wenger, K. R. Gelwicks, and K. A. Fesenmyer. 2011. Land use associations with distributions of declining native fishes in the upper Colorado River basin. Transactions of the American Fisheries Society 140:646–658.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. García Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Münkemüller, C. McClean, P. E. Osborne, B. Reineking, B. Schröder, A. K. Skidmore, D. Zurell, and S. Lautenbach. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46.

Downing, D. M., C. Winer, and L. D. Wood. 2003. Navigating through Clean Water Act jurisdiction: a legal review. Wetlands 23:475–493.

Erman, D. C., and V. M. Hawthorne. 1976. The quantitative importance of an intermittent stream in the spawning of Rainbow Trout. Transactions of the American Fisheries Society 105:675–681.

ESRI (Environmental Systems Research Institute). 2011. ArcGIS desktop: release 10. ESRI, Redlands, California.

Falke, J. A., K. D. Fausch, R. Magelky, A. Aldred, D. S. Durnford, L. K. Riley, and R. Oad. 2011. The role of groundwater pumping and drought in shaping ecological futures for stream fishes in a dryland river basin of the western Great Plains, USA. Ecohydrology 4:682–697.

Fraser, G. S., D. L. Winkelman, K. R. Bestgen, and K. G. Thompson. 2017. Tributary use by imperiled Flannelmouth and Bluehead suckers in the upper Colorado River basin. Transactions of the American Fisheries Society 146:858–870.

Hooley-Underwood, Z. E., S. B. Stevens, and K. G. Thompson. 2017. Short-term passive integrated transponder tag retention in wild populations of Bluehead and Flannelmouth suckers. North American Journal of Fisheries Management 37:582–586.

Labbe, T. R., and K. D. Fausch. 2000. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. Ecological Applications 10:1774–1791.

Laub, B. G., G. P. Thiede, W. T. Macfarlane, and P. Budy. 2018. Evaluating the conservation potential of tributaries for native fishes in the upper Colorado River basin. Fisheries 43:194–206.

Levick, L., J. Fonseca, D. Goodrich, M. Hernandez, D. Semmens, J. Stromberg, R. Leidy, M. Scianni, D. P. Guertin, M. Tluczek, and W. Kepner. 2008. The ecological and hydrological significance of ephemeral and intermittent streams in the arid and semi-arid American Southwest. U.S. Environmental Protection Agency, EPA/600/R-08/134 and U.S. Department of Agriculture, Agricultural Research Service, Southwest Watershed Research Center, ARS/233046, Washington, D.C.

Miller, A. M., and S. W. Golladay. 1996. Effects of spates and drying on macroinvertebrate assemblages of an intermittent and a perennial prairie stream. Journal of the North American Benthological Society 15:670–689.

Minckley, W., and J. E. Deacon. 1968. Southwestern fishes and the enigma of "endangered species." Science 159:1424–1432.

Modde, T., and D. B. Irving. 2011. 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.

Neuheimer, A. B., and C. T. Taggart. 2007. The growing degree-day and fish size-at-age: the overlooked metric. Canadian Journal of Fisheries and Aquatic Sciences 64:375–385.

Nunn, A. D., G. H. Copp, L. Vilizzi, and M. G. Carter. 2010. Seasonal and diel patterns in the migrations of fishes between a river and a floodplain tributary. Ecology of Freshwater Fish 19:153–162.

Olden, J. D., N. L. Poff, and K. R. Bestgen. 2006. Life-history strategies predict fish invasions and extirpations in the Colorado River basin. Ecological Monographs 76:25–40.

Ovidio, M., E. Baras, D. Goffaux, C. Britles, and J. C. Philippart. 1998. Environmental unpredictability rules the autumn migration of Brown Trout (*Salmo trutta* L.) in the Belgian Ardennes. Hydrobiologia 371–372:263–274.

Paukert, C., and R. S. Rogers. 2004. Factors affecting condition of Flannelmouth Suckers in the Colorado River, Grand Canyon, Arizona. North American Journal of Fisheries Management 24:648–653.

Pearson, K. N., W. L. Kendall, D. L. Winkelman, and W. R. Persons. 2015. Evidence for skipped spawning in a potamodromous cyprinid, Humpback Chub (*Gila cypha*), with implications for demographic parameter estimates. Fisheries Research 170:50–59.

Pope, K. L., and D. W. Willis. 1996. Seasonal influences on freshwater fisheries sampling data. Reviews in Fisheries Science 4:57–73.

R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: http://www.R-project.org/. (January 2019).

Raney, E. C., and D. A. Webster. 1942. The spring migration of the common White Sucker, *Catostomus c. commersonii* (Lacépède), in Skaneateles Lake Inlet, New York. Copeia 1942:139–148.

Rice, S. P., P. Kiffney, C. Greene, and G. R. Pess. 2008. The ecological importance of tributaries and confluences. Pages 209–242 *in* S. P. Rice, A. G. Roy, and B. L. Rhoads, editors. River confluences, tributaries and the fluvial network. Wiley, West Sussex, UK.

Schloerke, B., J. Crowley, D. Cook, F. Bariatte, M. Marbach, E. Thoen, A. Elberg, and J. Larmarange. 2018. GGally: extension to 'ggplot2'. R package version 1.4.0. Available: https://CRAN.R-project.org/package=GGally. (January 2019).

Snyder, D. E., R. T. Muth, and C. L. Bjork. 2004. Catostomid fish larvae and early juveniles of the upper Colorado River basin – morphological descriptions, comparisons, and computer-interactive key. Colorado Division of Wildlife, Technical Publication 42, Fort Collins.

UDNR (Utah Department of Natural Resources). 2006. Range-wide conservation agreement and strategy for Roundtail Chub *Gila robusta*, Bluehead Sucker *Catostomus discobolus*, and Flannelmouth Sucker *Catostomus latipinnis*. UDNR, Publication Number 06-18, Salt Lake City.

Weiss, S. J. 1993. Spawning, movement and population structure of Flannelmouth Sucker in the Paria River. Master's thesis. University of Arizona, Tucson.

Weiss, S. J., E. O. Otis, and O. E. Maughan. 1998. Spawning ecology of Flannelmouth Sucker *Catostomus latipinnis* (Catostomidae), in two small tributaries of the lower Colorado River. Environmental Biology of Fishes 52:419–433.

Werner, R. G., and M. J. Lannoo. 1994. Development of the olfactory system of the White Sucker, *Catostomus commersonii*, in relation to imprinting and homing: a comparison to the salmonid model. Environmental Biology of Fishes 40:125–140.

Wigington, P. J. Jr., J. L. Ebersole, M. E. Colvin, S. G. Leibowitz, B. Miller, B. Hansen, H. R. Lavigne, D. White, J. P. Baker, M. R. Church, J. R. Brooks, M. A. Cairns, and J. E. Compton. 2006. Coho Salmon dependence on intermittent streams. Frontiers in Ecology and the Environment 4:513–518.

SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.