Migration timing, return patterns, and tradeoffs for the early life stage of tributary spawning flannelmouth sucker (*Catostomus latipinnis*)

by

Sophia Marie Bonjour

B.S., Southern Illinois University, 2014
M.S., Southern Illinois University, 2018

AN ABSTRACT OF A DISSERTATION

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Abstract

Tributary streams can be important aspects of temporal and spatial heterogeneity in river networks impacted by anthropogenic activities. Tributaries are critical in the life history of some species and may be essential to support large-river fish populations through portfolio effects, whereby multiple spawning locations increase recruitment success. Migration timing, site fidelity, and the experience for offspring within tributaries can have population-level impacts throughout river networks. I examined how flannelmouth sucker, *Catostomus latipinnis*, use tributaries for spawning and the implications for larvae and juveniles hatched in these systems. In Chapter 2, I evaluated the relationship between the timing and duration of sucker migration and environmental cues across four tributaries in the Colorado River basin. For the San Juan River, I also quantified the use of a tributary, McElmo Creek, based on the proximity of fish to the tributary and movement in the mainstem prior to and following spawning. More than half of the fish tagged within 10 km of McElmo Creek spawned in the tributary the following spring with decreased use by fish tagged farther from the confluence. Fish staged at the mouth of McElmo Creek an average of 8 days before entering the tributary, coming from both upstream and downstream. Arrival and residence times varied across years with greater discharge, across years or sites, associated with extended tributary use. This suggests conservation actions prioritizing a natural flow regime, connectivity, and limited water extraction may benefit migrating fish, including flannelmouth sucker. In Chapter 3, I created detection histories from long-term passive integrated transponder (PIT) data to assess the site fidelity of spawning flannelmouth sucker to McElmo Creek. Encounter rates of PIT-tagged fish and apparent survival exhibited interannual variation and were dependent upon length at tagging. Annual site fidelity was generally high, averaging 0.93 across years and ranging from 0.80 to 0.98, which may benefit individuals by minimizing energetic costs associated with habitat exploration and selection but may be maladaptive in systems with rapid anthropogenic changes. Individual fish demonstrated consistency in relative arrival timing across years with stronger relationships in years with longer spawning seasons. Partial migration and separation of migration timing may act as two forms of bet-hedging in dynamic systems. In Chapter 4, I examined the differences in early life history sucker experiences based on spawning location by conducting an enclosure experiment in combination with observational data. Whether juvenile fish grew more in the mainstem or tributary depended upon year and environmental conditions. Spawning occurred earlier in the tributary than the mainstem in 2022 and 2023, which could lead to a competitive advantage against individuals with shorter growing times. However, suckers grew more in mainstem enclosures in 2023, perhaps due to negative effects of abundant non-native crayfish at tributary sites. Differences in experience during early life stages between tributary and mainstem habitats, and among years support the idea that tributary spawning acts as a population-level bet-hedging strategy that may contribute to the persistence of flannelmouth sucker where other native species are threatened or endangered. This work contributes to our understanding of the movement and reproductive ecology of flannelmouth sucker and the role of tributaries in their life history. Conservation or degradation of tributary attributes, such as connectivity, flow and temperature regimes, and larval habitat, will impact the resilience of native fishes, including flannelmouth sucker.

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Table of Contents

List of Figures

List of Tables

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Dedication

To my grandmother, Ora Roider. I have fond memories mucking around in the pond during summer visits, her covered in scales from cleaning the fish we caught, squeezing way too many people around her Thanksgiving table, and, of course, going for walks. She was the nearest relative during undergrad and masters, and always sent me back to Carbondale with angel food cake and a 7 Up. My time as a PhD student was bookended by her passing during the first month and the birth of her first great grandchild, my niece, the week before my defense, and somewhere in between, Michael and I were married in her garden.

Preface

Chapters 2 - 4 of this dissertation have been prepared and formatted for submission to a peer-reviewed journal and include co-authors. Chapter 2 is in press with *Journal of Fish Biology* and has been adapted with permission from **John Wiley and Sons**: License number 1408483-1. Chapter 3 has been formatted for submission to the journal *Ecology of Freshwater Fish*. Chapters 3 and 4 will be submitted for publication following the defense.

Chapter 1 - The role of tributaries in large-river fish conservation

Rivers, lakes, and reservoirs cover only 2.3% of Earth's land surface but contain 9.5% of described animal species (Reid et al. 2019) and provide freshwater for much of the human population. Diversions and water withdrawals have tripled in the past 70 years (Albert et al. 2021) such that few free-flowing rivers remain in industrialized countries (Grill et al. 2019). Human changes to the environment, including habitat destruction and overexploitation, (Caro et al. 2022), have led to the extirpation of many species. Freshwater biodiversity loss is faster than that of terrestrial environments, with the most threatened vertebrates being those in freshwater (Reid et al. 2019). The Colorado River basin in the American Southwest is a prime example of effects of human population expansion (Goodrich et al. 2018): alterations and management are pervasive (Castle et al. 2014), and native fish assemblages are imperiled (Minckley et al. 2003, Budy et al. 2015). A long isolation period of the basin has led to high endemism (Carlson and Muth 1989) and fish adapted to historical flow regimes, trophic dynamics of a native assemblage, and access to various habitats throughout their life history. The large number and diverse interests of stakeholders makes management actions for conservation difficult. The focus of this dissertation is on tributaries, which provide likely important resources and have smaller watersheds than mainstem rivers making tributaries potentially easier to protect (Pracheil et al. 2013, Laub et al. 2018).

Bouska et al. (2023) identified habitat diversity, connectivity, ecological asynchrony, and density-dependent processes as properties of tributaries that support populations of large-river fish. Many species use different parts of a watershed throughout their life history for spawning, feeding, and dispersal (Fausch et al. 2002); however, the exact contribution to large-river fish populations is often unknown (Healy & Omana Smith, In Press; Bouska et al., 2023). Tributaries are not exempt from human modifications and are often not included in critical habitat designation for large-river fish (Bottcher et al. 2013). Water development in tributaries is associated with the extirpation of native fish (Budy et al. 2015); current megadrought conditions magnify the stressors impacting native species (Gido et al. 2023). Understanding how fish use tributaries could aid managers in prioritizing conservation actions throughout the watershed (Bouska et al. 2023). My dissertation aims to better understand the use of tributaries by flannelmouth sucker (*Catostomus latipinnis*) for spawning. This species has experienced declines from its historical range (Budy et al. 2015) and is managed as part of an interstate compact (UDWR 2006) but persist in many locations from tributary and mainstem spawning (McKinney et al. 1999, Clarkson and Childs 2000, Cathcart et al. 2019, Fraser et al. 2019). The partial migration of flannelmouth sucker to tributaries may allow for a bet-hedging strategy that balances reproduction between large river and tributary spawning locations which could have different responses to temporal changes of climate and disturbances such as floods and fires (Chapman et al. 2012).

Identifying migration patterns, including timing, purpose, direction, and return interval (Moser et al. 2015), and movement ecology is necessary for species conservation (Marra et al. 2015). Migratory species are particularly vulnerable to human modifications to the environment that may disrupt movement of these species (Runge et al. 2014, 2015; Bauer et al. 2019). The same constriction points that make these species vulnerable can be leveraged as monitoring points for the acquisition of long-term data through the installation of passive integrated transponder (PIT) antenna arrays. I assessed interannual variation in migration timing and residence time and how these relate to environmental factors in Chapter 2 using multi-year PIT data. I found that arrival and residence times varied across years with greater discharged, across years or sites, associated with extended tributary use. In the San Juan River, more than half of the fish tagged within 10 km of McElmo Creek, both upstream and downstream, spawned in the tributary the following spring with decreased use by fish tagged farther from the confluence. Further investigation of PIT data in Chapter 3 demonstrated that the fish using McElmo Creek also returned to the tributary annually for spawning and with high site fidelity. Interannual variation interacted with total length at tagging of individual, but the mechanism for this relationship requires additional investigation. Individuals returned in consecutive years, as opposed to skip spawning, and showed consistency in their relative arrival timing, which was more pronounced in wetter years. Fish may not return to McElmo Creek in years where greater runoff from snowmelt makes other intermittent tributaries accessible or following monsoon events that cause fish to exit the population by movement below impassable barriers.

The population implications of spawning in tributary or mainstem rivers are regulated by the recruitment of offspring (Healy & Omana Smith, In Press). Tributaries likely have different biotic and abiotic conditions than mainstem rivers (Poff et al. 2007, Thornbrugh and Gido 2010, Sabo et al. 2012, Rice 2017, Dunn and Paukert 2021). These conditions can result in different growth and survival rates among early life stage fish (Papoulias and Minckley 1992, Clarkson and Childs 2000, Carpenter 2005, Bestgen 2008). In Chapter 4, I used observational and experimental data to assess the effects of tributary and mainstem habitat on growth of early life stage flannelmouth sucker. These methodologies evaluate different components of spatial and temporal dynamics between the two system types. Juvenile fish sampled in mid-summer were larger in the mainstem in 2021 but larger in the tributary in 2023. This difference may reflect later spawning or slower growth rates in the mainstem during a higher water year in which temperatures remained cooler longer. Growth patterns in our enclosure experiment in 2023 did not match observational data as tributary enclosure fish grew less than mainstem enclosure fish. Non-native virile crayfish (*Orconectes virilis*) were abundant in the tributaries in both years, but the longer experiment time later in the season may have increased competition during the 2023 deployment. Differences across years support the hypothesis that partial migrations act as a bet hedging strategy where contribution to the flannelmouth population may be higher in some years than in others from tributary spawning individuals. Additionally, increased water development and the invasion of non-native species in tributaries may decrease their value as a spawning and rearing habitat for flannelmouth sucker.

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Chapter 2 - Migration timing and tributary use of spawning flannelmouth sucker (*Catostomus latipinnis*)

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Abstract

Spawning phenology and associated migrations by fishes are often regulated by factors such as temperature and stream discharge, but flow regulation of mainstem rivers coupled with climate change might disrupt these cues and affect fitness. Flannelmouth sucker *(Catostomus latipinnis)* persisting in heavily modified river networks are known to spawn in tributaries that might provide better spawning habitat than neighboring mainstem rivers subject to habitat degradation (e.g., embedded sediments, altered thermal regimes, and disconnected floodplains). Passive integrative transponder (PIT) tag data and radio telemetry were used to quantify the timing and duration of flannelmouth sucker tributary spawning migrations in relation to environmental cues in McElmo Creek, a tributary to the San Juan River in the American Southwest. We also tested the extent of the tributary migration and assessed mainstem movements prior to and following tributary migrations. Additionally, multi-year datasets of PIT detections from other tributaries in the Colorado River basin were used to quantify interannual and cross-site variation in the timing of flannelmouth sucker spawning migrations in relation to environmental cues. The arrival and residence times of fish spawning in McElmo Creek varied among years with earlier migration and a three-week increase in residence time in relatively wet years compared to drier years. Classification tree analysis suggested a combination of discharge and temperature determined arrival timing. Of fish PIT tagged in the fall, 56% tagged within 10 km of McElmo Creek spawned in the tributary the following spring, as did 60% of radio-tagged fish, with a decline in its use corresponding to increased distance of tagging location. A broader analysis of four tributaries in the Colorado River basin, including McElmo Creek, found photoperiod and temperature of tributary and mainstem rivers were the most important variables in determining migration timing, but tributary and mainstem discharge also aided in classification success. The largest tributary, the Little Colorado River, had more residential fish or fish that stayed for longer periods (median = 30 days), while McElmo Creek fish stayed an average of just 10 days in 2022. Our results generally suggest that greater discharge, across years or across sites, results in extended use of tributaries by flannelmouth suckers. Conservation actions that limit water extraction and maintain natural flow regimes in tributaries, while maintaining open connection with mainstem rivers may benefit migratory species including flannelmouth suckers.

Keywords: classification tree, Colorado River Basin, environmental cues, movement, telemetry

Introduction

Understanding animal movement and ecology is necessary for species conservation (Marra et al. 2015). Habitat requirements often change throughout the life of an organism

(Rodewald 2015) and animals move between habitats to access different resources across time and space. For aquatic species, movement among these critical habitats is constrained to waterways and often includes movements from large rivers to smaller tributaries (Ma et al. 2020). Migratory species are particularly vulnerable to human interference that interrupts the cyclic movement of these species or destroys habitats that are critical for part of their life history (Runge et al. 2014, 2015, Bauer et al. 2019). Migration patterns can be described by the path, timing, direction, speed, and purpose of movement among habitats (Moser et al. 2015).

Fish migrate for a variety of purposes, over different time scales, and across multiple habitats (Brönmark et al. 2014). The decision to migrate is informed by environmental cues that presumably maximizes fitness (Weissburg and Browman 2005). Migration can be driven by spawning, feeding, or refuge-seeking behavior (Northcote 1978, Angermeier and Schlosser 1989). The timing of migrations can occur on seasonal, diel, or irregular cycles in response to environmental (Northcote 1978, Skov et al. 2010, McPherson and Kjesbu 2012, Serrat et al. 2019) and biological cues (Armstrong et al. 2016). However, migration may come at a cost, such as exposure to terrestrial predators (Koel et al. 2019) or energetic expense, leading to partial migration in which individuals in a population exhibit dissimilar migratory behavior, such as migrating or not (Chapman et al. 2012b, 2012a). Reproduction is a common reason for migrations, with movement between habitats linked to preferred incubating or rearing habitat (Jeffres et al. 2006, Ellsworth and VanderKooi 2011, Cathcart et al. 2019a, Dyer and Brewer 2020), rich food and energy resources (Humphries et al. 2020), aggregations of conspecifics (Anteneh et al. 2012), and escape from predation pressures or competition (Brönmark et al. 2008, Chapman et al. 2012a). Although salmonids are among the most studied fish with large freshwater spawning migrations, other groups such as eels (Anguillidae; Feunteun et al. 2003, Béguer-Pon et al. 2014, Carpenter-Bundhoo et al. 2020), sturgeons (Acipenseridae; Lindley et al. 2008, Lyons et al. 2016, Moore et al. 2022), and suckers (Catostomidae; Neely et al. 2009, Childress et al. 2014, Strohm et al. 2017, Acre et al. 2021, Swanson et al. 2021) make large-scale migrations among habitats.

In river networks, tributaries and confluences provide habitat and resources that are different from that of the mainstem, and can provide critical resources for multiple life stages of fish (Schlosser 1995, Fraser et al. 2017, Laub et al. 2018, Cathcart et al. 2019b, 2019a). Tributary and mainstem confluences may have higher localized species richness (Benda et al. 2004, Hitt and Angermeier 2008) by blending both large and smaller stream communities, providing connections between spawning and rearing habitats, and enhancing habitat heterogeneity (Thieme et al. 2001, Thornbrugh and Gido 2010, Dunn and Paukert 2021). Flow regime (Poff et al. 2007), canopy cover (Vannote et al. 1980), temperature (Sabo et al. 2012), and substrate (Rice 2017) typically vary between tributaries and mainstems. For example, tributaries can be easily fragmented, isolated, degraded, or dewatered (Whipple 2007, Flanigan and Haas 2008, Udall 2020), which could prevent fish migration. Tributaries are often excluded from critical habitat designations (Bottcher et al. 2013), but they could be an important component of large-river fish conservation through portfolio effects (Bouska et al. 2023).

Many suckers (family Catostomidae) migrate in spring or early summer for spawning, often in small tributary streams (Billman and Belk 2009, Childress et al. 2014, Hooley-Underwood et al. 2019). Flannelmouth suckers (*Catostomus latipinnis* Baird and Girard 1853) are endemic to the Colorado River basin in the American West, but currently occupy <50% of their historical range (Budy et al. 2015). Throughout the Colorado River basin, some individuals migrate into tributaries during the spring for spawning (Weiss et al. 1998, Bower et al. 2008, Cathcart et al. 2015, Fraser et al. 2017) or make long-range movements in the mainstem that are not necessarily migratory, in that they may not return to their starting location (Chart 1987, McKinney et al. 1999). Spawning occurs over gravel where eggs attach or occupy interstitial spaces (Sigler and Sigler 1996, Weiss et al. 1998). After eggs hatch, larvae drift downstream as mesolarvae roughly one month post spawn (Snyder and Muth 2004), occupying near-shore, low velocity habitat (Robinson et al. 1998). The relatively short larval period has a large impact on recruitment due to high mortality rates, so timing of adult migration and reproduction might influence environmental conditions experienced by offspring (Schiemer et al. 2003). Previous research from the San Juan River in the American Southwest, found mainstem water temperature to be the best predictor of flannelmouth sucker migration from the mainstem into a tributary for spawning (Cathcart et al. 2015, 2018a), but those observations only accounted for two spawning seasons and focused on within-year movement patterns. Multiple years of data can improve understanding of migration cues because timing of migration might be controlled by a suite of environmental variables, such as photoperiod, temperature, and hydrology (Bogaard et al. 2023). Furthermore, physical characteristics and biotic composition of the river-tributary system might influence migratory patterns, making comparisons across sites or populations (i.e., tributaries) useful for contextualizing patterns.

We quantified nine years of migratory behavior of flannelmouth sucker spawning in McElmo Creek, a tributary to the San Juan River in Utah, using passive integrated transponder (PIT) tags and radio telemetry. Specifically, we evaluated (1) the relationship between the timing and duration of sucker migration and environmental cues; (2) origin and migration distance of fish using spawning sites in McElmo Creek; and (3) movement in the mainstem before and after spawning. We hypothesized that (1) interannual variability in arrival timing and residence time would exist and that temperatures and increases in discharge would cue migration; (2) probability of tributary migration would decrease with the distance fish were tagged from the tributary confluence due to the energetic expense of migration; and (3) tributary migrating fish would stage or gather at the confluence before moving into the tributary for spawning and return to tagging locations after spawning.

Additionally, we compared the timing and residence time of the flannelmouth sucker migration into McElmo Creek with migrations at three other tributaries in the Colorado River basin (Figure 2.1). We predicted that migration timing followed similar cues among tributaries with the hypothesis that environmental variables may be generally helpful for predicting spawning migrations throughout the Colorado River basin. Quantifying the proportion of the population using tributaries for spawning and environmental conditions that cue spawning migrations will help explain the importance of tributary spawning and inform future management considerations for tributary protection and flow management.

Methods

Colorado River basin and study tributaries

The Colorado River basin covers 637,000 km^2 of southwestern United States and northwestern Mexico, with the river network being an important and overallocated source of water in a relatively dry climate (Schmidt 2007). The need for additional water with growing populations and aridification has increased water stress and intermittency of tributaries (Seager et al. 2013, Udall and Overpeck 2017, Goodrich et al. 2018).

The San Juan River flows through Colorado, New Mexico, and Utah before joining the Colorado River at Lake Powell (Figure 2.1). Navajo Dam regulates flow for more than 400 km of the river, limiting natural flow variability, but additional flow enters the river through unregulated tributary inputs. McElmo Creek joins the San Juan River 217 km downstream of Navajo Dam. Draining 1,818 km^2 of Colorado and Utah, McElmo Creek flows most of the year but may be fragmented into isolated pools during some months. Although McElmo Creek was historically intermittent, the creation of McPhee Reservoir in 1986 and associated projects for irrigation rerouted water from the Dolores River basin resulting in more continuous flow within McElmo Creek (Fresques et al. 2013). Row crop agriculture and grazing occurs in the watershed, while Russian olive (*Elaeagnus angustifolia* L.) and salt cedar (*Tamarix* spp.) have invaded much of the riparian zone, with implications for altered channel structure and flow regimes (Pollen-Bankhead et al. 2009).

To compare migration patterns of the flannelmouth sucker across tributaries throughout the Colorado River basin, we identified three additional mainstem-tributary systems with similar PIT tagging and antenna data (Figure 2.1, Table 2.1). The Little Colorado River (LCR) and Bright Angel Creek (BAC) are perennial, spring-fed tributaries to the Colorado River within Grand Canyon National Park (GCNP; Figure 2.1). Both the LCR and BAC experience elevated runoff due to late winter or early spring snowmelt or storms that are associated with increased recruitment of native fishes (Van Haverbeke et al. 2013, Healy et al. 2020). Water withdrawals and encroaching invasive vegetation have altered the flow regime in the LCR (Dean and Topping 2019), while GCNP diverts ~20% of baseflow from BAC to meet municipal water needs (Bair et al. 2019). These tributaries join the Colorado River between Glen Canyon Dam and Lake Mead; relative to pre-dam conditions, this segment is subjected to seasonally stable but higher daily fluctuations due to load following regulation from Glen Canyon Dam (Schmidt 2007). Roubideau Creek is a mostly intermittent tributary to the Gunnison River in the upper Colorado

River basin (Figure 2.1). The lower 12 km of Roubideau Creek are perennial, presumably due to irrigation associated groundwater overcharge during summer and fall. Snowmelt between April and June drives annual discharge peaks in Roubideau Creek and its tributaries, and irrigation returns supplement flow between March and November (Hooley-Underwood et al. 2021). The LCR is the largest of these tributaries, draining 69,857 km^2, and BAC is the smallest, draining 262 km^2 (Table 2.1). Roubideau Creek has a drainage area roughly half that of McElmo Creek but with higher discharge (Table 2.1).

Detection data and data analysis

Objective 1: Interannual variation in the timing and residence time of sucker migration and related environmental cues

Roughly 6,800 flannelmouth suckers were tagged with PIT tags (12 mm, full duplex; Biomark, Boise, Idaho) in the San Juan River basin from 2011 to 2021. More than three-quarters of individuals observed in this study were tagged in McElmo Creek prior to 2016 as described in Cathcart et al. (2015, 2018, 2019a), with additional periodic tagging efforts in McElmo Creek and the San Juan through 2021. The median total length at tagging was 434 mm; fish less than 250 mm (representing 13% of individuals) were excluded from further analysis to focus on adult spawning migrations (Compton et al. 2008). In 2012, a pass-over style PIT antenna array was installed in McElmo Creek 0.15 km upstream of its confluence with the San Juan River in southern Utah. This antenna spanned the width of the creek and detection ranges were tested during the initial 3-year study and ranged from 10-51 cm above the array (more detailed description in Cathcart et al 2015). The initial PIT antenna arrays have remained active since 2012 but decreased in reliability and areal coverage due to seasonal storms and sedimentation. A second pass-over style PIT antenna array spanning McElmo Creek was installed 0.3 km upstream of the confluence on 11 January 2017. Data from both antennas were uploaded to an online database managed by the Colorado Natural Heritage Program (STReaMS 2023) and all flannelmouth sucker encounters were downloaded on 03 May 2022.

To assess inter-annual variation in the migration timing and residence time of flannelmouth sucker in McElmo Creek, detections were pooled from both antenna arrays, and we identified the first (arrival) and last (departure) detection date of individuals each spawning season (January – June) from 2013-2022. Although spawning is typically restricted to early spring, the wide window allowed us to detect outliers while avoiding any monsoon-driven movement into McElmo Creek (Cathcart et al. 2015). Due to antenna malfunctions, 2016 was not included. Analyses were restricted to individuals with a residence time of two or more days to exclude fish making exploratory movements or those not detected upon both arrival and departure. To predict the arrival timing across years, we first calculated the proportion of total flannelmouth sucker arrivals for a given year occurring in each week (Cathcart et al. 2018a). This temporal scale allowed our study to be comparable with other studies in the basin (Cathcart et al. 2018a, Bogaard et al. 2023), account for time between cue and movement, and minimize overfitting based on high variability of detections at a finer scale and temporal autocorrelation. We converted migration to a binary response factor and used week as our response unit. Either a week was classified as having migratory fish present or not (absent). If more than 2% of the fish that used McElmo Creek that year arrived during that week, that week was classified as a migratory week. This value was used to reduce inclusion of exploratory movements (only a few individuals) and because 2% represented a natural break in the data. We also considered 1% and 5% cutoffs, but error rates were higher with these cutoffs. (All analyses were conducted using Program R version 4.0.5, R Core Team 2021).

Next, we compiled hydrological variables summarized by week to obtain mean weekly discharge and water temperature for the San Juan River, discharge and air temperature for McElmo Creek, and also included all above-mentioned variables with a one-week time lag. Hydrological data were obtained from U.S. Geological Survey (USGS) gaging sites on the San Juan River (USGS gaging station 09379500; USGS 2022) and in McElmo Creek (USGS gaging station 09372000; USGS 2022b) (using the 'importDV' function in package *waterData*, Ryberg and Vecchia 2017, Table 2.1). Because water temperature is not measured for McElmo Creek at the USGS site, a set of linear regressions using air temperature, discharge, and an interaction between the two was used to predict water temperature for all years (R-squared = 0.90). Pendant temperature loggers (HOBO model: UA-002-64; Onset Computer Corp., Bourne, Massachusetts, USA) were deployed in McElmo Creek 2021-2022 and we used air temperature data for each of the tributaries (obtained through PRISM via the Climate Engine; Huntington et al. 2017, "Climate Engine" 2022). The most parsimonious regression was determined using Akaike's Information Criterion corrected for small sample size (AICc, Burnham and Anderson 2002). The model with the lowest AICc was used to estimate water temperature for all years (equations in Table 2.1). Photoperiod was calculated at each site (using the 'daylength' function in package *geosphere*, Hijmans 2019).

A classification tree analysis was used to identify environmental thresholds corresponding to the arrival timing cues(i.e., binary response described above) of flannelmouth suckers into McElmo Creek ('rpart' function and visualized using the 'prp' function in package *rpart,* Therneau and Atkinson 2019). Classification trees allowed discrimination between weeks with and without flannelmouth sucker arrivals at McElmo Creek using recursive partitioning, where predictive variables were not required to have linear relationships, but values were used to split observations into groups such that the sum of squares of end members is minimized. The weeks were divided into a training and testing set (50/50 split) with Cohen's Kappa used to test observed versus predicted values ('cohen.kappa' function in package *psych* (Revelle 2021)). Variables were back-transformed for result interpretation.

Linear mixed effects models were used to assess relationships between environmental factors (tributary temperature and discharge) and residence time. We included daily mean water temperature at arrival and departure, daily mean discharge at arrival and departure, and photoperiod (as a surrogate for general trend of increasing temperature over the season) as fixed effects after checking for correlations among variables. Year was included as a categorical random effect. Predictor variables were scaled and centered at a mean of zero to allow for comparison of coefficients. All variables were examined simultaneously ('dredge' function in package *MuMIn,* Barton 2020), and only variables significant in the top models (as determined by delta AICc < 2) were considered further and compared using model weights and evidence ratios, the ratio of model weights for a pair of models.

Objective 2: Tagging origin and proportion of flannelmouth suckers using McElmo Creek

To quantify the proportion of flannelmouth suckers using McElmo Creek, we conducted intensive PIT tagging and radio telemetry studies in 2020-2021 and 2021-2022. We captured 647 adult flannelmouth suckers using raft electrofishing in the San Juan River, sampling between river kilometer (rkm) 288 and 173 in December 2020 and between rkm 229 and 142 in November 2021. Sex, length, and preexisting tags were recorded for all fish, and untagged individuals received new PIT tags. Fish were returned to the river near original capture locations and the nearest rkm recorded to calculate distance from the McElmo Creek–San Juan River confluence. A subset of the fish caught in December 2020 also received radio transmitters. Forty-five fish (total length 476.73 ± 4.96 mm, range 415 – 555 mm) were surgically implanted with a 300-day coded radio transmitter (model F1225C ATS, Isanti, MN, 17g). Fish were anesthetized with tricaine methanesulfonate prior to surgery and received continuous irrigation of river water across gills during surgery. Incisions were made posterior to the left pelvic fin and closed with two interrupted monofilament sutures (3-0, PDS 2; Ethicon, Sommerville, NJ). Fish were allowed to recover in an aerated live box before being released. Care and use of fish complied with Kansas State University Animal Care and Use permit KSU IACUC#4494 for the use of PIT and radio transmitters in fish.

We used active and passive telemetry to obtain fish locations. Mobile surveys were conducted on the San Juan River by raft every 3-4 weeks during 2021 with a radio receiver and handheld Yagi antenna. The receiver scanned through active frequencies and an attached GPS unit recorded the location of the receiver during detections. The position of the strongest signal strength was used as the fish's longitudinal location. Eight stationary radio receivers were distributed along the San Juan River, including one approximately 100 m downstream of the McElmo Creek confluence. The stationary receivers included two four-element Yagi antennas, one aimed upstream, and one aimed downstream. Receivers cycled through active frequencies every 6-12 seconds and were equipped with external batteries, a solar panel. A test tag was used to verify proper functioning of antennas. For this study, we only used the coordinates of the receiver for fish location on a given day.

We used logistic regression ('glm' in the *stats* package) to estimate the proportion of flannelmouth suckers PIT tagged in fall 2020 and 2021 spawning in McElmo Creek the following spring and quantify how probability of use varied with fall tagging location (i.e., distance from tributary). We also calculated the proportion of tributary use by radio tagged fish since we could verify absence from the tributary with other location data, unlike undetected PIT tagged fish.

Objective 3: Staging time and movement after spawning

We used mobile and stationary radio telemetry detections to determine adult flannelmouth sucker locations before and after the spawning season of March and April. We selected flannelmouth suckers that were detected on the McElmo Creek stationary radio antenna between March 1 and April 1 to focus on the subset potentially using McElmo Creek for spawning. Staging time was determined by the difference between the first detection on the stationary radio receiver and the first detection on the PIT antenna for individuals that entered McElmo Creek. PIT antenna data was also used to verify which individuals entered the tributary, as opposed to just being in the vicinity. Telemetry data available for those individuals were used to describe patterns of movement in the mainstem immediately following spawning. Because we were primarily interested in spawning migrations, we only considered location data prior to July.

Objective 4: Comparison of sucker migration timing and related environmental cues among basins

To contextualize the results from Objective 1, we compared flannelmouth sucker migration timing in McElmo Creek to other tributaries with multiple years of PIT detections during the spawning season. Within the Grand Canyon, National Park Service (NPS), Arizona Game and Fish Department, US Fish and Wildlife Service (USFWS), and USGS Grand Canyon Monitoring and Research Center (GCMRC) tagged 34,355 flannelmouth suckers >150 mm total length from 2017 through 2020 during a variety of research and monitoring projects, with additional tags deployed previously. Capture records managed by GCMRC from these studies were used to identify individuals detected on antennas located in Bright Angel Creek and the Little Colorado River (Table 2.2). Colorado Parks and Wildlife (CPW) and USFWS have tagged roughly 7,600 flannelmouth sucker in the Gunnison River basin since 2005. Tagging and detection records are managed by CPW (Hooley-Underwood, unpublished data) and the database managed by the Colorado Natural Heritage Program (STReaMS 2022). An array of four (arranged in pairs such that the entire channel is covered in two locations) PIT tag antennas (Biomark, IS1001 Readers and IS1001 MC) in Roubideau Creek have operated year-round since 2015, with no interruptions. These antennas are located 0.58 km upstream of the Roubideau Creek–Gunnison River confluence. Read ranges (up to 74cm) are typically sufficient to encompass the creek's depth in all but extreme (i.e. > 23 m^3/s) flow events. Discharge exceeded 23 m^3/s for several weeks in 2019, and directional movement data derived from the array indicates that many immigrating individuals were not detected (Hooley-Underwood unpublished data). CPW downloads data several times per year. For this study, only spawning season (March – June) detections were used.

Hydrological data for the Little Colorado River (USGS gaging station 09402300; USGS 2022c), Bright Angel Creek (USGS gaging station 09403000; USGS 2022d), the Colorado River (USGS gaging station 09402500; USGS 2022e), and the Gunnison River (USGS gaging station 09144520; USGS 2022f) were obtained from a USGS gaging sites (packages *waterData* and GCgage, Ryberg and Vecchia 2017, Muehlbauer 2020, Table 2.1). Discharge for Roubideau Creek at the PIT array location was estimated by creating a rating curve relating measured discharge (via channel depth-velocity measurement) to depth as recorded by a pressure transducer logger (Onset U20-001, corrected for barometric pressure), and temperature was recorded with temperature logger (Onset U22). We used a set of linear regressions, as described in Objective 1, to estimate water temperature where data were missing in the USGS dataset (equations in Table 2.1).

Arrival times across tributaries were calculated the same as in Objective 1. To describe the range of temperatures at which movement into tributaries occurred, cumulation plots were created for each tributary for January through June of the sampling years. We used random forest analysis (package *randomForest*, Liaw and Wiener 2002) to predict weeks when migration happened across tributaries based on photoperiod, mainstem and tributary temperature, and mainstem and tributary discharge. Covariates were centered and scaled (mean = 0; SD = 1) within sites to allow comparisons across tributaries. We calculated the weekly proportion of total flannelmouth sucker arrivals occurring at each site for all years (Cathcart et al. 2018). The 2% threshold for binary migration used for McElmo Creek in Objective 1 was also used for BAC and Roubideau Creek, while a 5% threshold was used for LCR so that 20-30% of weeks were considered migration weeks, like the other tributaries. Detections in the LCR were more distributed across time and the 5% threshold allowed us to identify weeks with the highest activity levels. The data were divided into a training and testing set (70/30 split, ‘tuneRF’ was used to set ‘m.try’ for the ‘randomForest’ function), and 500 trees were run. Variable importance and partial dependence plots were used to visualize individual independent variables. Chi-squared test and Cohen’s Kappa were used to test observed versus predicted values. Variables with a mean decrease in Gini greater than 10 were used to create a classification tree to visualize environmental cues for migration. Gini importance can indicate variable relevance by how well it divides nodes into pure groupings. This classification tree was assessed as in Objective 1.

Results

Objective 1: Interannual variation in the timing and residence time of sucker migration and related environmental cues

Distinct fish arrival and exit pulses were evident most years with some interannual variation in McElmo Creek driven primarily by discharge or an interaction between temperature and photoperiod (Figure 2.2A). Models included 4922 known migrations out of 9636 detected individuals after accounting for missing arrival dates (primarily for fish tagged in McElmo during the spawn) or arrival and departure dates less than the 2 days apart (Figure 2.2A). Our classification tree identified discharge from McElmo as the first split in defining migration weeks, where discharge ≥ 0.62 cms corresponded to migration into the creek (Figure 2.2B). Subsequently, San Juan River temperatures were identified to parse data with more migration occurring at water temperatures greater than 8.2 oC and photoperiod of more than 13 h. The testing set of data classified 86% of weeks correctly (Chi-squared = 33.39, df = 1, $p < 0.001$). One week with migration and five weeks without were misclassified when using the results from the training tree to classify the remaining weeks (Table 2.3, Cohen's kappa = 0.76). Weeks with migration as predicted by the classification tree showed a general concordance with the observed arrival timing of individuals (Figure 2.2A).

Within and across years, the top model relating the five environmental variables to residence time included all variables except air temperature at arrival. Air temperature was included with all others in the second candidate model with ΔAICc 0.5 but represents an uninformative parameter (Arnold 2010). The two top models had a combined weight of > 0.99, with an evidence ratio of 1.28 between the two (Table 2.4). The coefficient for scaled photoperiod had the largest absolute value indicating that when fish arrived later in the season, they also had shorter residence times. Discharge values were negatively related to residence time while temperature had a positive relationship. During years with higher spring tributary discharge (2017 and 2019 discharge Jan–April was 184% more than other years included, Figure S1) fish moved into McElmo Creek earlier (median arrival 23 days earlier, Feb 18 vs Mar 13) and stayed longer (median residency time 45 vs 20 days, Figure 2.3A), with 2017 being the earliest arrival, 2019 the longest residence time. The year with the lowest spring discharge, 2022, had the latest arrival and shortest residence time. In a post-hoc test, mean discharge (January–June) explained 63% of the variance in residence days among years (Figure S2, F(1,6) = 16.08, p = 0.007, Adjusted R-squared = 0.63).

Objective 2: Tagging origin and proportion of flannelmouth suckers using McElmo Creek

Of the 647 individuals captured in the mainstem during fall sampling, 34% of PIT-tagged fish and 29% of the radio-tagged fish entered McElmo Creek. Our regression model suggested the proportion of tagged fish entering McElmo Creek from the San Juan River declined from 56% of fish tagged within 10 km of McElmo Creek to 50 % of those tagged within 25 km to zero of the 14 fish tagged > 50 km from the confluence (Figure 2.4). Similarly, of the 45 radio-tagged fish, 60% tagged in the San Juan River within 5-13 km of the confluence in December moved into the tributary the following March, in contrast to 14% of fish radio-tagged 35-42 km from the confluence.

Objective 3: Staging time and post-spawning movement

Of the 13 radio-tagged flannelmouth suckers from the San Juan River detected on the McElmo Creek PIT antenna, four individuals tagged upstream and nine tagged downstream of the McElmo Creek–San Juan River confluence remained near their tagging location in the San

Juan River until March (Figure 2.5). One individual moved 24 km downstream in the San Juan River before returning to McElmo Creek. Fish were detected on the stationary radio antenna 100 m downstream of the McElmo Creek–San Juan River confluence an average of 8 days (range 0-20 days, SD = 6.6) before moving into McElmo Creek. A mobile survey conducted by foot in McElmo Creek March 29-30, 2021 detected 12 radio-tagged individuals 0.7 to 11.4 km upstream of the confluence, confirming they entered the tributary. We observed spawning behaviors by several thousand flannelmouth suckers while performing this mobile survey. Following the spawning period in McElmo Creek, all fish that were tagged upstream from the McElmo Creek–San Juan River confluence moved back upstream. Of the fish tagged in the San Juan just downstream of McElmo Creek, four moved downstream, two moved upstream, and five remained near McElmo Creek after spawning in McElmo Creek. In addition to the 13 radio tagged fish that entered McElmo Creek, five fish were detected on the radio receiver near the confluence during the spawning period but did not appear to enter the tributary as determined by the lack of detection on the PIT antenna in McElmo Creek or during a mobile radio telemetry survey in McElmo Creek. Three of those five fish made subsequent substantial upstream movements (in one case more than 100 km) in the San Juan River during what we still consider the spawning season.

Objective 4: Comparison of sucker migration timing and related environmental cues among basins

Migration timing across tributaries was not synchronous. The earliest arrivals occurred in McElmo Creek, which also had the most variation in arrival time across years (Figure 2.6 and S3). In examining migration timing relative to environmental factors, arrival of fish in McElmo Creek, Roubideau Creek and BAC occurred at notably cooler temperatures than in LCR (Figure

2.7). Temperatures in which 90% of fish arrived ranged between 5.5 and 15.1 ˚C in McElmo Creek compared to 7.7 to 12.4 ˚C in Roubideau Creek, 9.9 to 15.9 ˚C in BAC, and 12.8 to 22.6 ˚C in LCR.

Random forest models corroborated that both temperature and discharge were important predictors of arrival timing of migrating flannelmouth suckers, but photoperiod was ranked as the strongest predictor (Figure 2.8, Figure S4). The default of mtry = 2 minimized out-of-bag error rate which was 15% with 83% accuracy on test data and better than random assignment of migration weeks (Chi-squared = 48.54, df = 1, $p < 0.001$, Cohen Kappa = 0.53). Tributary identity was the least important variable, had a relatively small mean decrease in Gini, and was the most distal branch in the classification tree. The classification tree used photoperiod as the first split, such that weeks with longer photoperiods corresponding to weeks after March were less likely to have migrations. After accounting for photoperiod tributary temperature was the next most important variable related to spawning migration followed by tributary flow (Figure 2.9). Low relative tributary temperatures predicted weeks without migration unless tributary discharge was high and mainstem discharge low. During relatively warmer tributary temperatures, migration was more likely with elevated tributary discharge and mainstem temperatures (Figure 2.9). The testing set of data had 80% of weeks classified correctly (Chi-squared = 36.61, df = 1, $p < 0.001$). The classification tree predicted 83% of weeks without migration correctly and 70% of weeks with migration correctly (Table 2.3, Cohen’s kappa = 0.46).

Discussion

The timing and duration of flannelmouth sucker spawning migrations in tributaries were predicted by temperature and discharge. Years with more water coincided with earlier arrival and longer residence time in tributary streams. Arriving earlier may give fish an opportunity to refuel (feed or rest) before spawning, to obtain priority habitats, or to avoid intraspecific competition for mainstem resources. Although early migration could result in the depletion of resources by adults, thus limiting those available for larval fish, many of the shared resources (algae, small invertebrates) have high turnover rates and might also be enhanced by nutrient subsidies from migrating fish (Childress et al. 2014). Much of Roubideau Creek and its tributaries are intermittent, and as such, aquatic derived resources are minimal. Still, fish enter the intermittent sections of these creeks when there is sufficient flow to move between pools – often more than one month before the bulk of spawning occurs – presumably to spawn as soon as water temperatures are appropriate or to take advantage of terrestrial resources such as leaf litter (Hooley-Underwood et al. 2019). Higher discharge in wetter years might allow for early migration by reducing risk of bird predation through decreased visibility of prey (Cathcart et al. 2018) or facilitating passage over barriers (Thompson and Hooley-Underwood 2019). Higher flow increases habitat space and persistence and may improve survival by providing habitats that are not available at lower discharge. Moving into the tributary earlier and during higher water could permit farther upstream movements or exploration for ideal spawning habitat. At the other extreme, migration into intermittent tributaries is limited by the absence of water, and migration cannot begin until discharge sufficient to allow physical movement of fish into and through tributaries is present (Hooley-Underwood et al. 2019).

Integrating data across streams allowed us to compare the general importance of environmental variables in predicting migration timing cues. The importance of photoperiod most likely represented a suite of characteristics pertaining to the time of year spawning occurs, but across year variation suggests other cues determine exact migration timing. Water temperature in tributaries and mainstem rivers appeared to be generally important across tributaries, having high variable importance in random forest models, with migration being conditional on a series of interactions between tributary and mainstem temperature and discharge (Figure 2.9). Temperature is the predominant factor regulating physiology in fish (Beitinger and Fitzpatrick 1979), but is often difficult to disentangle from collinear variables (Currey et al. 2015). Specifically, temperature is often linked to discharge with winter floods resulting in colder water temperatures. Temperature was the primary determinant of flannelmouth sucker tributary migration and spawning dates in the White River, northern Colorado (Fraser et al. 2017, 2019), while temperature was weakly correlated to flannelmouth sucker immigration in Cottonwood Creek, tributary to Roubideau Creek (Hooley-Underwood 2019). San Juan River temperatures also cue upstream razorback sucker (Xyrauchen texanus Abbott 1860) migration (Bogaard 2023), while Utah Lake June suckers (Chasmistes liorus Jordan 1878) cue primarily from discharge (Hines 2011) and blue suckers (Cycleptus elongatus Lesueur 1817) use both temperature and discharge to cue migrations, with discharge being the stronger cue (Tornabene et al. 2020). However, the combination of discharge and temperature may confuse spawning cues when environmental regimes are mismatched (Acre et al. 2022). High discharge spawning seasons in this study (2017 and 2019) were outside of the time range examined by Cathcart et al. (2018) but lead to the primary split in our McElmo Creek classification tree, highlighting the usefulness of multiple years of data across a variety of flow conditions. Presumably, the timing of spawning migrations is such that resource availability and climatic conditions are favorable for offspring, and alterations to timing cues could lead to a mismatch between larval development periods and environmental conditions (Asch et al. 2019, Brosset et al. 2020).

The thermal window for migration varied among streams and with discharge. The LCR had the highest thermal window for migration but did not get as cold as the other tributaries due to the large spring source 21 km upstream of the confluence. The LCR also had the highest baseline discharge, behaving less like a tributary than the other streams with the largest temporal spread of detections and perhaps more resident individuals. Fifty percent of the migration into BAC occurred between 11.4 and 13.2 ˚C, just below the temperature range previously noted for spawning by BAC flannelmouth sucker of 13-15 ˚C (Weiss et al. 1998, Table 2.5). Weiss et al. (1998) noted dissimilar ranges in spawning temperature among Grand Canyon tributaries with spawning in the Paria River, 26 km downstream of Glen Canyon Dam, occurring between 9 and 18 ˚C, which was similar to the range in temperatures at arrival across all four tributaries in this study (Figure 2.7). Flannelmouth suckers also spawn in Kanab Creek, Havasu Creek, and Shinumo Creek (Utah Division of Wildlife Resources 2006), all tributaries in the Grand Canyon where tributary spawning and timing allows larvae to grow in warm tributary water before entering the mainstem where reproduction and growth of native fish was limited by cold dam discharge (Hansen et al. In Review, Dzul et al. 2017, Yackulic et al. 2018, Dibble et al. 2021, Gilbert et al. 2022). Although flannelmouth sucker physiology may dictate a general thermal window for spawning, variation between tributaries suggests population adaptations or other important environmental factors, such as discharge and local habitat features may be important.

The partial migration by flannelmouth suckers into tributaries for spawning represents a bet-hedging strategy for populations where timing is an important part of the cost-benefit analysis. Environmental conditions, resource availability, and biotic interactions vary between tributaries and mainstem rivers. The wide distribution of spawning effort across locations may be part of the reason flannelmouth suckers are relatively abundant in contrast to other native fish in this region, like the razorback sucker (USFWS 1991). The absence of peak flows following impoundment has resulted in mostly embedded substrates in the mainstem as compared to the loose gravel/cobbles preferred for spawning where eggs can settle into interstitial spaces (Weiss et al. 1998). Higher abundances of young-of-year native fishes following late winter and spring flooding in Grand Canyon tributaries (Van Haverbeke et al. 2013, Healy et al. 2020) may be attributed to scouring of fine sediment from spawning areas, increased productivity, or displacement of nonnative fish. Smaller systems like tributaries also have less thermal inertia allowing for faster warming, given adequate distance from thermally stable springs, and increased larval fish growth (Robinson and Childs 2001).

The difference in communities between tributaries and mainstem rivers also likely represents tradeoffs in biotic interactions (Shaw 2020), both for adult and larval fish. Avian predation of adults flannelmouth sucker is likely greater in tributaries, but piscivory of larvae and juveniles might be greater in the mainstem (Cathcart et al. 2018). In the Grand Canyon, the abundance of nonnative predators (e.g. Rainbow Trout; Oncorhynchus mykiss Walbaum 1792) has varied substantially over time (e.g., Korman et al. 2016) leading to periods during which juvenile survival of another native fish species (humpback chub; Gila cypha Miller 1946) was greater or less than in the LCR (Yackulic et al. 2014, 2018). In BAC, nonnative predators have declined due to concerted removal efforts and juvenile flannelmouth suckers began rearing once invasive salmonid populations were suppressed by >60% in BAC (Healy et al. 2020).

Fish tagged farther from McElmo Creek were less likely to migrate to the tributary the following spring and may reflect the energetic costs associated with migration. However, our radio telemetry data show that some individuals moved toward McElmo Creek during the spawning season, but then made large upstream migrations (i.e., up to 100-kilometer displacements) without entering McElmo Creek, indicating other considerations besides the energetic costs of migration. Exploring factors leading a fish to either wait at a tributary for a spawning cue or move to a different area could elucidate components of the cost-benefit analysis. Regardless, ~ 50-60% of tagged flannelmouth sucker inhabiting the San Juan River within 15 km of McElmo Creek entered the creek during spawning season. This is a remarkable number of fish when one considers annual discharge from McElmo Creek is approximately two percent of San Juan River discharge. The use of this tributary suggests a large dependence on tributary spawning for this species and highlights the responsive nature of flannelmouth suckers regarding spawning behaviors to a mainstem alternative. Additionally, high flow events in McElmo Creek might condition substrates to make suitable spawning habitat, contrasting the regulated mainstem that lacks regular high flow events (Pennock et al. 2022).

Habitat fragmentation and alterations to flow regimes impact many fishes, particularly, migratory species (Tamario et al. 2019). Water diversion structures may limit available habitat in tributaries during low water years as passage appears to be discharge dependent. None of our radio tagged fish were detected above a McElmo Creek diversion structure ~12 km upstream of the confluence. Additionally, only two individuals were captured in the ‘oilfield’ reach ~28 km upstream of the confluence during ongoing sampling in spring 2022 (a particularly low flow year) compared with hundreds of fish detected and captured upstream during earlier studies (Cathcart et al. 2018, 2019a) and during 2020 tagging. Our radio-tagged individuals exhibited a variety of long-distance movements during the spawning season (Figure 2.5) and movements of 340 km have been documented in the Grand Canyon, indicating the potential importance of habitat connectivity (Yackulic, written communication 06 January 2023).

Conclusions and future directions

Our research illustrates that inter-annual variation in temperature and hydrology affects the timing of flannelmouth sucker migrations into tributaries for spawning. These tributaries serve as an important component of the life cycle of flannelmouth sucker populations, but their conservation value might be overlooked with a focus on mainstem rivers (Utah Division of Wildlife Resources 2006). Although this study begins to examine this seasonal migration, better estimates of the contribution of tributary-spawned flannelmouth sucker to river populations would help identify their importance as a spawning area. While only a proportion of the mainstem flannelmouth sucker populations use tributaries for spawning, tributary-spawned larvae may have higher survival rates or better habitat conditions than mainstem-spawned larvae. We did not measure resource availability, predator threat, or water chemistry in this study, and comparing resources between tributaries and mainstem rivers could suggest reasons why flannelmouth suckers spawn in tributaries and contribute to a mechanistic understanding of any differences in larval survival between these habitats.

While classification trees provide a general assessment of migration patterns, future work may consider finer temporal resolution and intraspecific variation in behavior. Summarizing tributary occurrences by week, for example, smoothed over some potentially important nuances of environmental factors and migration extremes that are important on a daily or hourly basis. For example, McElmo Creek had 60% of individuals arrive in a single day in 2020 and over 3 days in 2018. Conversely, the LCR in general had more intra-annual variations in arrival timing than the other systems, except for McElmo Creek in 2017 and BAC in 2019 which were both higher flow years. While there were many detections used in this study, they represent a small portion of the population. Recaptures in the San Juan River basin generally represent less than 5% of individuals handled during tagging events. It is also likely that individual characteristics (such as sex, age, size, genetics, and experience) might help explain variable migration behaviors (Rasmussen and Belk 2017). For example, sex-specific resource requirements could alter migration timing (Green et al. 1966). Examination of the diversity of individual behaviors and which of these factors may be important to migration timing should be considered to avoid managing to the mean migratory experience that may obscure different yet successful life histories (Holyoak et al. 2008).

The ability of flannelmouth sucker to recruit to adulthood in the wild is more promising than other native sucker species in the region (i.e., razorback suckers). Many sucker species use tributaries for spawning and these habitats can be fragile (Hines 2011, Bottcher et al. 2013, Strohm et al. 2017). In some cases, tributary spawning may be the primary source for sustaining native fish populations including in the Grand Canyon in much of the post-Glen Canyon Dam period (e.g., Kaeding and Zimmerman 1983, Robinson and Childs 2001). As basin-wide reservoir water storage declines and thermal regimes change, the relative importance of tributary and mainstem habitats to flannelmouth sucker life stages may increase (Dibble et al. 2021). Continued monitoring of PIT tagged individuals throughout the basin will provide a robust dataset of flannelmouth sucker movement that could be useful as an indicator of river conditions and informative on the role of tributaries for these populations. Assuring water availability and connectivity to tributaries could benefit suckers by allowing access to spawning habitats, while natural flow and thermal regimes should allow fish to time migrations to optimize recruitment of offspring.

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Figures

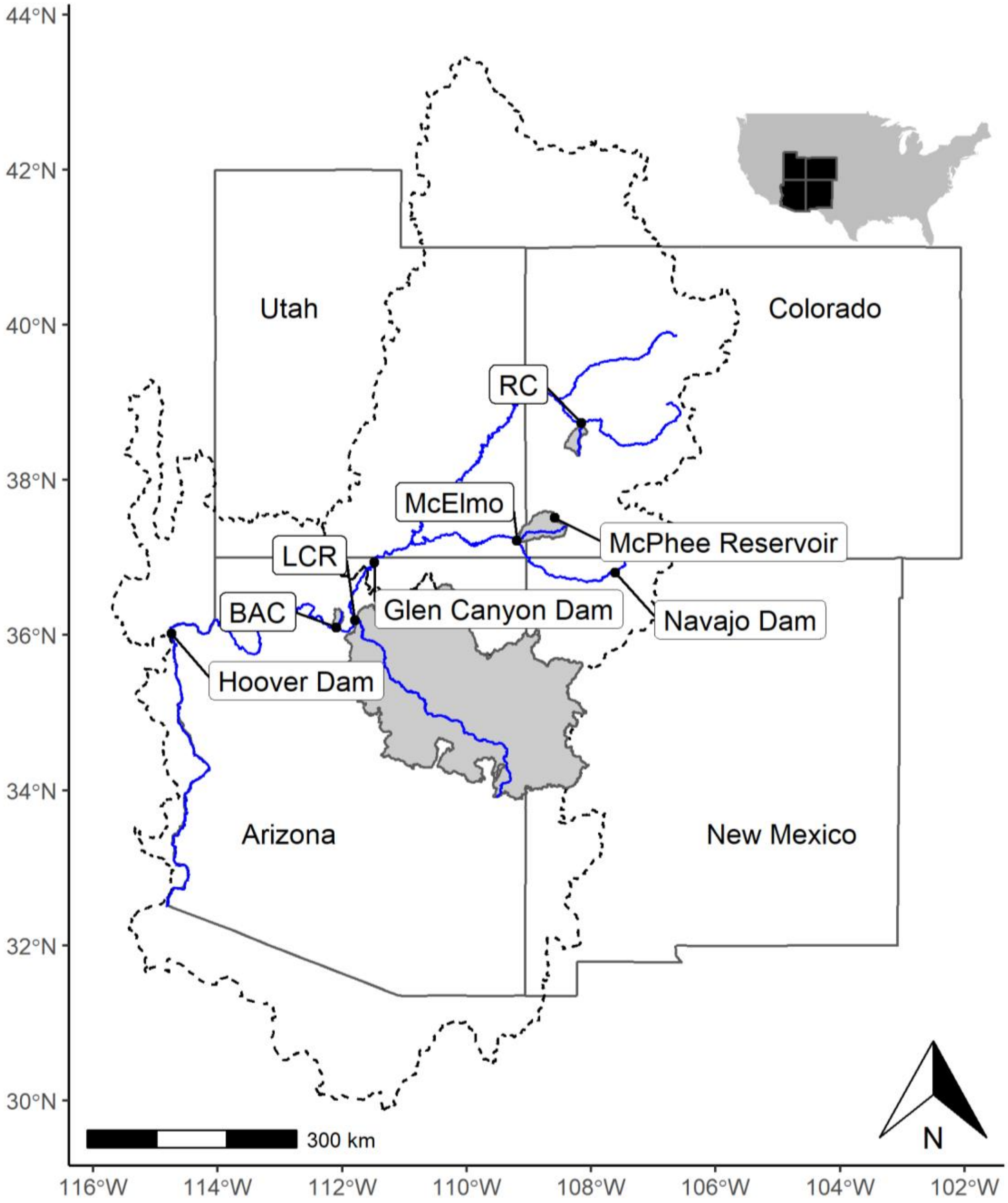

Figure 2.1. Map of tributary sites in the Colorado River basin (dashed line). Tributary watersheds are shaded grey (watershed area in Table 2.1), and antenna sites are denoted by dots. Map shows study tributaries to the Colorado River (Bright Angel Creek, BAC, and Little Colorado River, LCR), San Juan River (McElmo Creek), and Gunnison River (Roubideau Creek, RC).

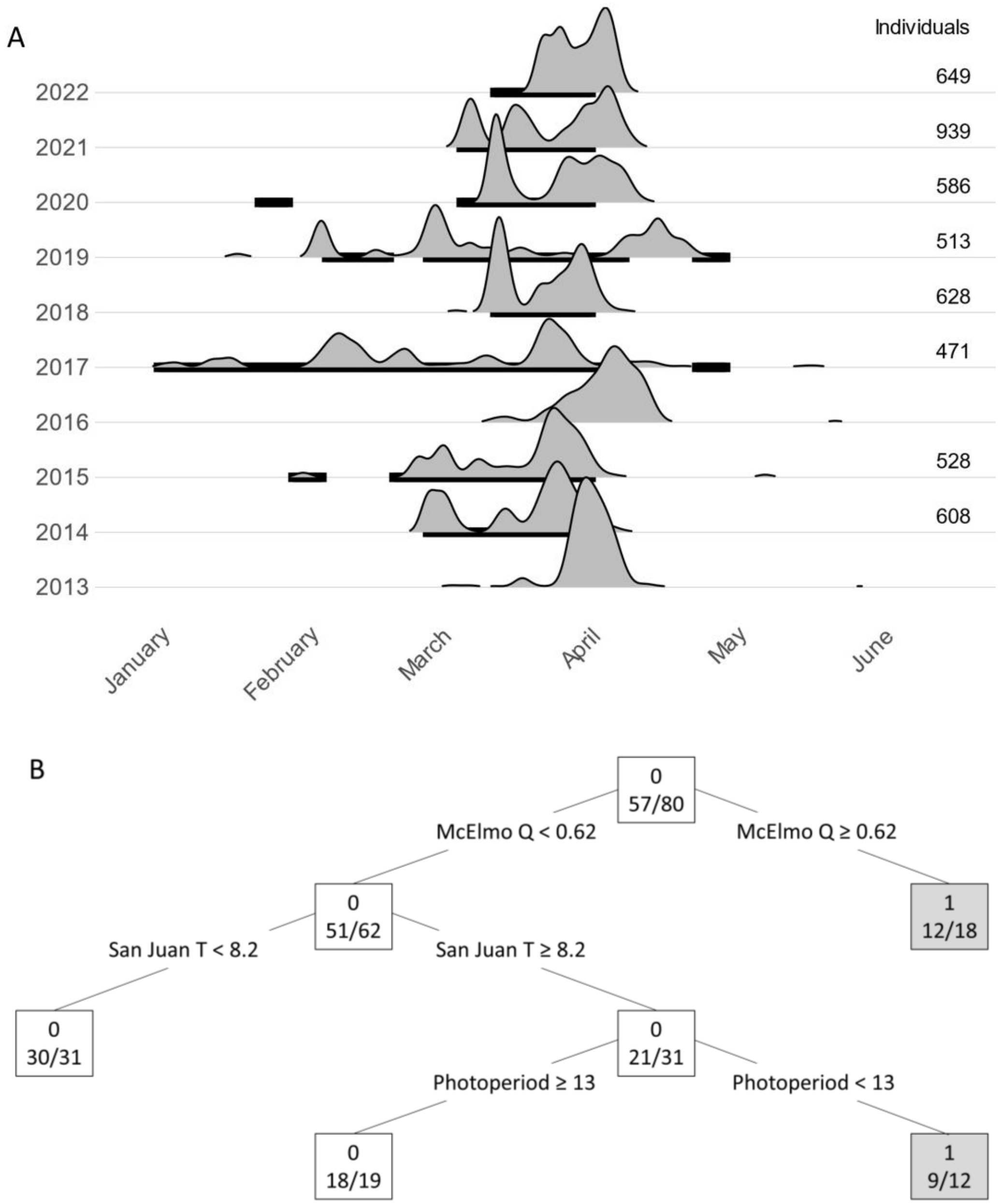

Figure 2.2. A) Ridgeline plot showing the timing of individual fish detection on the PIT antenna array near the mouth of McElmo Creek across years. Height of peaks show relative numbers of individuals smoothed over time since a small portion of the population is tagged. Black bars indicate which weeks the classification tree model predicted fish arrival based on environmental cues (2013 and 2016 not included in analysis). Numbers on the right indicate the number of individual fish for each year included in the models. B) Classification tree built from a subset of the flannelmouth sucker (*Catostomus latipinnis)* migration data. Zeros represent weeks without major migrations into McElmo Creek whereas 1 represents weeks with migration. Proportions in boxes represent the number of individuals from each group correctly identified. Discharge (Q) in cms, temperature (T) in degrees C, photoperiod in hours.

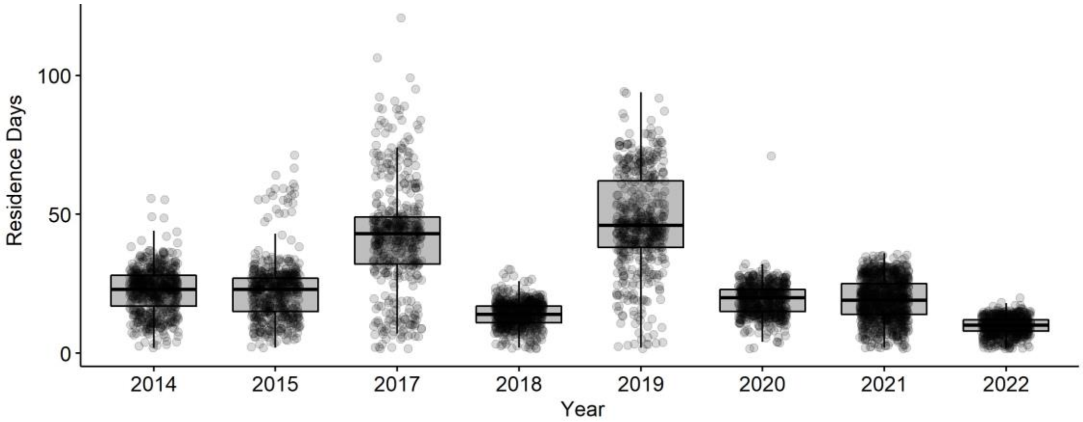

Figure 2.3. Residence time for McElmo Creek flannelmouth suckers (*Catostomus latipinnis)*. Time was calculated as a difference between date of first and last PIT antenna detection of an individual fish detected on two separate days at least two days apart. Boxes show median and inner 50% of data, whiskers indicate 1.5 times the inner quartile range.

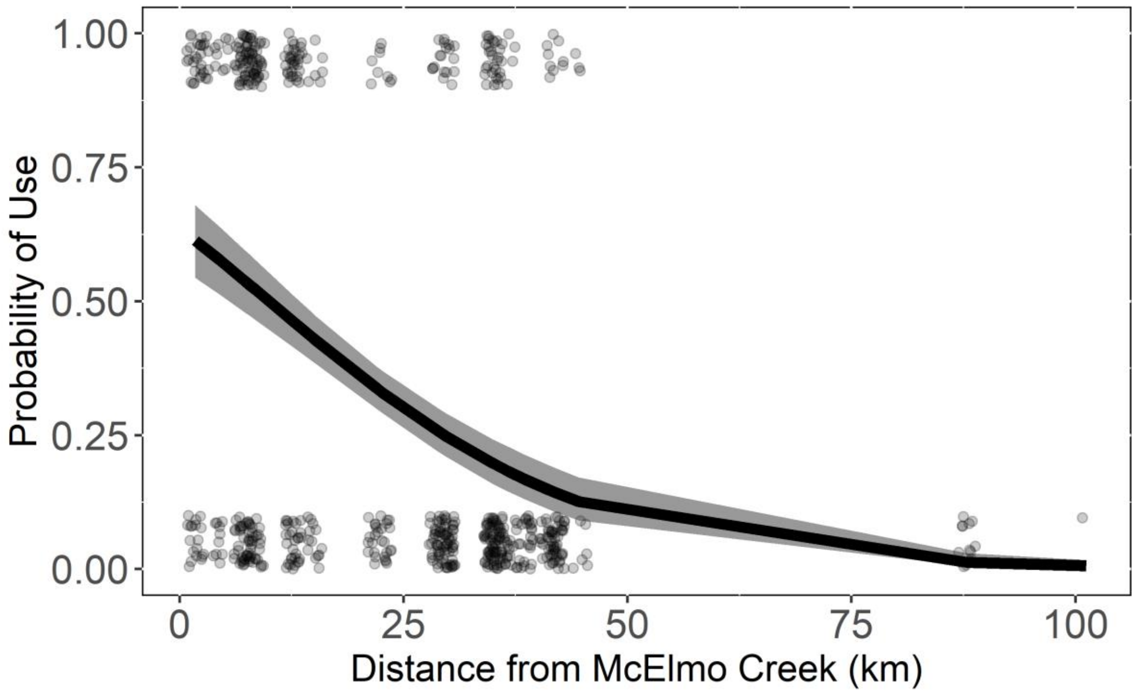

Figure 2.4. Logistic regression of a fish being detected on the McElmo PIT antenna in spring following fall tagging event based on the initial distance from McElmo Creek during the fall tagging events. Grey band represents 95% confidence interval. Points represent distribution of fish tagging locations with those that used McElmo plotted near 1 and those that did not near 0 (points jittered for visualization). Plot was symmetrical when considering upstream or downstream distance.

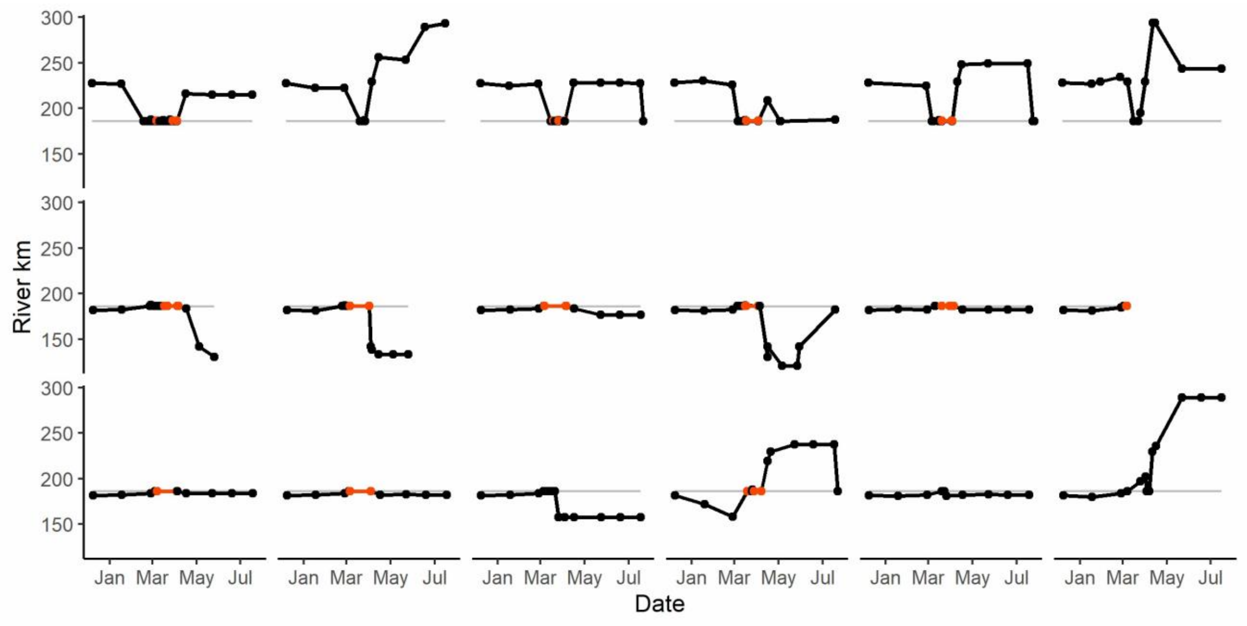

Figure 2.5. Individual longitudinal movement of 18 radio tagged (December 2020) flannelmouth suckers (*Catostomus latipinnis)* in the San Juan River that were detected on the McElmo radio antenna during the spawning season (spring 2021). Orange segments indicate detections on the McElmo Creek PIT antenna. The first point is the tagging location. The horizonal grey line indicates river mile of the McElmo confluence.

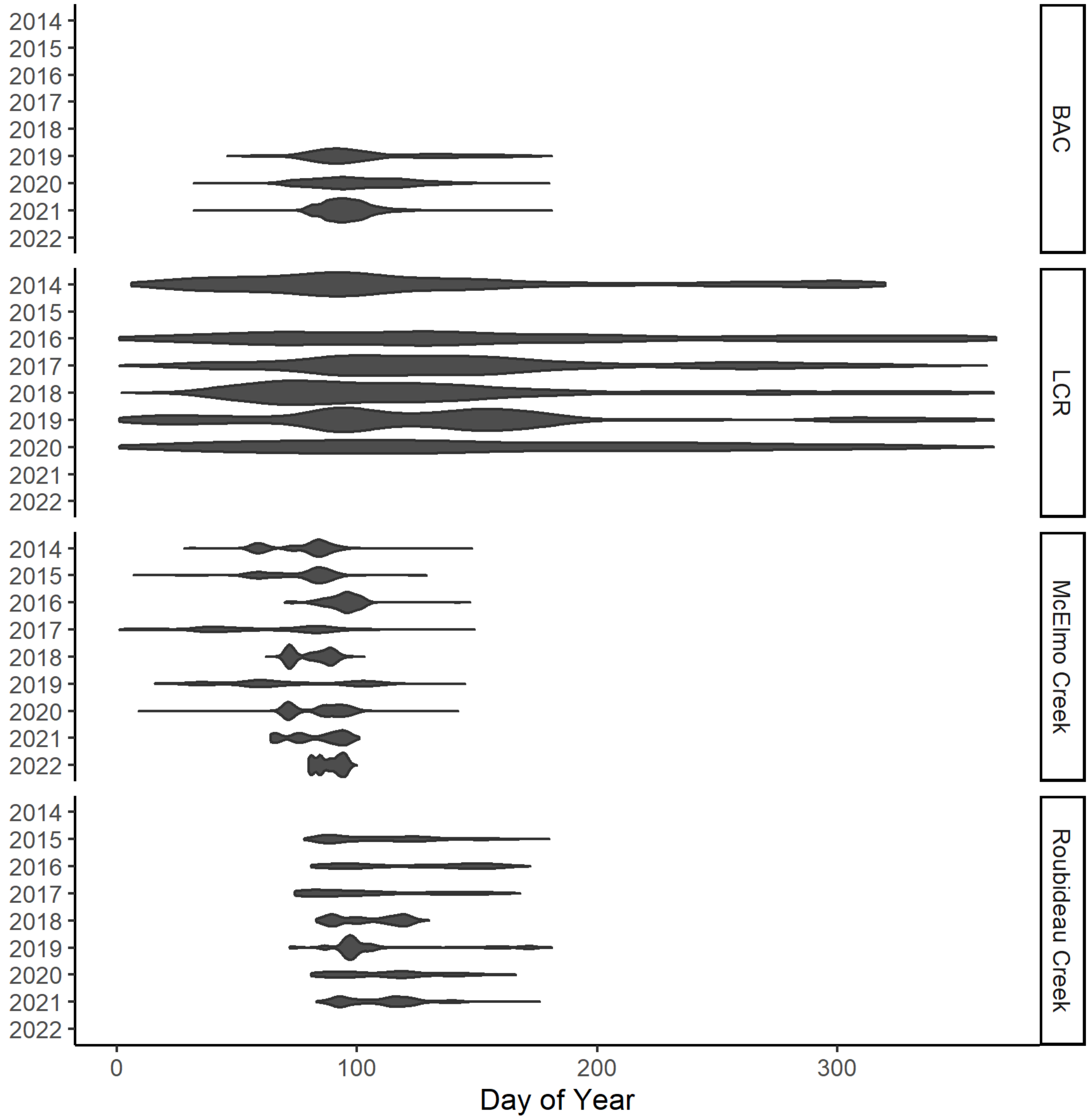

Figure 2.6. Unique PIT tags detected each day at each creek indicating movement into the creeks across the Colorado River Basin during the spawning season, or full year in the case of the Little Colorado River (LCR). Short residence times (< 2 days) filtered out. Full year shown for LCR due to extended detection peaks not seen in other tributaries. Low detection efficiency for antenna issues at McElmo Creek 2016 and high water at Roubideau Creek 2019. BAC = Bright Angel Creek.

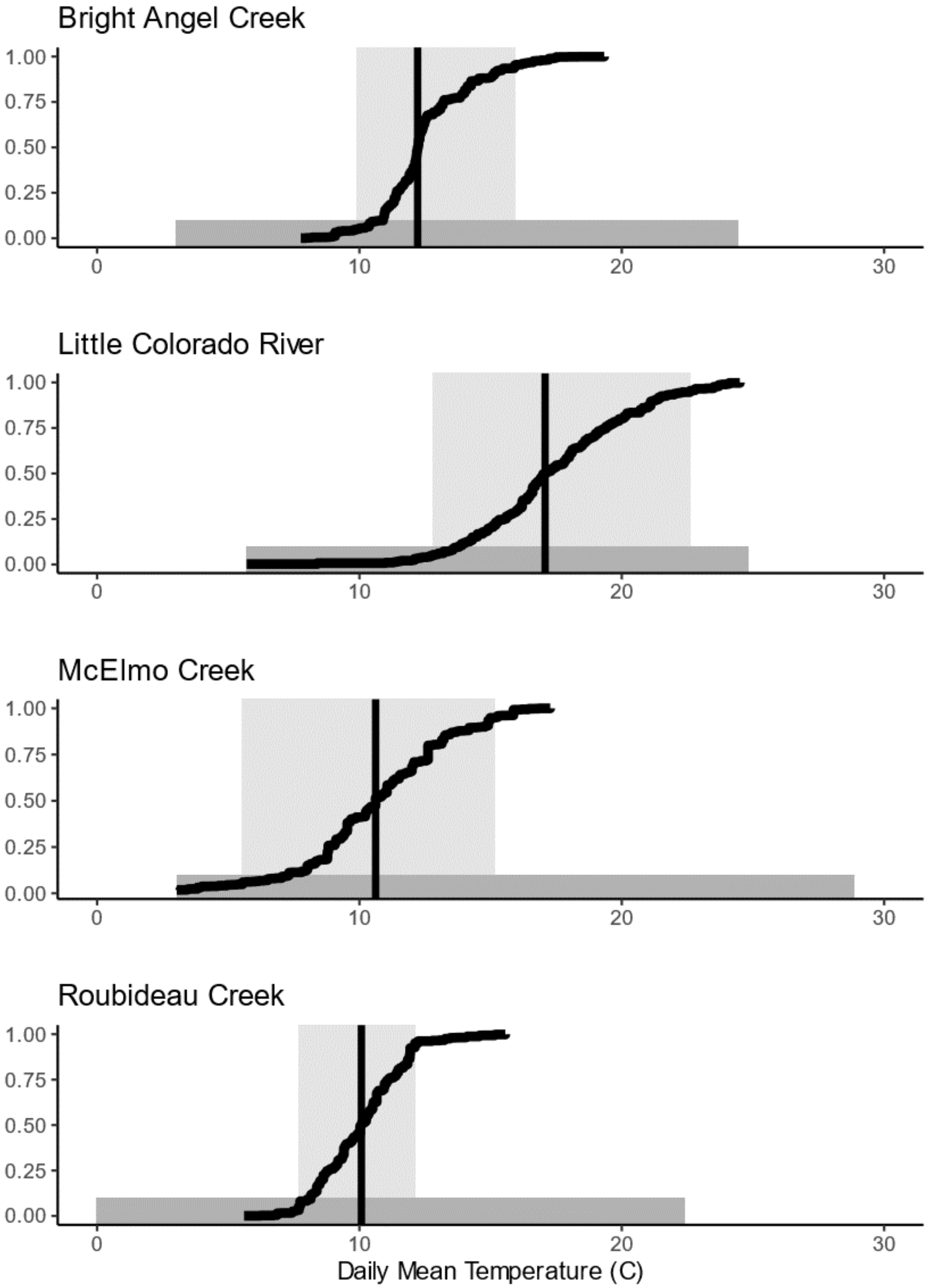

Figure 2.7. Cumulative density functions of the arrival of migrating flannelmouth sucker (*Catostomus latipinnis)* into tributaries. Verticle lines are migration medians (50% of fish migrated on days at or below that temperature) and the light grey region indicates the inner 90% of migration. Dark grey region indicates temperature range (January to June) for years included in this study.

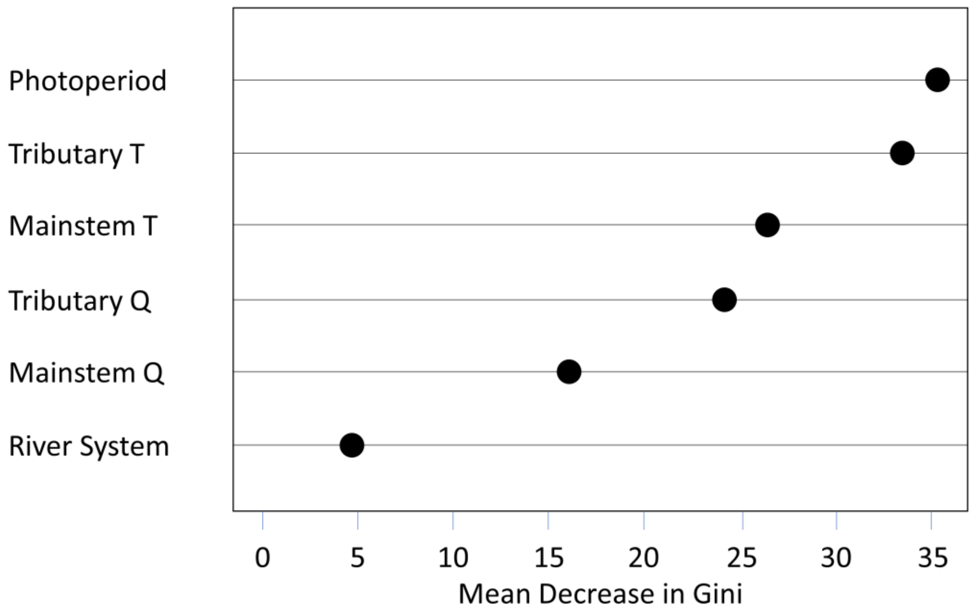

Figure 2.8. Variable importance for environmental factors in random forest model for all tributaries. Factors are sorted by mean discrease in Gini, the mean decrease in node impurity for each variable, weighted for samples parse by the node across trees. T = temperature, Q = discharge.

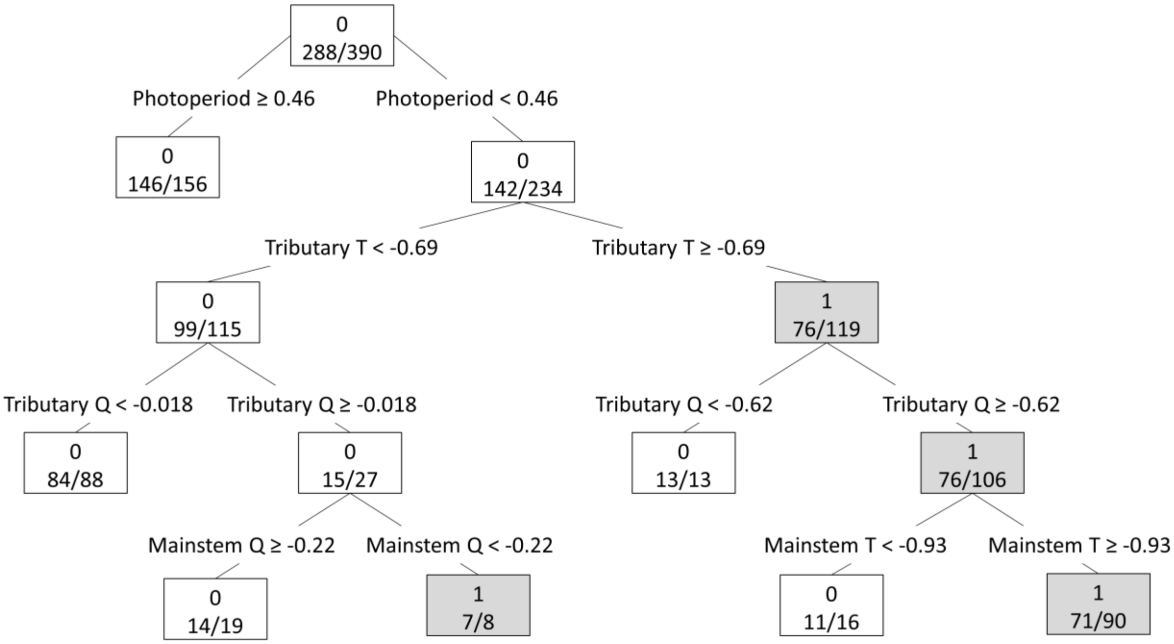

Figure 2.9. Classification tree predicting the occurrence of weekly tributary spawning runs by flannelmouth suckers (*Catostomus latipinnis)* based on environmental conditions in both tributaries and mainstem rivers. Data were combined from four tributary systems and tree was pruned based on class probabilities. Zeros represent weeks without major migrations into McElmo Creek whereas 1 represents weeks with migration. Proportions in boxes represent the number of individuals from each group correctly identified. The five environmental variables used in the model were scaled for each tributary to standardize relative effects across tributaries (T = temperature, Q = discharge).

Tables

Table 2.1. Stream characteristics for the tributaries and mainstems in this study. Discharge statistics were calculated for January through June of years with spawning data. Gage numbers represent U.S. Geological Survey (USGS) gaging stations (Figure 2.1). Temperature equations used for gap filling missing water temperature data from air temperature (T_A) and discharge (Q).

Stream	Mainstem	Gage	Elevation (m)	Drainage Area (km^2)	Discharge (m^3/s)		Temperature equations
					Mean	Median	
McElmo Creek	San Juan River	09372000	1,360	1,818	0.566	0.543	$3.04 + 0.79T_A$
Little Colorado River	Colorado River	09402300	838	69,857	10.1	6.29	$14.32 + 0.37T_A - 3.42^{-3}Q$
Bright Angel Creek	Colorado River	09403000	742	262	1.30	0.510	$1.90 + 0.64T_A + 0.35Q - 2.27^{-3}T_A{:}Q$
Roubideau Creek	Gunnison River	Hooley-Underwood, Thompson	1,488	628	3.45	1.81	
San Juan River		09379500	1,233	59,570	41.4		
Colorado River		09402500	737	366,742	354		
Gunnison River		09144250	1,497	14,597	51.9		

Table 2.2. Antenna array information for flannelmouth sucker (*Catostomus latipinnis*) telemetry data collection used in this study. Antenna installations were each for different projects contributing to the differences in antenna setups and locations within the streams. Data used were determined by functioning of antennas and time of installation relative to migrations. Tributary locations shown in Figure 2.1. Notable omissions reflect time periods when data was unavailable due to equipment issues.

Tributary	Antenna setup	Distance from confluence (km)	Dates used	Notable omissions
McElmo Creek	1 - 2 Multiplexer pass-over	0.3	2014 - 2022	2016
Little Colorado River	2 - 3 Multiplexer pass-over arrays	1.8	2014 – 2020	2015, 2016-04-15 to 2016-04-24, 2019-03-19 to 2019-03-29
	Submersibles		2017 - 2021	
Bright Angel Creek	3 Multiplexer pass-over arrays	0.6	2019 - 2021	
Roubideau Creek	1 – 4 Multiplexer pass-over array	0.6	2015 - 2021	

Table 2.3. Error matrix for flannelmouth sucker (*Catostomus latipinnis)* migration observations compared with predictions from classification tree of environmental factors for McElmo Creek alone and all tributaries together (McElmo Creek, Roubideau Creek, Little Colorado River and Bright Angel Creek; Figure 2.1).

		Classification Tree Predictions	
	Observations	Weeks without migration	Weeks with migration
McElmo Creek	Weeks without migration	34	5
	Weeks with migration	1	16
All tributaries	Weeks without migration	111	23
	Weeks with migration	10	23

Table 2.4. Top five model for residence time of flannelmouth suckers (*Catostomus latipinnis)* in McElmo Creek (Figure 2.1) as related to environmental factors. Variables were all scaled and centered, and ‘year’ was included in each candidate model as a random variable. Photoperiod was calculated at date of arrival, McElmo Creek discharge was calculated at arrival (Q_A) and departure (Q_D), and air temperature was calculated at arrival (T_A) and departure (T_D) for each individual. K = number of parameters, AICc = Akaike’s Information Criterion corrected for small sample sizes, ΔAICc = difference in AIC compared to top-ranked model, AICcWt = Akaike weight, LL = log likelihood.

Model	K	AICc	ΔAICc	AICcWt	LL
-Photoperiod - Q_A - Q_D + T_D	7	31396.6		0.562	-15691.29
-Photoperiod - Q_A - Q_D + T_A + T_D	8	31397.1	0.5	0.438	-15690.54
-Photoperiod - Q_D + T_D	6	31415.9	19.28	0	-15701.93
-Photoperiod - Q_D + T_A + T_D	7	31416.7	20.11	0	-15701.35
-Photoperiod - Q_A - Q_D	6	31752.4	355.83	0	-15870.21

Table 2.5. Temperature ranges for tributary migration or spawning for flannelmouth suckers (*Catostomus latipinnis)* from this and similar studies.

Tributary	Mainstem	Study	Years	Migration (˚C)	Spawning (˚C)
Bright Angel Creek	Colorado River	Weiss et al 1998	1993		13-15
Bright Angel Creek	Colorado River	This study	2019-2021	9.9-15.9	
Little Colorado River	Colorado River	This study	2014-2020	12.8-22.6	
Paria River	Colorado River	Weiss et al 1998	1992-1993		9-18
Roubideau Creek	Gunnison River	This study	2015-2019	9.9-15.9	
Cottonwood Creek	Roubideau Creek	Hooley-Underwood et al 2019	2016-2017	6.0-12.0	
McElmo Creek	San Juan River	This study	2014-2022	5.5-15.1	
Coal Creek	White River	Fraser et al 2017	2012-2013	13.5-18.0	

Supplemental Information

Supplemental information: Migration timing and tributary use of spawning flannelmouth sucker (*Catostomus latipinnis)*

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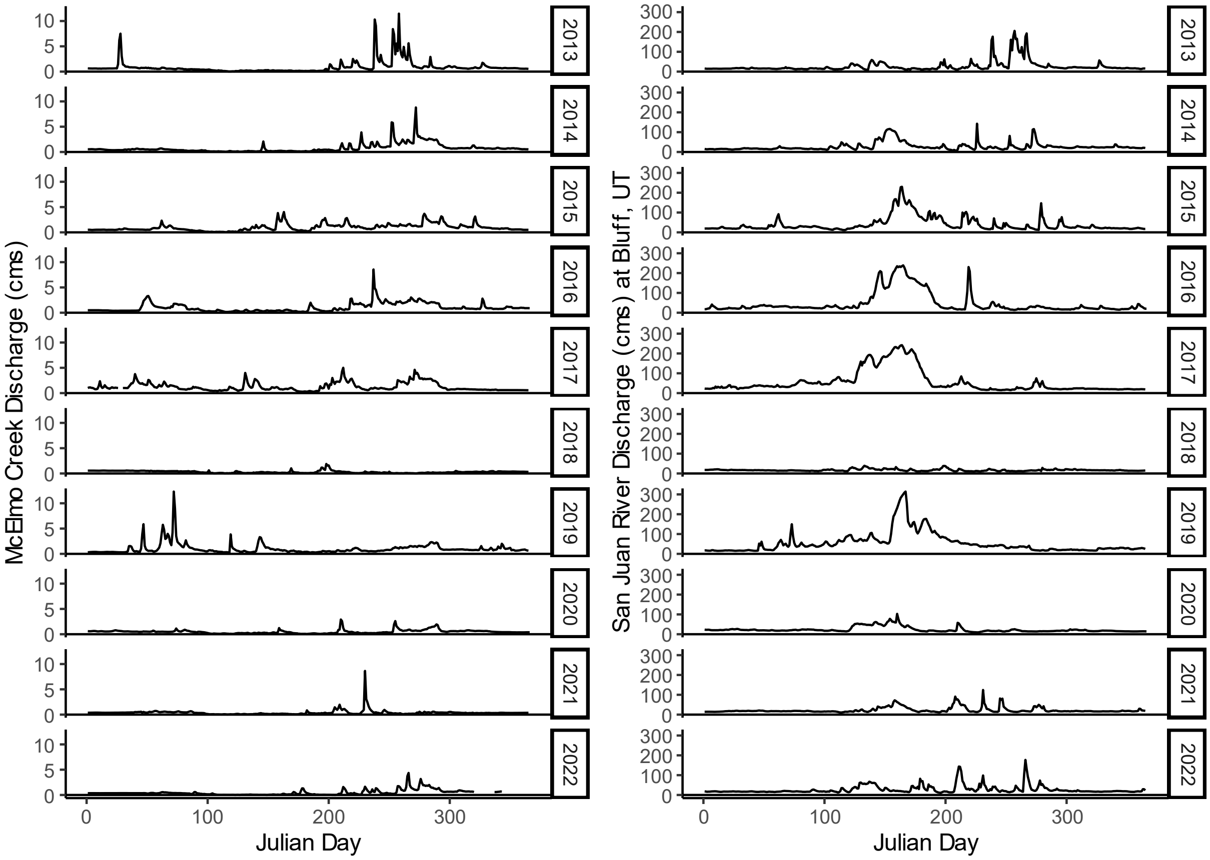

Figure S1. Mean daily discharge for McElmo Creek (USGS 09372000) and the San Juan River (USGS 09379500).

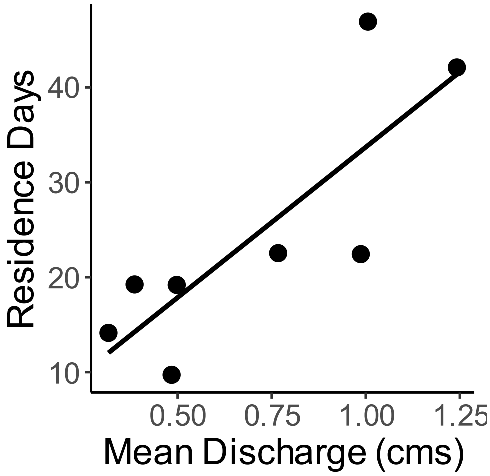

Figure S2. Mean residence days in McElmo Creek, Utah and mean discharge between January and June. $F_{(1,6)}$ = 16.08, p = 0.007, Adjusted R-squared = 0.63.

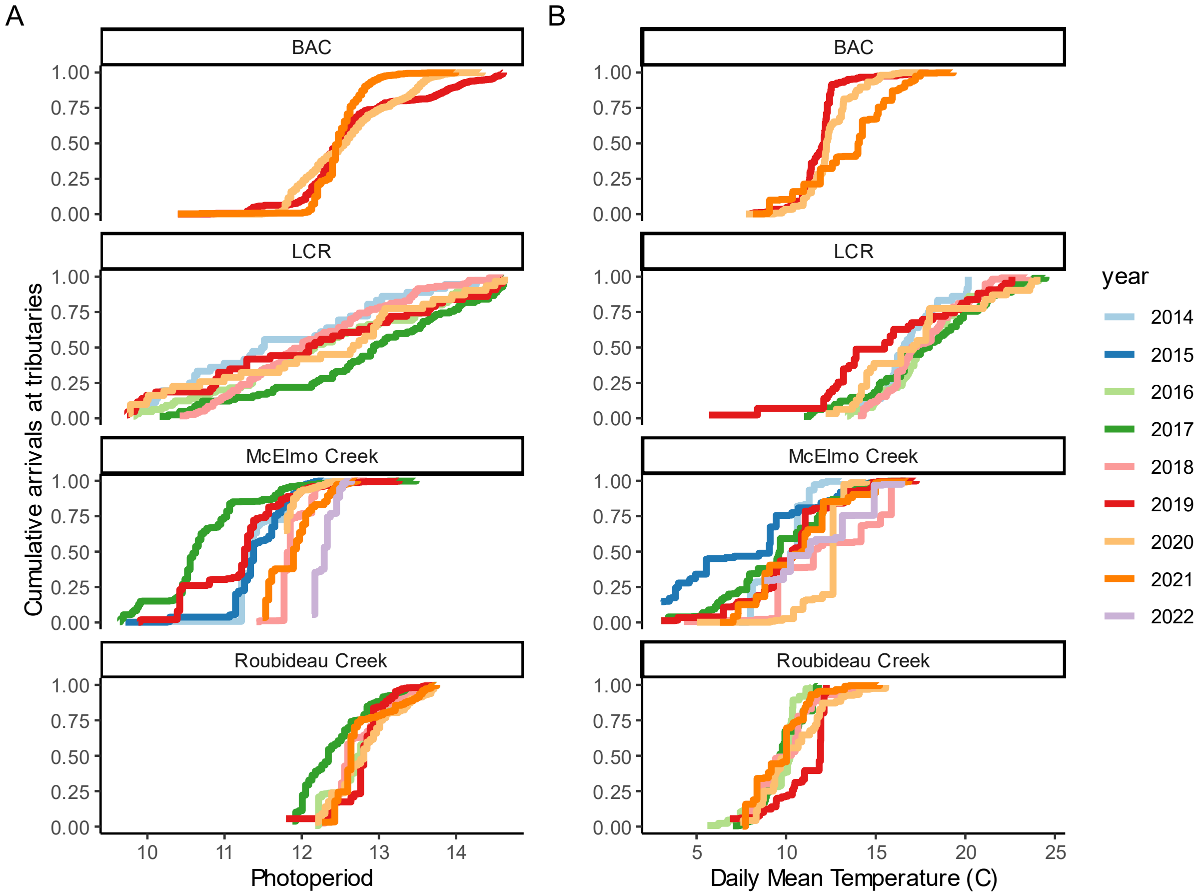

Figure S3. Cumulative plots of flannelmouth sucker (*Catostomus latipinnis*) arrivals for each year across sites. The x-axis shows A) photoperiod (h) to represent time of year but also account for some of the latitudinal displacement among sites and B) tributary mean daily temperature. BAC = Bright Angel Creek, LCR= Little Colorado River.

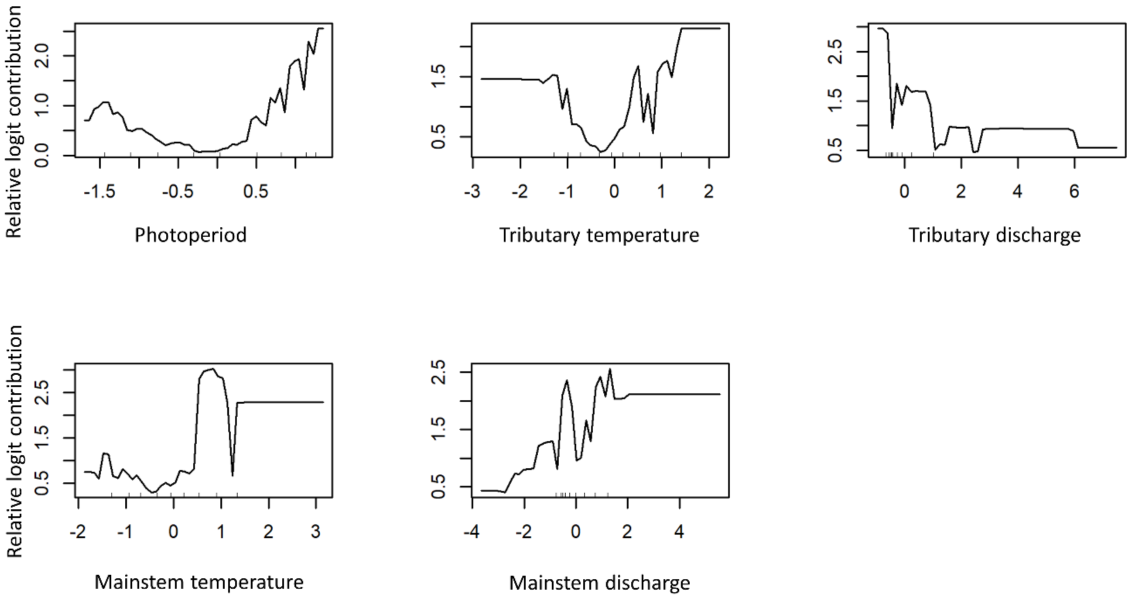

Figure S4. Partial dependence of environmental factors in random forest model for all tributaries.

Chapter 3 - Individual return patterns of spawning flannelmouth sucker (*Catostomus latipinnis*) to a desert river tributary

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Abstract

Tributaries provide temporal and spatial habitat heterogeneity in river networks. Migratory species that use these habitats may return to the same locations to reduce time and energy spent exploring new areas and to take advantage of previous experience. Although tributaries can be critical for parts of a species life history, anthropogenic activities can fragment or degrade these systems. Throughout the Colorado River Basin, flannelmouth suckers (*Catostomus latipinnis*) migrate from mainstem rivers into tributaries for spawning. Movement of passive integrated transponder (PIT) tagged fish between the San Juan River and its tributary McElmo Creek has been monitored since 2013 with a passive antenna array. We used Cormack-Jolly-Seber models to estimate the proportion of fish returning to spawn each year (i.e., tributary fidelity) based on PIT detection data from 2013 - 2022. Encounter rates and apparent survival varied among years and were dependent upon length of fish at initial tagging. Site fidelity, the proportion of the population returning to a specific tributary each year to spawn, was generally high, averaging 0.93 across years and ranging from 0.80 to 0.98. Average annual apparent survival across years was 0.82 and suggests 64% of tributary spawners die or emigrate from the population after 5 years. Individuals also showed consistency in relative arrival timing across years with ranked arrival order of individuals being positively correlated, averaging 0.40 and ranging from r = 0.23 to 0.74. The highest correlations generally occurred during years with higher spring discharge and extended tributary residence time. Site fidelity to McElmo Creek may reflect natal homing or habitat suitability and could benefit individuals by minimizing energetic costs in exploratory movements. However, the behavior may be maladaptive in systems where tributaries are vulnerable to human alterations. Flannelmouth sucker that use McElmo Creek for spawning likely have an important role in the maintenance of the mainstem San Juan River population and their spawning habitat should be protected.

Introduction

Within populations, individual variation in reproductive strategies can inform our ecological understanding of population dynamic response to environmental variation. One classic example of this is male bluegills (*Lepomis microchirus*) that exhibit alternative reproductive strategies such as parental care or cuckoldry, the second of which reduces parental investment (Gross and Charnov 1980). Another example is early return migrations of salmon jacks (*Oncorhynchus* spp.), which have less relative reproductive success after spending just a year in the ocean than full-size males who spend 3-7 years growing in the ocean, albeit jacks still sire almost a quarter of recruited individuals (King et al. 2023). Individual Sakhalin taimen (*Parahucho perryi*) may also vary in spawning migration timing, with some individuals consistently moving earlier than others (Fukushima and Rand 2023). Iteroparous steelhead trout (*Oncorhynchus mykiss*) may invest less energy into their first spawning season to improve their survival to a second spawning season as opposed to semelparous individuals (Seamons and Quinn 2010). Return pattern of migratory spawners can depend upon sex, as seen with male blue sucker (*Cycleptus elongatus*) that return annually to spawning tributaries while female suckers skip years (Lyons et al. 2016). 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 (Copeland et al. 2019). 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 (Chapman et al. 2012a). Recognizing how riverine fish express individual tendencies to balance trade-offs among spawning, migration, and survival and providing access to critical spawning habitats, such as tributaries, is important to conserving resilient native fish populations.

Tributaries influence river communities and ecosystem processes by providing habitat diversity, material transport, and connectivity (Kiffney et al. 2006, Tavernini and Richardson 2020). 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 (Fausch et al. 2002). Access to tributary habitat may be essential to support large-river fish populations through portfolio effects, whereby multiple spawning locations increase recruitment success (Bouska et al. 2023). Mainstem rivers altered for transportation, sport fisheries, agriculture, hydropower, and water storage may be more difficult to conserve than smaller, less degraded tributaries (Moyle and Mount 2007, Pracheil et al. 2013). 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 (Bottcher et al. 2013).

Preservation of tributary habitats is particularly important for iteroparous fish that demonstrate site fidelity by returning to the same tributary to spawn. Homing ability occurs in a number of species that return to previous spawning locations or natal sites (Harris et al. 2014), with mechanisms less researched in non-game species such as suckers (Cathcart 2021). Site fidelity benefits individuals by reducing energetic costs of searching for available habitat, increasing local experience and adaptation, and can be desirable if spawning habitat is limited (Zhao et al. 2011). These repeated migrations can shape population dynamics and genetic structure (Wilson et al. 2016). Genetic divergence among sites can result as a product of high site fidelity and reproductive isolation, potentially leading to increased population genetic diversity. However, site fidelity may be maladaptive in systems where these sites are rapidly degraded by human alterations (Merkle et al. 2022). 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.

Flannelmouth sucker is a long-lived species that use tributaries as a part of their reproductive strategy. Some flannelmouth suckers migrate into tributaries for spring spawning (Cathcart et al. 2019a, Hooley-Underwood et al. 2019), with probability of tributary use being greatest for fish closer to tributaries (Bonjour et al. 2023). Other studies have observed both long-range (> 200 km; Chart 1987, McKinney et al. 1999) or local (Bonjour, unpublished telemetry data) movement patterns. 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 (Molloy et al. 2020). Loose gravel, with aerated interstitial spaces for eggs to develop (Sigler and Sigler 1996, Weiss et al. 1998) may be more common in tributaries with natural flow regimes and bed material transport dynamics in contrast to regulated mainstem rivers with suppressed flows and increased embeddedness (Osmundson et al. 2002). Spawning migrations occur in spring when tributaries warm faster than mainstem rivers. This is likely important, as temperature is an important predictor of flannelmouth sucker migration timing (Bonjour et al. 2023).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 (Bezzerides and Bestgen 2002).

Passive integrated transponder (PIT) data have been integral for understanding migration behaviors (Fraser et al. 2017, Cathcart et al. 2018b, Pennock et al. 2020). 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 Cormack-Jolly-Seber (CJS) models to estimate site fidelity, or the proportion of the population returning to a specific tributary each year to spawn (Hayden et al. 2018). Two rates are estimated by the CJS model. Apparent survival (Phi) is the probability an individual survives to the following year and has not emigrated from the population and encounter rate (p) is the probability of an animal occurring and being detected at a site. We can derive site fidelity from these estimates using estimates of detection rate as the probability an animal will return to the site, given the animal is alive and does not emigrate. Apparent survival and site fidelity each contribute to the return patterns of migratory animals and advance the understanding of the ecology of a population. These models can also incorporate individual characteristics (sex, size, etc.) to examine the impact of individual variation on apparent survival and encounter rate estimates. 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 (Bonjour et al. 2023), less is known about individual behaviors 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 known spawning migrations. Our research questions were 1) what was the return pattern of individuals to McElmo Creek for spawning and how are annual apparent survival and site fidelity affected by individual variables (size, sex, cohort), time since tagging, interannual environmental variability, and handling effects, 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 (Merkle et al. 2022), including suckers (Hooley-Underwood et al. 2019, Dyer and Brewer 2020, Tornabene et al. 2020), so we anticipated relatively high site fidelity in McElmo Creek. As tributary migration is more common for fish near the tributary (Bonjour et al. 2023), 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 greater site fidelity in larger fish. We expected interannual variation to affect apparent survival and site fidelity, as different environmental conditions across years, such as higher discharge or earlier warming, impact migration timing (Bonjour et al. 2023). Similarly, time since tagging was anticipated to affect both estimates as fish age. Previous research noted handling effects associated with PIT tagging on exit time, with captured flannelmouth suckers exiting within 48 hours while suckers detected only by PIT antenna arrays remained in the tributary for 10-12 days (Fraser et al. 2017), so we tested if handling affected apparent survival in our system. A subset of fish using the tributary on an exploratory basis instead of as a regular spawning location would have the same pattern as handling effect. For the second question, we predicted that fish not returning to McElmo Creek to spawn might be spawning in other tributaries, the mainstem, or have emigrated from the system. Finally, we hypothesized that relative return timing of individuals in the population would be consistent across years, but more apparent in years with prolonged spawning seasons. Understanding the individual variation in return patterns of flannelmouth suckers to tributaries provides context for other research and management decisions associated with the reproductive ecology of this native species.

Methods

Study Location

McElmo Creek is the tributary to the lower San Juan River with the most consistent flow (Figure 3.1). Historically, McElmo Creek flowed intermittently, but the creation of McPhee Reservoir on the Dolores 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 dip in spring after early runoff and peak with late summer monsoons (Figure 3.S1). Discharge from the creek represents approximately two percent of the San Juan River discharge.

Passive integrated transponder data

Fish were tagged as described in Cathcart et al. (2015, 2018) and Bonjour et al. (2023). Approximately 7,000 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 arrays 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. 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 (Cathcart et al. 2018a). The second array was installed 0.3 km upstream of the confluence at a bridge crossing near Aneth, UT in January 2017. Data from the McElmo Creek arrays are uploaded as 'Aneth Confluence' and 'Aneth Bridge' into the Species Tagging, Research and Monitoring System (STReaMS, https://streamsystem.org/) 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 were retrieved from STReaMS on 03 Mar 2023, filtered for flannelmouth suckers that had any records in McElmo Creek. Fish measuring < 300 mm TL at tagging were excluded to focus on spawning individuals (Compton 2007). Data from the spawning season before the second PIT antenna installation (2016) were excluded from our analyses because of reduced reliability. Detections from both arrays were pooled to increase detection efficiency.

Data Analysis

1. Return patterns, apparent survival, and encounter rates

We tracked individuals tagged in McElmo Creek during the 2013, 2014, and 2015 spawning events to examine the proportion that returned annually for spawning. Encounter histories were created for 2013-2022 that summarized whether a fish was detected or not at the McElmo Creek PIT antenna during the first six months of the year. Although spawning generally occurs in March and April (Bonjour et al. 2023), this elongated time allowed us to include early and late spawning movement while excluding movement associated with late-summer monsoons. We focused on these three tagging cohorts because the McElmo Creek PIT antenna was not installed until after the spawning season in 2012 and efforts to tag fish spawning in McElmo Creek were reduced after 2015. 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. All analyses were conducted using Program R version 4.2.1 (R Core Team 2022).

Cormack-Jolly-Seber (CJS) open-population models were used to estimate annual apparent survival (survival less emigration) and encounter rates (Lebreton et al. 1992) and has previously been used to assess tributary spawning fidelity when a detection rate can be estimated (Hayden et al. 2018). Models were specified and fit using maximum likelihood methods in the package *marked* (Laake 2013). Candidate models were built to test if apparent survival and encounter rates differed by individual covariates for total length at tagging (TL), sex, and tagging cohort (cohort), which represented unmeasured factors that could limit fish migrating in a certain year (Table 3.1). For apparent survival, we considered models that differed over time since tagging (time), by yearly environmental characteristics (year), by handling where apparent survival was distinct in the first year after tagging and constant across subsequent years (tag event), and as constant (null). For encounter rate, we considered models that differed by time, year, or were constant. Although we had 10 years of data, that time frame was insufficient to address all potential environmental factors contributing to migration, so we used years (year) as a latent variable representing unmeasured response to interannual variation in environmental conditions. To examine handling effects, we added the variable ‘tag event’ in which survival in the year following tagging (i.e., handling) is different than survival in the subsequent years based only on detections. Only individuals with sex and length data were included in the models. In models where year was included as a parameter for estimating both apparent survival and encounter rates, estimates for the last time period were confounded (Lebreton et al. 1992, Hayden et al. 2018). For those models, apparent survival was fixed at 1 so the encounter rate estimate represents a joint probability of surviving and returning to the tributary during 2022.

Time-dependent models for each combination of tagging cohort and sex were used to calculate the degree of overdispersion ($\hat{c}$) individually and then combined to get an overall test statistic from goodness of fit with 'overall_CJS' in package *R2ucare* (Gimenez et al. 2018). Goodness of fit testing for the data indicated minor overdispersion $\hat{c} = 1.55$, which was accounted for in model comparison. We also examined the goodness of fit test 3.SR, as it is the component of the overall goodness of fit test that specifically compares apparent survival of redetected individuals to individuals not previously captured and can be used to examine handling effects in CJS models (Lebreton et al. 1992). Test 3.SR indicated that individuals with previous marks had different apparent survival rates than first-time captures ($\chi^2 = 8.61$, df = 2, p = 0.013). An initial model was fit considering tag event as a factor in apparent survival, but 95% confidence intervals overlapped for individuals handled and those only detected, with handled individuals having similar apparent survival estimates (Table 3.S1). As such, handling did not appear to negatively affect fish and we did not consider further models including tag event.

Model selection was performed sequentially to reduce the number of candidate models. First, apparent survival was estimated using a series of variable combinations with the global model for encounter rates (Table 3.2). The $\hat{c}$ estimate was used to correct Akaike's Information Criteria (AICc). Models were compared using corrected AIC (QAIC) and model weights. Second, the top apparent survival model was paired with a series of variable combinations for encounter rate. The most parsimonious model from this step was used for further interpretation.

To derive estimates of site fidelity from encounter rates, it was necessary to correct for detection rates. Detection rates were estimated for each antenna in McElmo Creek and combined to get an overall detection probability for each year. The Confluence and Bridge PIT antenna arrays each consist of two antennas that were installed to span the stream. We created detection histories that summarized whether individual fish were detected on each antenna any time during the first six months of the year, matching the time scale used in the CJS models, and estimated detection probabilities for each antenna by treating them as independent detectors. This method of estimating detection probability does not account for variation in detection rate within a year and assumes all antennas are functional at the same time. An antenna outage during the 2016 migration season resulted in only capturing the detection pulse as fish exited the tributary after spawning, so we adjusted detection rates for 2016 using average detection rates during the exiting pulse of similar years. Encounter rates were divided by detection rates to estimate site fidelity.

2. 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 (STReaMS 2023). Regardless, detections at these arrays provide data on annual or seasonal patterns of dispersal 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.

3. Relative individual arrival timing across years

We ranked individuals based on their arrival time in McElmo Creek each year from 2013-2022 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 two 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 (Bonjour et al. 2023). 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 not, we pooled these data.

Results

1. Return patterns, apparent survival, and encounter rates

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 (Figure 3.2), with an average of 81% of fish returning each successive year (Figure 3.3). Individuals tended to return in consecutive years (Figure 3.2) with gaps in returns only occurring for 18% of individuals detected across multiple years, and 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 each year since initial tagging in McElmo Creek through 2022 (Figure 3.2).

The apparent survival model with a dependence upon an interaction between year and length at tagging was retained in subsequent models to estimate encounter rate. The most parsimonious model for encounter rate included a negative relationship with length at tagging and variability across years (Table 3.2). This model received 89% of the model weight. The next ranked model had a delta QAICc of 4.67. Variability across years was included in the top four models for apparent survival and the top eight ranked models for encounter rates (Table 3.2). Tagging cohort and sex were not included in top models. Averaged across years, apparent survival was 0.82 and encounter rate was 0.86 (Table 3.S2). Apparent survival of the largest fish tended to decrease by the end of the study with greatest survival in 2013-2015 and 2019 and reduced survival in 2016. For fish tagged at lengths between 300 and 400 mm, survival tended to be lower in 2014-2016 and greatest in subsequent years (Figure 3.4A). Fish tagged at ~450 mm had consistent survival across years. Smaller fish had lower apparent survival estimates in 2013-2015. Contrary to our prediction, encounter rates decreased with size at tagging and were lowest in 2016-2018 (Figure 3.4B).

Annual detection rates were estimated using two to four individual antennas depending upon the year. Individual antenna detection rates were variable and ranged from 0.03 (Confluence-Upstream in 2017) to 0.99 (Bridge-Downstream in 2018, Table 3.3). Overall detection rates of combined antennas were more consistent, ranging from 0.79 in 2016 to 1.00 in 2021. The detection rate for 2016 reflects a correction using the probability of detection for individuals exiting McElmo Creek that were known to enter the tributary, which ranged from 0.70 to 0.93, with an average of 0.85 (estimate was multiplied by 0.85 to get 0.79, Table 3.3). High detection efficiency resulted in site fidelity estimates mirroring encounter rates (Figure 3.5, Table 3.S2) with site fidelity lowest in 2016 (0.74) and highest in 2014 (0.98).

2. 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 certain years, 72 of 117 (62%) detections were from the PIT antenna below Piute Farms Waterfall (186 rkm downstream of McElmo Creek), with 57 of those detections occurring during the 2022 spawning season (Figures 3.1,3.6). In addition to the waterfall, several individuals known to have spawned in McElmo Creek were detected near PNM Weir 121 km upstream of McElmo Creek, primarily in 2014 and 2015. Detections for all locations mostly occurred during the spawning season when flannelmouth suckers are presumably most mobile (Figure 3.6). 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 other records of flannelmouth sucker moving between the San Juan River Basin and the remainder of the Upper Colorado River Basin.

3. Relative individual arrival timing across years

Relative arrival timing was not sex dependent ($p > 0.05$), so data were pooled for males and females. As predicted, fish showed consistency in relative arrival timing across years (Figure 3.7). All contrasts between years had positive correlation coefficients and were significant (alpha = 0.05). Higher correlation coefficients were more common in wet 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 where fish exited the tributary sooner than wetter years.

Discussion

McElmo Creek spawning flannelmouth suckers 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 population represents a bet-hedging strategy made possible by high survival and spawning site fidelity. This individual variation in 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 during the spawning season ranged from 0.25 to 1.16 cms. The average site fidelity of flannelmouth suckers (0.93) was greater than estimates from tributary spawning blue suckers in Texas (0.83 probability of returning to a tributary, 0.65 of returning to the same tributary; Dyer and Brewer 2020). 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 the lack of a “handling effect” or apparent survival being lower in the year post-tagging. The average apparent survival of flannelmouth suckers (0.82) was similar to that of Lost River suckers (0.88) and shortnose suckers (0.76), even though that study assumed these values were equivalent to true survival because of lack of emigration in their system (Janney et al. 2008). Using our estimated apparent survival rate of 0.82, 64% of tributary spawners die or emigrate from the population after 5 years.

The inclusion of a latent variable (year) representing unknown interannual variation in our models suggests environmental variability as a driver of both apparent survival and site fidelity. Site fidelity was lowest in 2016 - 2018, even accounting for lower detection rates in 2016 (Figure 3.5). Higher water in 2016 and 2017 relative to the previous three years may have given fish the opportunity to explore other nearby tributaries (such as the Mancos River 40.5 km upstream of McElmo Creek). Conversely, 2018 was a low water year and 2019 was a higher water year with greater site fidelity, so factors other than discharge are likely to contribute to site fidelity. Specific features of either the water year or other environmental variability may also have significant impacts on return patterns. A monsoon in late July 2021 resulted in observed mortality and emigration of flannelmouth suckers downstream (Whitney et al. In Press) and highlights how acute environmental conditions impact true survival and emigration from a system. However, the general patterns of similar apparent survival and site fidelity across years suggested that environmental effects on migration behavior may have been relatively muted among years.

Patterns of larger/older individuals dying or leaving the McElmo Creek spawning population later in the study was generally supported for years early and late in the study; however, there was an unexpected interaction between fish length and year in the middle period of the study for apparent survival. Encounter rates were also lower for larger individuals between 2016 and 2018 (Figure 3.4B). Because detection rate was not likely size dependent, lower site fidelity of these larger individuals was most likely driving lower encounter rates in those years. As mentioned above, discharge in these three years did not seem to explain the low encounter rates. Because these were not mechanistic models, it was difficult to surmise why individuals of different sizes responded differently across 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 (Holyoak et al. 2008). Larger individuals tend to be more fecund (Dowling et al. 2014) and, while length and age are not perfectly correlated, larger individuals likely have more experience in the system. Individual variation within relative return time means individuals may not be interchangeable through individual-specific responsiveness to environmental cues (Fukushima and Rand 2023), particularly in years with longer spawning periods. This individual variation in arrival timing likely performs an additional bet hedging strategy to mainstem versus tributary spawning, but more research is needed to understanding mechanisms driving the observed variation in individual responses across years.

As flannelmouth suckers in our system exhibit high levels of spawning site fidelity, we had limited detections outside of the tributary, but some individuals moved long distances and returned to McElmo Creek in subsequent years. A small fraction of fish was detected on upstream PIT antennas during the spawning season in years they did not spawn in McElmo Creek. Some of these individuals may have been in search of greener spawning pastures. 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 (Bonjour, unpublished data). 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 (Pennock et al. In Review). These observations of individual fish spawning elsewhere or unintentionally permanently emigrating from the system 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 (Warkentin and Hernández 1996, Merkle et al. 2022) 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 Winemiller and Rose 1990), 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 disproportionally 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 low number of recruits, the tributary may be acting as an ecological trap in which reproductive efforts are being wasted in a hostile 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 (Bonjour unpublished data, Cathcart et al. 2019). Tracking reproductive output and recruitment, for example through genetic parentage analysis, might be a way to evaluate the true value of this tributary.

River connectivity is vital for these spawning migrations, allowing suckers to access habitat and resources in tributaries and link mainstem and tributary systems through energy and nutrients, process subsidies, and the coupling of communities (Bauer and Hoye 2014, Childress et al. 2014). Similarly, removing barriers within tributaries, protecting watersheds from further dewatering or degradation, and limiting the introduction and spread of non-natives 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. Regardless, our observations of site fidelity by McElmo Creek flannelmouth suckers suggest this habitat with less flow regulation than the mainstem is of critical importance to the San Juan River population and conservation measures to maintain access and enhance habitat in this tributary should be a top priority.

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Figures

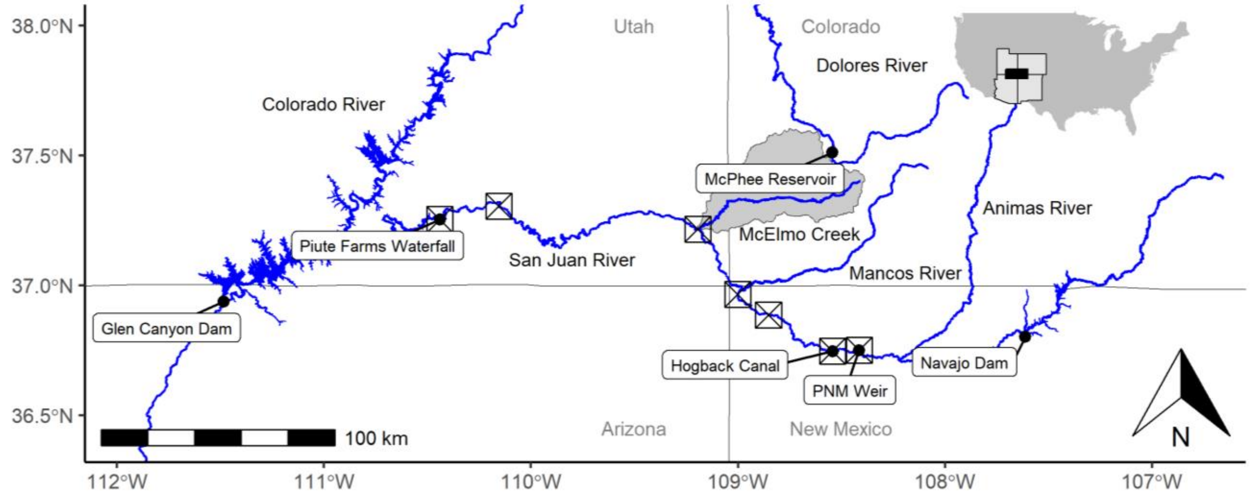

Figure 3.1 The Colorado and San Juan rivers along with the focal tributary, McElmo Creek (watershed area in grey). Permanent passive integrated transponder (PIT) tag antenna locations are indicated by squares with an x. Black dots represent barriers.

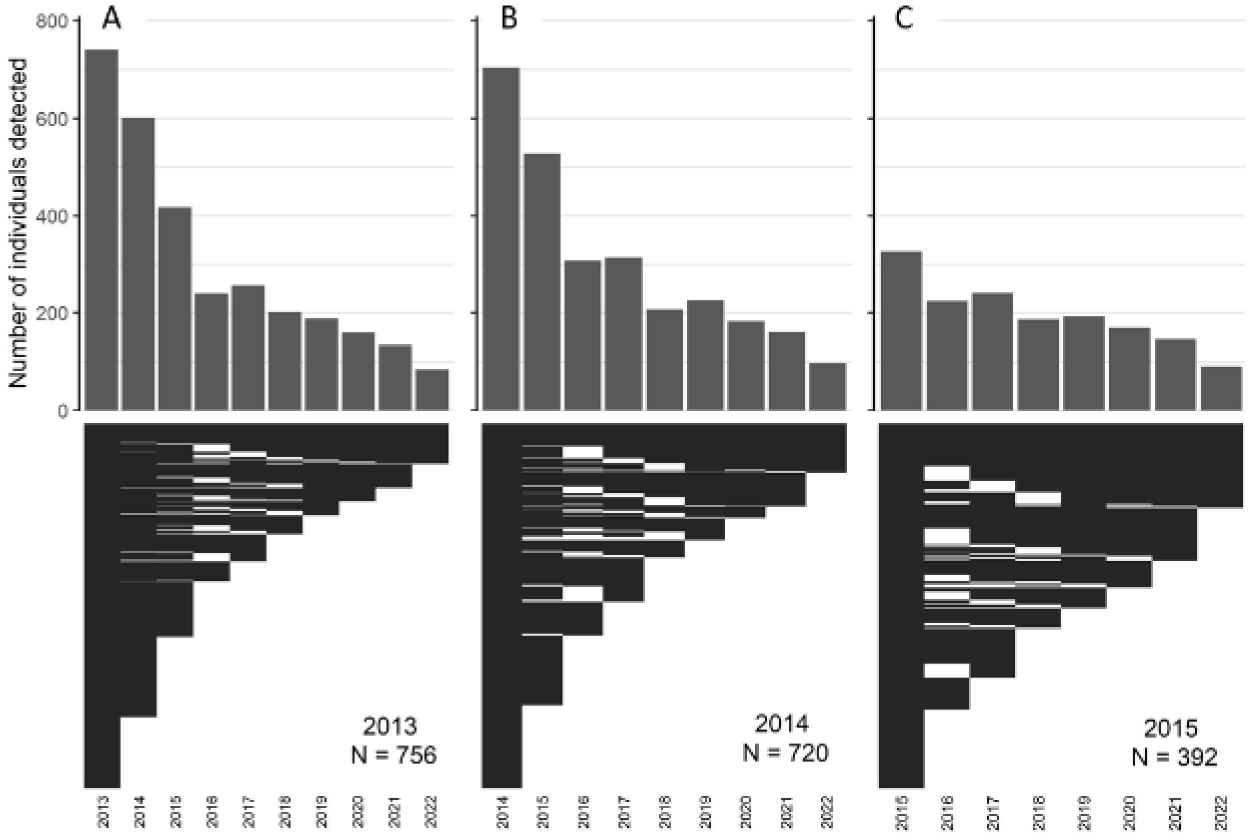

Figure 3.2 The top panels depict the number of flannelmouth suckers tagged in McElmo Creek during (A) 2013, (B) 2014, and (C) 2015 and subsequently detected on McElmo Creek PIT antenna each year to the tributary. Bottom panels: Visualization of detection histories of individual flannelmouth suckers migrating 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 left 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.

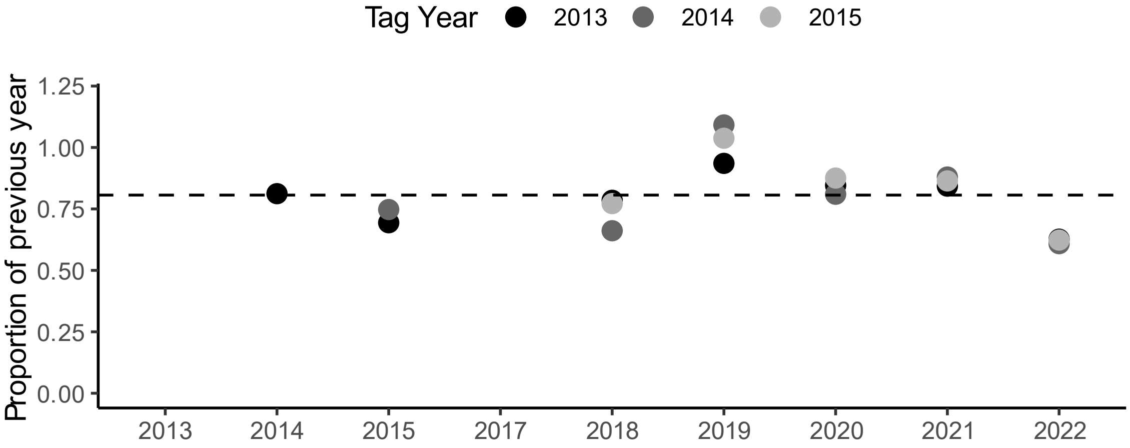

Figure 3.3 The proportion of flannelmouth suckers returning each year to McElmo Creek relative to the previous year. Dashed line shows mean value of 0.81 calculated from all points. Values over 1 indicate that more fish showed up in 2019 than in 2018.

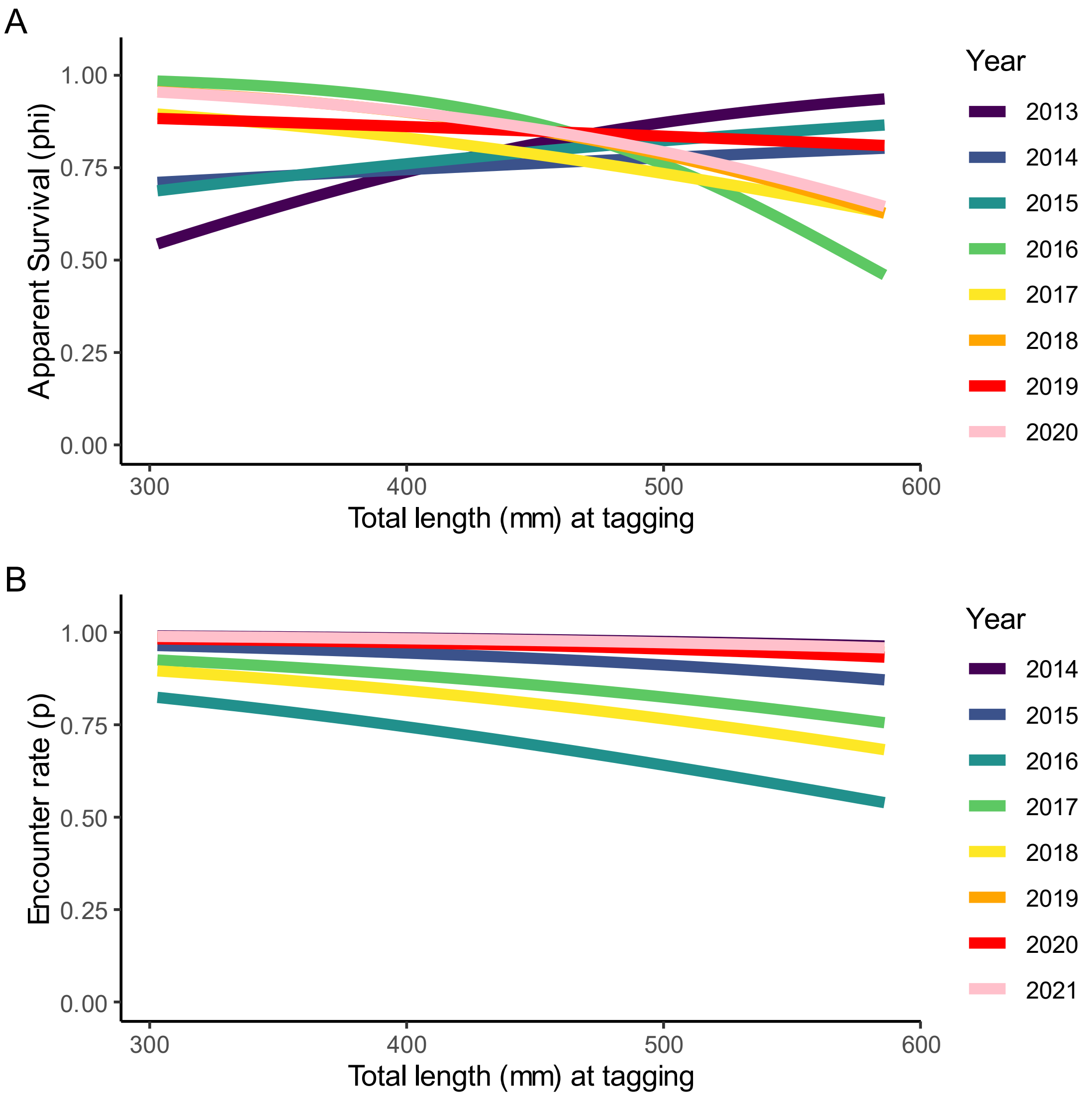

Figure 3.4 Interaction between total length at tagging and year for apparent survival (Phi) and encounter rate (p) estimates for flannelmouth sucker at McElmo Creek where apparent survival is predicted by an interaction with year and total length at tagging and encounter rate is predicted by an additive effect of year and total length.

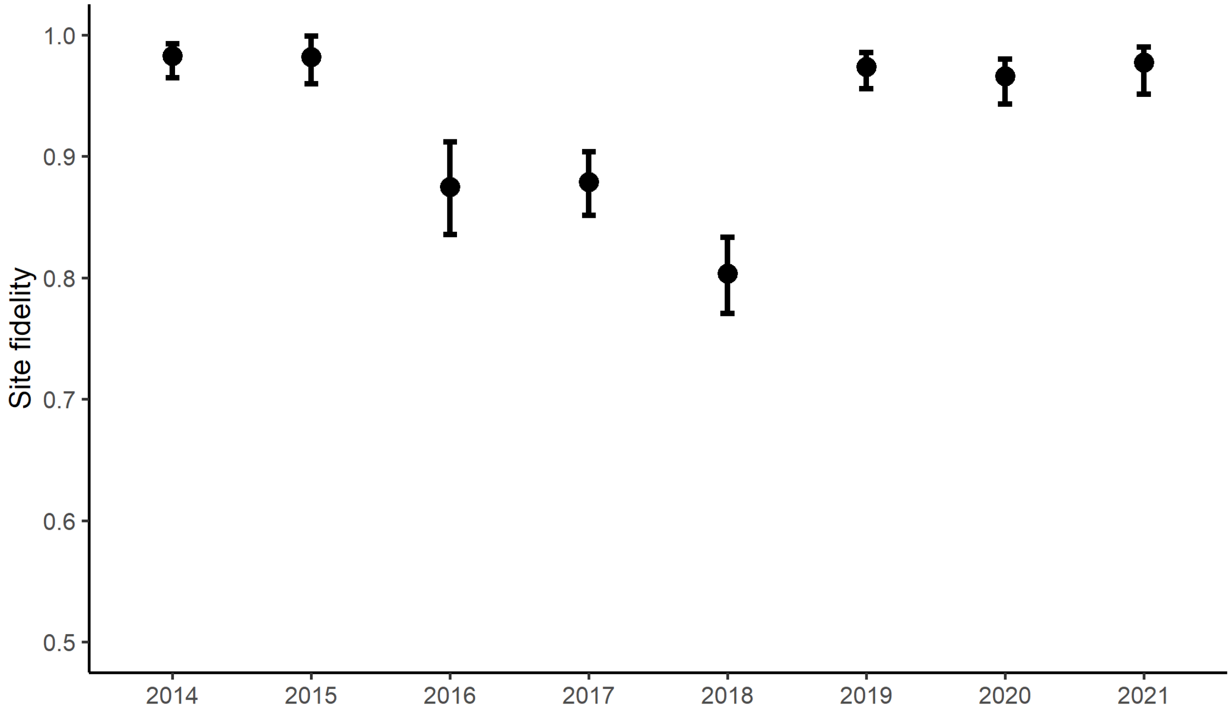

Figure 3.5 Estimates of site fidelity (calculated as encounter rate / detection probability) for flannelmouth sucker spawning in McElmo Creek. Bars represent 95% confidence intervals from encounter rates.

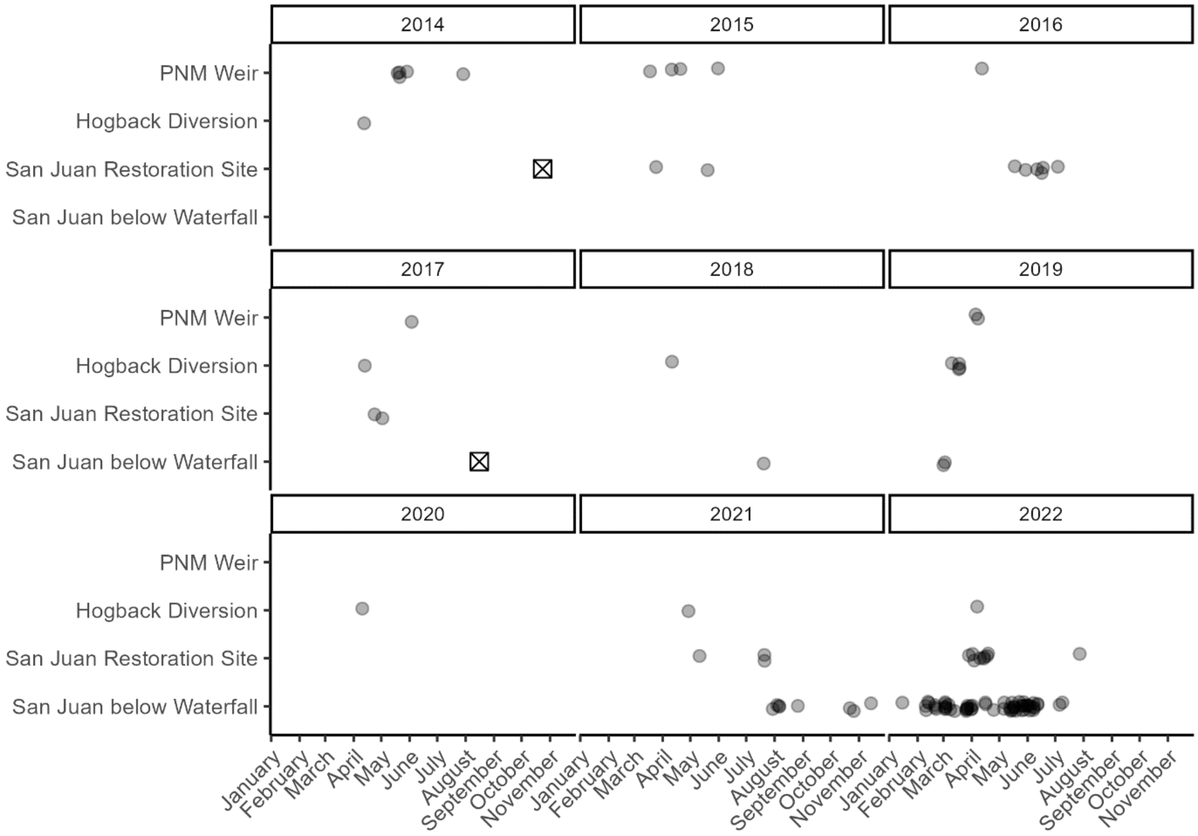

Figure 3.6 Detections of flannelmouth sucker (*Catostomus latipinnis*) on the four longest running passive interrogation arrays in the San Juan River during years the individuals were not detected in McElmo Creek after having previously spawned in the tributary. Points are slightly transparent and jittered for visualization purposes. Squares indicate when antennas were installed if not before 2014. Locations are arranged from upstream to downstream.

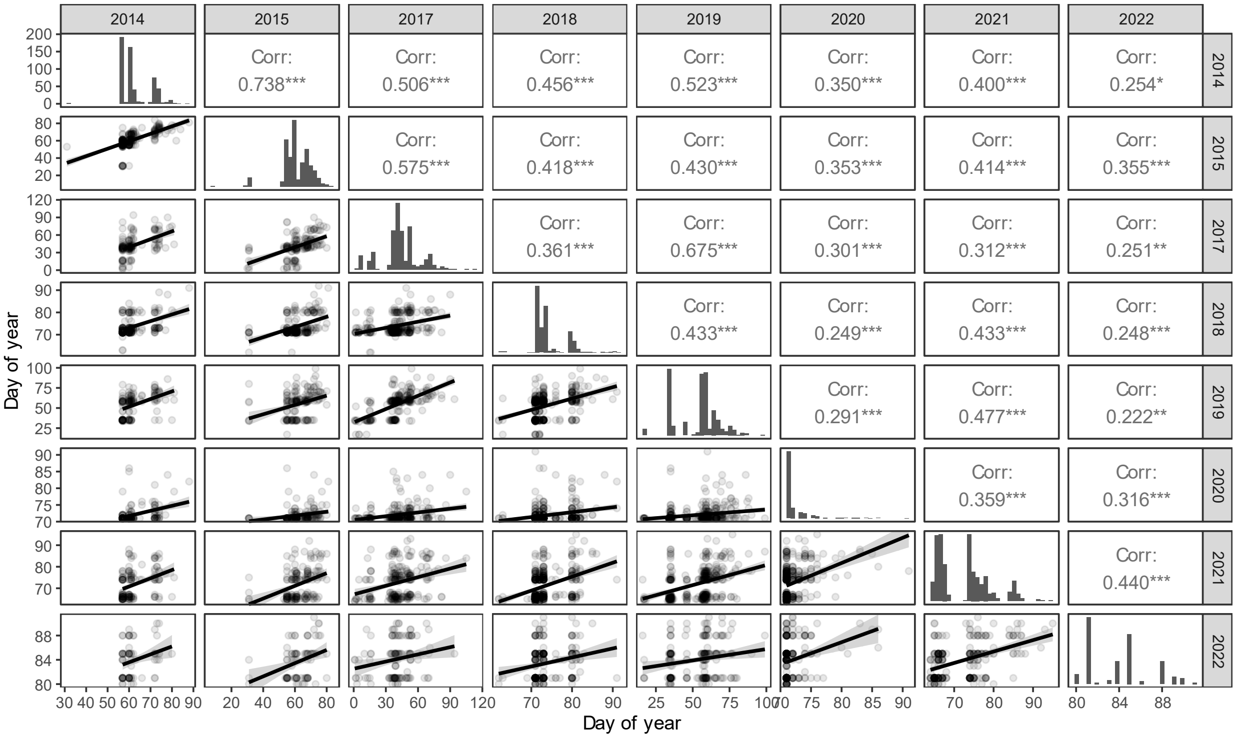

Figure 3.7 Spearman correlation for individual flannelmouth sucker day of arrival to McElmo Creek across years. Correlation coefficients given in the upper-right half with asterisks indicating significance of *0.05, **0.01 and ***0.001. Bar plots along the diagonal show the distribution of arrival times for each year. Points set to 0.1 transparency so that darker points represent multiple individuals. Lines reflect linear correlation for visualization purposes.

Tables

Table 3.1 Descriptions of models and variables tested for apparent survival (AS) and encounter rate estimates, including model variables and which hypotheses are supported by each model. IV = Individual variability, Env = environmental variability across years, TL = total length

Hypothesis	Model	Description
Null		AS is constant
IV	TL	AS differs by length at tagging
IV	Sex	AS differs by sex
IV	Cohort	AS differs by tagging cohort
Time	Time	AS differs by time since tagging
Time, IV	time*TL	AS differs by time since tagging, depending on length at tagging
Time, IV	time*sex	AS differs by time since tagging, depending on sex
Time, IV	time*TL+sex	AS differs by time since tagging, depending on length at tagging and sex
Env	Year	AS differs across years
Env, IV	year*TL	AS differs across years, depending on length at tagging
Env, IV	year*sex	AS differs across years, depending on sex
Env, IV	year*cohort	AS differs across years, depending on cohort membership
Env, time	year*time	AS differs across years, depending on time since tagging
Env, IV, time	year+TL*time	AS differs across years and time since tagging, depending on length at tagging
Handling	tag event	AS differs following tagging
Handling, IV	tag event*TL	AS differs following tagging, depending on length at tagging
Handling, IV	tag event*sex	AS differs following tagging, depending on sex
Handling, Env	tag event + year	AS differs following tagging and across years
Handling, IV, Env	tag event + year*TL	AS differs following tagging and across years, depending on length at tagging
Null		Encounter rates are constant
IV	TL	Encounttner rates differ by length at tagging
IV	Sex	Encounter rates differ by sex
IV	sex+TL	Encounter rates differ by sex and length at tagging
Time	Time	Encounter rates differ by time since tagging
Time, IV	time*TL	Encounter rates differ by time since tagging, depending on length at tagging
Env	Year	Encounter rates differ across years
Env, IV	year*TL	Encounter rates differ across years, depending on length at tagging
Env, IV	year+TL	Encounter rates differ across years and length at tagging
Env, IV	year*sex	Encounter rates differ across years, depending on sex
Env, IV	year+sex	Encounter rates differ across years and sex
Env, IV	year*cohort	Encounter rates differ across years, depending on cohort membership
Env, time	year*time	Encounter rates differ across years, depending on time since tagging
Env, time	year+time	Encounter rates differ across years and time since tagging

Table 3.2 Cormack-Jolly-Seber models for apparent survival (Phi) and encounter rate (p) from flannelmouth sucker detections in McElmo Creek during spawning season. Variables considered were year, period in which an individual was total length at tagging (TL), sex, and time since tagging (time). Models were built sequentially, with a global model for encounter rate used to estimate apparent survival, and the top model for survival used when estimating encounter rate. Npar = number of parameters, QAICc = Quasi-Akaike's information criteria, DeltaQAICc = change in AIC, weight = support for model compared to others in the table. Models adjusted for ĉ = 1.55.

Equations	npar	QAICc	DeltaQAICc	weight
*Model set for estimating apparent survival, with encounter rate as p ~ time + time:year + year * TL + year * sex*				
~year * TL	87	7095.39	0	1.00
~time * TL + year	94	7112.01	16.62	0.00
~year	79	7119.15	23.76	0.00
~cohort	74	7121.34	25.95	0.00
~time * TL	89	7127.41	32.02	0.00
~TL	73	7128.58	33.19	0.00
~year * sex	87	7128.77	33.38	0.00
~time * TL + sex	90	7128.88	33.49	0.00
~sex	73	7130.04	34.65	0.00
~1	72	7130.62	35.23	0.00
~time	80	7131.04	35.65	0.00
~year * cohort	95	7133.57	38.18	0.00
~time * sex	89	7140.64	45.25	0.00
~time + time:year + year * TL + sex	123	7152.69	57.30	0.00
~year * time	114	7172.71	77.32	0.00
*Model set for estimating encounter rate, with apparent survival as Phi ~ year * TL*				
~year + TL	26	6994.71	0.00	0.89
~year * TL	34	6999.38	4.67	0.09
~year + sex	26	7003.06	8.35	0.01
~year	25	7003.48	8.77	0.01
~time + year	33	7014.61	19.91	0.00
~year * sex	34	7017.85	23.14	0.00
~cohort * year	43	7031.86	37.15	0.00
~time * year	69	7084.69	89.98	0.00
~time * TL	34	7282.09	287.38	0.00
~time	25	7285.98	291.28	0.00
~TL	18	7417.03	422.32	0.00
~sex + TL	19	7419.01	424.30	0.00
~sex	18	7424.92	430.21	0.00
~1	17	7425.13	430.43	0.00

Table 3.3 Detection probabilities for antenna arrays in McElmo Creek by year and the overall probability of an individual being detected in a year. DS and US are downstream and upstream, respectively. Probabilities were calculated using detection of individuals on a single antenna compared to being detected on the other. * indicates probability corrected for antenna only functioning during the exit pulse.

Year	Bridge DS	Bridge US	Confluence DS	Confluence US	Overall
2013			0.780	0.935	0.986
2014			0.961	0.927	0.997
2015			0.866	0.589	0.945
2016			0.848	0.592	0.938
					*0.789
2017	0.113	0.059	0.715	0.880	0.972
2018	0.992	0.921	0.054	0.360	1.000
2019	0.930	0.773	0.552	0.634	0.997
2020	0.705	0.845	0.768	0.834	0.998
2021	0.910	0.956	0.939	0.947	1.000
2022	0.960	0.962	0.000	0.033	0.999

Supplemental Information

Table 3.S1. Cormack-Jolly-Seber models for apparent survival (Phi) from flannelmouth sucker detections in McElmo Creek during spawning season with the inclusion of tag event. A global model for encounter rate was used to estimate apparent survival. Models including tagging events (highlighted in grey) were added after the initial model run (Table 3.2). Npar = number of parameters, QAICc = Quasi-Akaike's information criteria, DeltaQAICc = change in AIC, weight = support for model compared to others in the table. Models adjusted for ĉ = 1.55.

Equations	npar	QAICc	DeltaQAICc	weight
Model set for estimating apparent survival, with encounter rate as *p ~ time + time:year + year * TL + year * sex*				
~tag event + year * TL	88	7092.37	0.00	0.82
~year * TL	87	7095.39	3.02	0.18
~time * TL + year	94	7112.01	19.64	0.00
~year	79	7119.15	26.78	0.00
~cohort	74	7121.34	28.96	0.00
~tag event * TL	75	7122.41	30.04	0.00
~time * TL	89	7127.41	35.04	0.00
~TL	73	7128.58	36.20	0.00
~year * sex	87	7128.77	36.40	0.00
~time * TL + sex	90	7128.88	36.50	0.00
~tag event * year	87	7129.20	36.82	0.00
~sex	73	7130.04	37.67	0.00
~1	72	7130.62	38.25	0.00
~time	80	7131.04	38.67	0.00
~tag event	73	7132.64	40.26	0.00
~tag event * sex	75	7133.22	40.85	0.00
~year * cohort	95	7133.57	41.19	0.00
~time * sex	89	7140.64	48.27	0.00
~time + time:year + year * TL + sex	123	7152.69	60.31	0.00
~year * time	114	7172.71	80.34	0.00

Table 3.S2. Apparent survival (Phi) and encounter rate (p) estimates across years of flannelmouth sucker at McElmo Creek using the top Cormack-Jolly-Seber model Phi(~year *length)p(~year + length) with joint probability for the final year. SE = Standard error, LCI = lower confidence interval, UCI = upper confidence interval.

Parameter	Year	Estimate	SE	LCI	UCI
Phi	2013	0.821	0.015	0.790	0.848
	2014	0.763	0.012	0.738	0.786
	2015	0.797	0.014	0.768	0.822
	2016	0.862	0.015	0.829	0.889
	2017	0.781	0.016	0.748	0.811
	2018	0.846	0.015	0.813	0.873
	2019	0.847	0.015	0.816	0.875
	2020	0.849	0.017	0.814	0.879
p	2014	0.980	0.007	0.962	0.990
	2015	0.928	0.009	0.907	0.944
	2016	0.690	0.015	0.659	0.719
	2017	0.854	0.013	0.827	0.878
	2018	0.803	0.016	0.770	0.833
	2019	0.971	0.007	0.953	0.983
	2020	0.964	0.009	0.941	0.978
	2021	0.977	0.009	0.951	0.990
Phi*p	2022	0.601	0.024	0.554	0.646

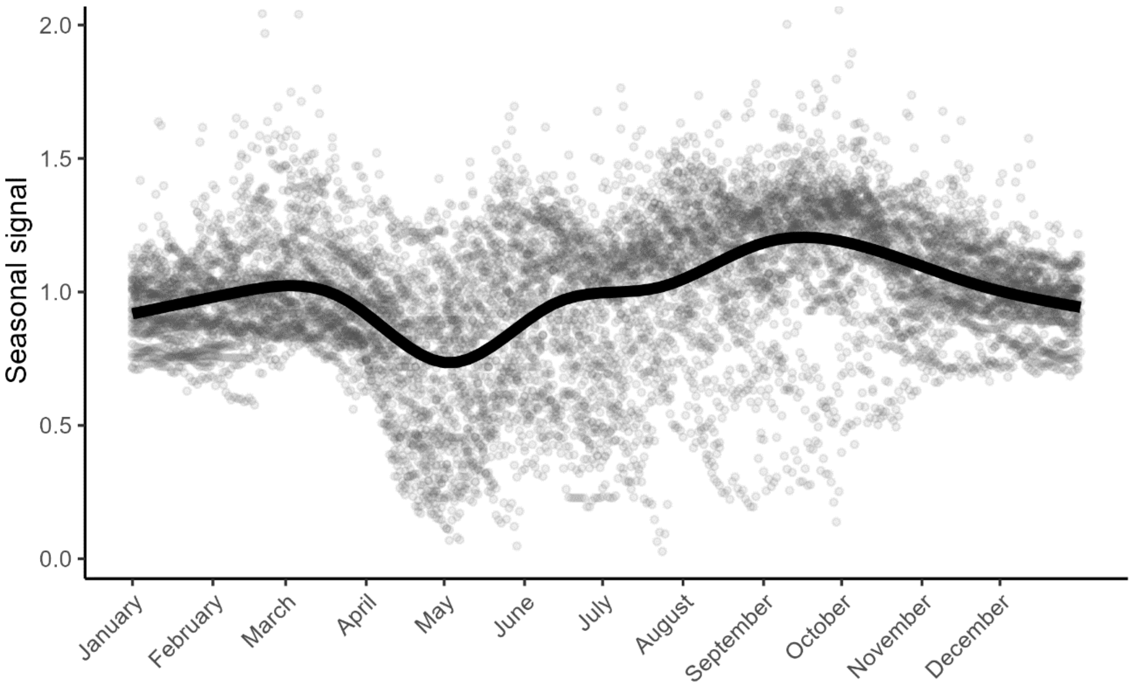

Figure 3.S1. Seasonal signal of discharge in McElmo Creek extracted using discrete fast Fourier transform (Sabo et al. 2008, 2017) with the black line indicating the mean from 1990 - 2022 and points are daily normalized discharge values.

Chapter 4 - Are tributaries for suckers? Growth of an early life stage sucker in desert tributary and mainstem habitats

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Abstract

Rivers in the American Southwest face multiple human-caused pressures, including flow alteration, non-native species introduction, and climate change, leading to negative impacts on native fish. Tributaries provide habitat diversity and environmental asynchrony within river networks, but the tradeoffs associated with the use of these habitats by early life stage fish are unknown. We examined the growth of early life stage flannelmouth sucker (*Catostomus latipinnis*) observationally through periodic seining and experimentally using enclosures in mainstem and tributary habitats. Differences in size structure among habitats depended upon year and environmental conditions with larger juveniles captured in the mainstem compared to tributaries in 2021 and the opposite pattern of larger individuals in the tributary in 2023. However, fish grew more in mainstem enclosures in 2023, perhaps due to the negative impacts of abundant non-native crayfish at tributary sites. Spawning occurred earlier in the tributary than the mainstem in 2022 and 2023. Variation in experience during early life stages between tributary and mainstem habitats, and among years supports the idea that tributary spawning acts as a population-level bet-hedging strategy. Partial migration to tributaries for spawning may contribute to the persistence of flannelmouth sucker in altered rivers, but future water

development and increased abundance of non-native species homogenize stream networks and lessen the advantage multiple spawning locations.

Introduction

Many rivers are highly modified ecosystems (Poff and Zimmerman 2010) subjected to flow alteration, species introductions, and climate change (Reid et al. 2019) with impacts accumulating through the stream network (McCluney et al. 2014, Bouska et al. 2023). Continued water development and multidecadal megadrought further stress desert streams of the American Southwest (Baker et al. 2004, Williams et al. 2020), increasing native fish conservation challenges (Gido et al. 2023). Most large-river fish in the American Southwest have state or federal listings from ‘species of concern’ to ‘endangered’, some of which have minimal to no natural recruitment due to environmental degradation, habitat fragmentation, and invasive species interactions (Bestgen et al. 2006, Maloney 2017, Pennock et al. 2019, Farrington et al. 2023). The early life stages of fish represent a critical period of development, growth, and high mortality rates, with slower growth rates resulting in increased time in this vulnerable life stage (Bestgen 2008). Prescribing management strategies to improve the recruitment of juvenile native fishes remains elusive.

The availability of habitat supporting early life stages may be limiting the recruitment of native fish (Clarkson et al. 2005, Bestgen 2008, Humphries et al. 2020). Larvae of large-river fish are often associated with low-velocity habitats, such as backwaters and secondary channels (Gido and Propst 1999, Carman 2007, Maloney 2017). Flow regulation and modifications to the riparian community can lead to channelization, minimizing low-velocity habitats and reducing nutrient flow and macroinvertebrate diversity in edge habitats (Dudley and Platania 2007, Kennedy and Turner 2011), while increasing drifting distances of larval fish (Robinson et al. 1998). The creation of low-velocity spawning and rearing habitat has been a focus of conservation efforts in the Colorado River basin (Minckley et al. 2003, Speas et al. 2017, Gori et al. 2020). Among low-velocity areas, variations in habitat characteristics such as temperature (Clarkson and Childs 2000, Bestgen 2008), biotic interactions (Carpenter 2005), and food resources (Papoulias and Minckley 1992) can result in differential rates of growth and survival among young fishes.

Tributary confluence areas can provide consistently available low-velocity habitats and high abundances of larval fish (Clark Barkalow et al. 2020). Unregulated tributaries with natural flow regimes can also provide substrates with more interstitial space for protolarvae (Rice et al. 2001, Compton 2007), refuge from predation or competition during spawning and early life (Jeffres et al. 2006, Ellsworth and VanderKooi 2011, Cathcart et al. 2019a, Dyer and Brewer 2020) or may be an area rich in food and energy resources (Humphries et al. 2020). Moreover, tributaries themselves provide larval habitat (Cathcart et al. 2019a) and may be less degraded and easier to conserve than mainstem rivers because of smaller watershed sizes (Bouska et al. 2023) yet tributaries are often excluded from critical habitat designations for large-river fish (Bottcher et al. 2013). Fragmentation by dams and other infrastructure (Whipple 2007, Flanigan and Haas 2008), landcover change, and water extraction can all have large negative impacts in these smaller watersheds (Udall 2020). Tributaries represent critical habitat for desert fish, with different roles throughout their life (Schlosser 1995; Laub et al. 2018; Cathcart et al. 2019b, 2019a; Bouska et al. 2023). Several species of large-river fish migrate to tributaries for spawning either occasionally or with high site fidelity (Webber et al. 2013, Fraser et al. 2017, Cathcart et al. 2019a, Hooley-Underwood et al. 2019, Bonjour et al. 2023). Migration for spawning limits intraspecific interactions between adults and early life stage fish but site selection can impact growth, survival, and recruitment of offspring; even upstream migration distance within a tributary can affect growth rates (Cathcart et al. 2019a). Differences in flow (Poff et al. 2007) and temperature regimes (Sabo et al. 2012) across the river network allow for differences in the timing of spawning, with implications for the growth and survival of larvae (Donahue et al. 2015, Bouska et al. 2023).

The partial migration of spawning of flannelmouth sucker (*Catostomus latipinnis*) in which some fraction of the population spawns in mainstem rivers and the other fraction spawns in tributaries provides an opportunity to compare size structure and growth rates of early life stage fish between these habitats. We know thousands of flannelmouth suckers use McElmo Creek, a tributary to the San Juan River, for spawning with high fidelity (Cathcart et al. 2015, 2018, 2019a; Bonjour et al. 2023), but there is uncertainty in the trade-offs for larval fish growth and survival between mainstem and tributary habitats. Our three objectives were to: 1) quantify the distribution and size structure of early life stage flannelmouth sucker in tributary and mainstem habitats, 2) experimentally test for differences in growth between tributary and mainstem habitats using enclosures, and 3) contrast larval fish production in tributary and mainstem habitats. Observational and experimental data were both considered as they examine different aspects of early life stage experience. We also collected physical and biotic data from these habitats to consider potential advantages and disadvantages of being spawned in a tributary.

Methods

The San Juan River (Figure 4.1) drains approximately 98,400 km^2 of Colorado, New Mexico, Utah, and Arizona. Flow is primarily regulated by Navajo Dam and augmented by downstream additions from melting snowpack in the spring and early summer and by monsoon activity in late summer. Flow regulation, reduced sediment loading, and invasion by saltcedar (*Tamarix* spp.) and Russian olive (*Elaeagnus angustifolia*) have resulted in channelization of the river and armored banks (Bliesner and Lamarra 2000, Nagler et al. 2011, Cheek 2019). Restoration projects along the San Juan River have focused on creating more habitat for larvae of endangered fish species (secondary channel restoration at rkm 220 built in 2011 [Lamarra et al. 2017] and a wetland refuge at rkm 172 built in 2020 [Gori et al. 2020]), but these areas may also provide habitat for non-native fish (Franssen et al. 2015). Flow regimes of the San Juan River tributaries are generally less altered, although still modified. The creation of McPhee Reservoir and associated water projects have contributed to more continuous flow in McElmo Creek, with occasional fragmentation into isolated pools during summer months. It is one of only a few such tributaries joining the San Juan River downstream of Navajo Dam. This tributary supports the spring spawning of thousands of flannelmouth suckers (Cathcart et al. 2015, 2019a; Bonjour et al. 2023).

Discharge and temperature data

Mean daily discharge was obtained from U.S. Geological Survey (USGS) gaging sites on the San Juan River (USGS gaging station 09379500; USGS 2022) and in McElmo Creek (USGS gaging station 09372000; USGS 2022b) using the ‘importDV’ function in package *waterData* (Ryberg and Vecchia 2017). Water temperature for the San Juan River was obtained in the same manner. McElmo Creek water temperature was monitored using a HOBO pendant logger

(HOBO model: UA-002-64; Onset Computer Corp., Bourne, Massachusetts, USA) that recorded temperatures every 30 minutes and was anchored in a pool at site T2 (Figure 4.1). Temperature and discharge were plotted to visually assess differences between the tributary and mainstem. Flannelmouth sucker spawning migration timing was determined from detections of adult suckers on a passive integrated transponder antenna array in the tributary (data downloaded from (STReaMS 2023, accessed 07 August 2023).

Fish sampling to quantify distribution and size structure of larval suckers

Three sites were established in each the San Juan River and McElmo Creek for regular juvenile sucker sampling (Figure 4.1). Early life stage fish were sampled by periodically seining (1.6-mm mesh, 1.2 x 2.4-m) low-velocity habitats in late spring to early summer of 2021 and 2023. Suckers were preserved in 95% ethanol for laboratory processing. Larval and juvenile suckers were measured and identified (Snyder and Muth 2004). Lengths were compared between reaches (tributary versus mainstem) separately in 2021 and 2023. The variability across sites and for sites during a specific sampling week were addressed as random effects using ‘lmer’ in package *lme4* (Bates et al. 2015). We compared models including sample week as a fixed effect against models including reach, sample week, and an interaction between reach and sample week using likelihood ratio tests.

Growth of larval fish in tributary and mainstem enclosures

We constructed enclosures from 35.6 x 35.6-cm black wire grid panels connected by cable ties to form a 62.8 x 35.6-cm frame. The frames were encased in a polyester utility mesh fabric (5-mm). Fish were collected via seining at each site and handled minimally during measuring for standard length before being placed in enclosures. Enclosures were stocked with six juvenile suckers (2021: mean SL = 27 mm, range = 25 – 30 mm; 2023: mean SL = 35 mm, range= 30 – 42 mm) and six cobbles for cover and invertebrate sampling before being secured in a low-velocity area of the stream using rebar. Cobbles placed in enclosures were also collected from the stream at each individual site. Five enclosures were deployed at three tributary and three mainstem sites (only two mainstem sites were used in 2023 due to our inability to find juvenile suckers during setup). At each site, three sets of six cobbles each were also placed outside of the enclosures. Enclosures were checked every one to three days to ensure they remained in low-velocity habitat that would not dry during daily fluctuations in discharge. If warranted, enclosures were carefully moved to a more appropriate location within a few meters, often <1 m, of the original location. Temperature, dissolved oxygen, and water depth were periodically measured at each enclosure (data not presented). Enclosures were deployed for 15 days in 2021 beginning 01 June and 28 days in 2023 beginning 05 July. No enclosures were deployed at site M1 in 2023 because insufficient juvenile fish were captured at the site to initiate the experiment.

Fish from the enclosures were measured and preserved in 95% ethanol at the end of the experiment. Three low-velocity habitats at each site were sampled using a larval seine (2.4-m x 1.2-m, 1.6-mm mesh) to quantify the macroconsumer assemblage. Animals from the three hauls were combined, identified, measured, and released. In the lab, preserved suckers from the enclosures were identified (Snyder and Muth 2004) and measured. Daily growth rates of enclosure fish were determined as the difference in average beginning length and final length divided by the experiment length (16 days in 2021 and 29 days in 2023). Growth rates between the tributary and mainstem were analyzed with mixed effects linear models with site as a random variable. Variation in macroconsumer assemblage structure was assessed based on abundance using the Bray-Curtis dissimilarity index (Bray and Curtis 1957). Assemblages were visually inspected using two-dimensional non-metric multidimensional scaling (‘metaMDS’ in package *vegan*, Oksanen et al. 2022). Analysis of similarity (‘anosim’) was used to determine if assemblages differ between tributary and mainstem or between years and multi-level pattern analysis was used to determine the relative contribution of species to differences (‘multipatt’ in package *indicspecies* De Caceres and Legendre 2009).

Larval fish production in tributary and mainstem habitats

Larval fish were sampled in 2022 with drift nets to contrast the production of larval fish from McElmo Creek and the San Juan River and examine spawning chronology. Nets were set 50-300 m above the confluence during the spring of 2022. A drift net (30.5 cm x 30.5 cm, 500 µm mesh) was deployed at each site such that the top of the net was just below the water surface unless water depth was < 30 cm. Set times were dependent upon discharge and turbidity with nets pulled when organic matter filled the sample bottle to prevent backflow. Velocity was measured at three points across the opening of the net at the start of each deployment and at the end if the set length exceeded one hour. Net position relative to the channel, conductivity, and temperature were also recorded at the start of each deployment. At the end of the deployment, the contents from the drift net were transferred to a 500-µm sieve and rinsed before being transferred to a plastic sample bottle. Samples were kept refrigerated until being sorted (within 48 hours). Larval fish were measured and preserved in 95% ethanol. Two other sucker species, razorback sucker (*Xyrauchen texanus*) and bluehead sucker (*C. discobolus*), are sympatric with flannelmouth sucker and were not differentiated; however, flannelmouth sucker is the first catostomid to spawn (Clark Barkalow et al. 2020) and were most numerous in this reach during our sampling period (Farrington et al. 2023).

Drift densities were calculated as the number of larval fish per 1,000 m^3 of water filtered through the drift net. Set length, mean velocity, depth of water at the net entrance, and a net width of 30.5 cm were used to estimate the volume of water filtered during each deployment. Peak production rates from the tributary and mainstem were estimated by calculating the fraction of the river filtered through the drift nets and extrapolating the rate of fish collected in the drift net over an hour. This estimate assumes homogeneous concentrations of drifting larvae across the river, which is likely not the case (Robinson et al. 1998).

Results

Discharge and temperature data

Temperature and flow regimes were notably different in 2023 than in 2021 or 2022. Increased discharge from snowmelt runoff occurred in the mainstem after the McElmo Creek spawning migration in 2021 and 2022 but was larger and began during the migration event in 2023 (Figure 4.2 bottom). Similarly, discharge remained near baseflow (<1 cms) in McElmo Creek through the spawning migration and early summer in 2021 and 2022, but mean daily discharge peaked at 16.8 cms on 23 March 2023. Temperatures in the tributary and mainstem remained similar in 2021 and 2022 (Figure 4.2 top), but McElmo Creek was initially cooler than the mainstem during the 2023 spawning migration, and then 3-4 ˚C warmer from late May to mid-June.

Fish sampling to quantify distribution and size structure of larval suckers

Juvenile sucker length exhibited an interaction between site and sampling week in both tributary and mainstem habitats. Reach affected juvenile sucker length in 2021 ($\chi^2 = 28.40$, df = 2, $p < 0.001$), with lengths 4.2 ± 1.4 SE mm longer in McElmo Creek than in the mainstem

(Figure 4.3A). Fish grew 0.54 mm/day (total length, calculated from change in average length between sample events), but interactions between sampling week and reach resulted in noticeable differences in lengths by week 9, when juvenile suckers in the mainstem were 12.4 mm larger than those in the tributary ($t = 8.02$, $df = 42$, $p < 0.001$). The interaction of reach and sampling week also affected juvenile sucker length in 2023 ($\chi^2 = 17.76$, $df = 2$, $p < 0.001$, Figure 4.3B). Tributary fish were 14.3 mm larger than those in the mainstem ($t = 5.17$, $df = 34$, $p < 0.001$) by the sampling event during week 10.

Growth of larval fish in tributary and mainstem enclosures

Survival of juvenile suckers in enclosures was low (20% ± 3% SE fish per enclosure) and did not differ between years, reaches, or an interaction of the year and reach ($p > 0.1$ for all). Enclosures that were lost or dried were excluded from consideration in survival. Growth rates based on otoliths from 2021 fish in enclosures averaged 0.08 ± 0.03 SE mm/day and rates did not differ between tributary and mainstem habitats (Figure 4.5A, $\chi^2 = 1.68$, $df = 1$, $p = 0.19$). Fish grew an average of 0.22 ± 0.05 SE mm/day during the 2023 enclosure experiment, but the mainstem fish grew more than tributary fish (Figure 4.5B, 0.41 ± 0.05 SE mm/day, $\chi^2 = 13.37$, $df = 1$, $p < 0.001$).

Small non-native macroconsumers (crayfish, catfish, and killifish) could enter the enclosures through the mesh (Figure 4.6). Crayfish were abundant in tributary enclosures, particularly in 2021 (Figure 4.6). Crayfish were absent from the mainstem enclosures in 2023, while catfish were only present in 2023 and only in the mainstem. Macroconsumer assemblages sampled at each site reflected the pattern within the enclosures (Figure 4.7), with crayfish driving the separation between tributary and mainstem (ANOSIM $R = 0.392$, $p = 0.015$, crayfish $p =$

0.006). Assemblages also differed between years (ANOSIM R = 0.421, p = 0.009), with suckers more abundant in 2021 (p = 0.007).

Larval fish production in tributary and mainstem habitats

Drift nets were deployed for 44 sampling events (Figure 4.4C). Net set durations ranged from 30 minutes to 15 hours (average of nine hours) in McElmo Creek depending upon flow rates and debris build-up, and from nine minutes to 1.5 hours (average of 30 minutes) in the mainstem. Larval drift peaked on 27 April in McElmo Creek at 936 fish per 1000 m^3 filtered (Figure 4.4A). Very few larval fish were captured from the mainstem (eight total individuals), but the first fish was not detected until 15 May, a week after the last larval fish from McElmo Creek was collected. Suspended organic matter content was greater in the mainstem and increased with discharge ($r^2 = 0.705$, Figure 4.4D). Conductivity was initially similar at tributary and mainstem sites but was much greater in McElmo Creek beginning 14 April (average in tributary = 4834 µS, mainstem = 540 µS, t = 31.96, df = 35.5, p < 0.001, Figure 4.4E). Peak production of larvae in the mainstem was 657 times greater in the mainstem with McElmo Creek peaking at 70 fish per hour and the San Juan River peaking at 45810 fish per hour. Discharge at the peak of production in McElmo Creek was 0.02 cms, 3,096 times less than discharge at the peak of production in the San Juan River (64 cms).

Discussion

Periodically sampled juvenile suckers were larger in the mainstem than tributary following the 2021 spawning season, but this pattern was reversed following the 2023 spawning season (Figure 4.3). These years had vastly different discharge patterns in the mainstem with 2023 being a high-water year that led to cooler water temperatures during late spring and early summer (Figure 4.2). Tributary spawning may be more advantageous in years where spring runoff in the mainstem leads to later warming. Spawning in McElmo Creek, and likely the mainstem, was later in 2023 than in 2021 (Figure 4.2). Some smaller individuals (<20 mm SL) were captured during sample week 10 in the tributary but were relatively more abundant in the mainstem. Tributary and mainstem spawning and larval hatching can occur asynchronously (Figure 4.4A) and are likely controlled by thermal cues (Fraser et al. 2019). These smaller mainstem 2023 individuals may have spawned later and had less growing time or originated further upstream where the water was cooler.

The growth pattern in enclosures in 2023 (mainstem fish growing more, Figure 4.5) did not match the pattern we saw with periodic seining during the same time frame (Figure 4.3B), indicating an enclosure effect or influx of later spawned larvae in the mainstem. Enclosures and nearby low-velocity habitat in the tributary had greater abundances of non-native virile crayfish than mainstem sites (*Orconectes virilis*, Figure 4.6 and Figure 4.7). The 2023 enclosure experiment was carried out over a longer time frame than in 2021, which may have given crayfish more time to have an effect even though abundances were greater during the first year. The invasion of crayfish in McElmo Creek may degrade larval fish habitat as crayfish can limit juvenile flannelmouth sucker growth through competition (Carpenter 2005). Alternatively, the mainstem growth rate of flannelmouth suckers, as determined by size structure from periodic seining, may have been skewed by the influx of small individuals from subsequent spawning events in the mainstem. However, larger individuals were captured at each of the tributary sites than any of the mainstem sites during sampling week 10 (Figure 4.3), suggesting the maximum size was larger in the tributary, supporting the hypothesis of an enclosure effect, likely related to competition with crayfish.

Rapid growth is advantageous for survival through early life stages. Improved feeding ability and predator avoidance associated with size and rapid growth results in greater survival rates for larval fish (Rice et al. 1993, Fitzgerald 2023). Non-native red shiners (*Cyprinella lutrensis*) occur in the same habitats as early life stage flannelmouth suckers (Figure 4.7) and prey on larval sucker (Brandenburg and Gido 1999, Bestgen 2008). Early life stage fish are less vulnerable to predation once they are > 25 mm TL as they exceed predator gape limitations (Bestgen et al. 2006). Similarly, size-related gape limitations in flannelmouth suckers could limit resource acquisition, although Pennock et al. (2019) found that SL of larval flannelmouth suckers did not affect diet richness or isotopic signatures. However, reductions in low-velocity habitat in the San Juan River through changes to river flow regime and bank armoring (Nagler et al. 2011, Franssen et al. 2015) could increase competition and predation in remaining habitats (Pennock et al. 2019).

Spawning chronology and growth of flannelmouth suckers has important implications for their survival, but also might influence interactions with other San Juan River fish. Early life stage suckers provide forage for age-1 Colorado pikeminnow (*Ptychocheilus lucius*), particularly in years with higher spring discharge. In these years, suckers are generally more abundant, within gape limitations of pikeminnow, and red shiners spawn later so are unavailable as prey (Franssen et al. 2007). Predator and competitor abundance and activity peaks in warmer months (Cathcart et al. 2015), so earlier growth can better prepare early life stage suckers for these pressures. Early-spawned suckers might also better withstand changes in the physical and chemical environment. Conductivity increased in McElmo Creek in mid-April 2022 (Figure 4.4E), likely corresponding to irrigation returns. Increased salinity decreases the hatch rate in razorback sucker and the quick shift can negatively impact larvae (Strolberg and Horn 2010).

Additionally, backwaters are an important nursery habitat for early life stage fish, but physiochemical properties in these habitats can degrade in quality throughout the monsoon season (Hansen 2023). Tributary spawning occurred earlier in 2022 (Figure 4.4A) and likely before much of the mainstem spawn in 2023 (Figure 4.3). Fish that are spawned in the tributary also have the option to move into the mainstem if conditions are more desirable there. However, upstream tributary sites tend to have greater growth rates than downstream tributary sites (Figure 4.3, Cathcart et al. 2019a) and enclosures had almost no survival near the confluence (Figure 4.5, site T3). Advantages are normally given to early life stage fish that are larger earlier in the year, through faster growth or longer growth period; thus, spawning location and timing may dictate the success of young of year fish.

Our data support the idea that partial migrations into tributaries might benefit flannelmouth sucker due to interannual variation in juvenile success and tradeoffs between tributary and mainstem habitats. Observational and experimental data addressed different aspects of early life stage experience. Periodic sampling integrates the experience of early life stage fish up until the point of sampling, but the origin of these fish is likely upstream of that site. Conversely, the growth of fish held in enclosures reflects the experience of an individual in a known location, but the enclosure itself might magnify the experience. We could not completely explain variation between enclosure experiments and sampling results, but replicated sampling over additional years could be used to predict conditions favoring rapid growth across habitats.

Tributary spawning likely provides a bet-hedging strategy for large-river fish on a population level (Bouska et al. 2023). Even though the number of fish per hour drifting in the river at peak production was much larger in the mainstem, the density of fish was greater and three weeks earlier in the tributary (Figure 4.4A). Whether tributary spawning in an individual year is the “better choice” may depend on a variety of factors including spring and summer hydrology and temperature, the population dynamics of competitors and predators, and other environmental factors, such as conductivity. Tributary spawning may regularly occur earlier, which could allow for earlier growth out of the most vulnerable life stages. Our study provides information on some of the tradeoffs affecting the growth of early life stage flannelmouth sucker in tributary and mainstem habitats, but the contribution of tributary spawning flannelmouth suckers at the population level is still unknown. Further work examining reproductive output and recruitment to adulthood could elucidate the true value of this tributary. Management actions limiting non-native predators and competitors and preserving connectivity between rivers and their tributaries could benefit native fish including flannelmouth sucker.

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Figures

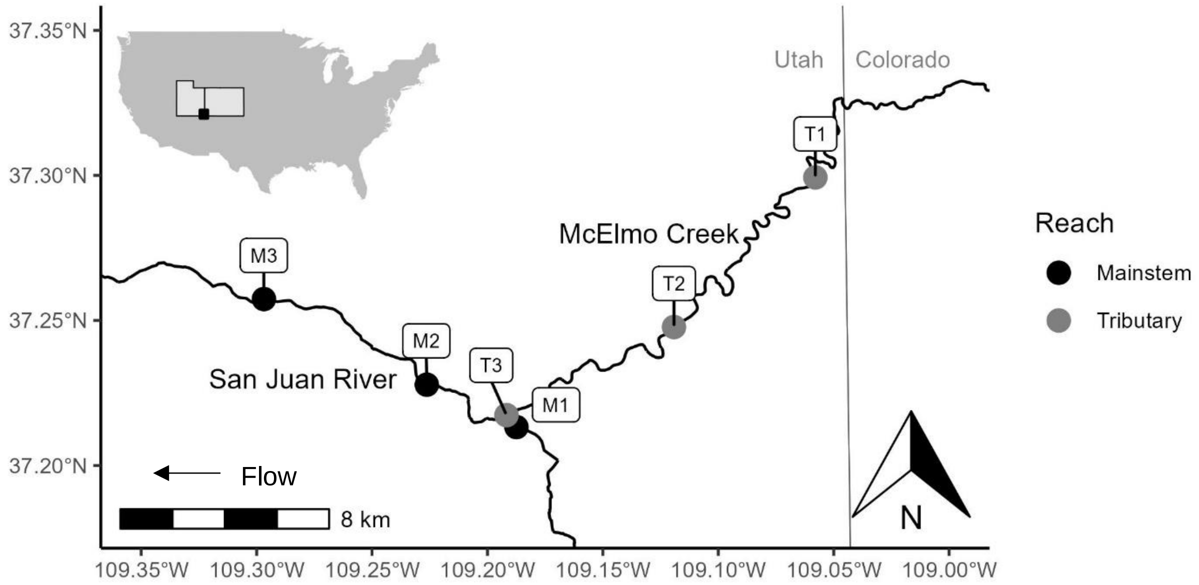

Figure 4.1. Sampling and enclosure locations in McElmo Creek and the San Juan River. Tributary sites are indicated by grey points and mainstem sites are indicated by black points.

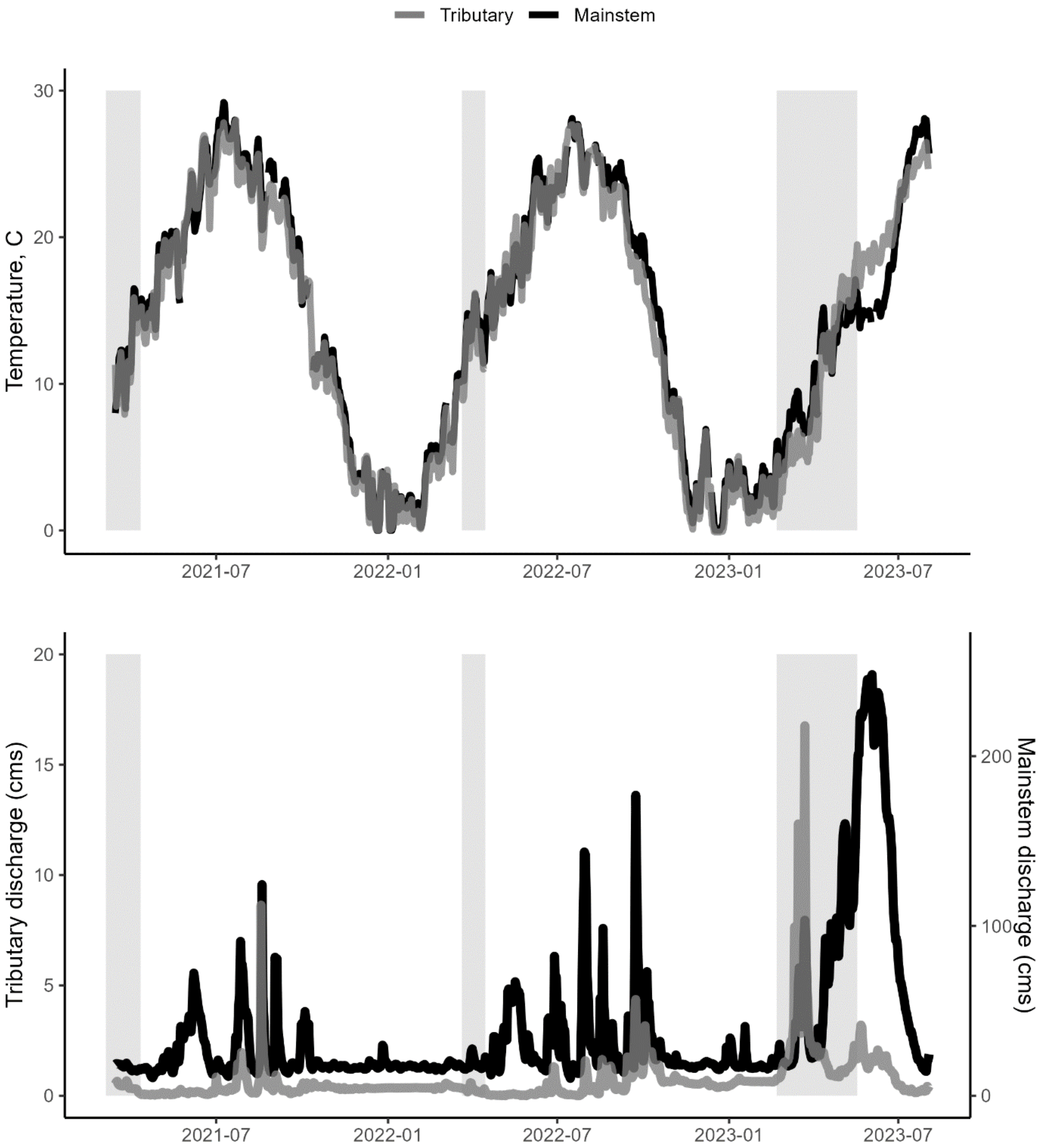

Figure 4.2. Mean daily temperature (top) and discharge (bottom) of McElmo Creek (grey line, U.S. Geological Survey (USGS) gaging station 09372000) and the San Juan River (black line, USGS gaging station 09379500). Light grey boxes indicate period of flannelmouth sucker (*Catostomus latipinnis*) migration into McElmo Creek as determined by passive integrated transponder detections in the tributary (STReaMS, 2023).

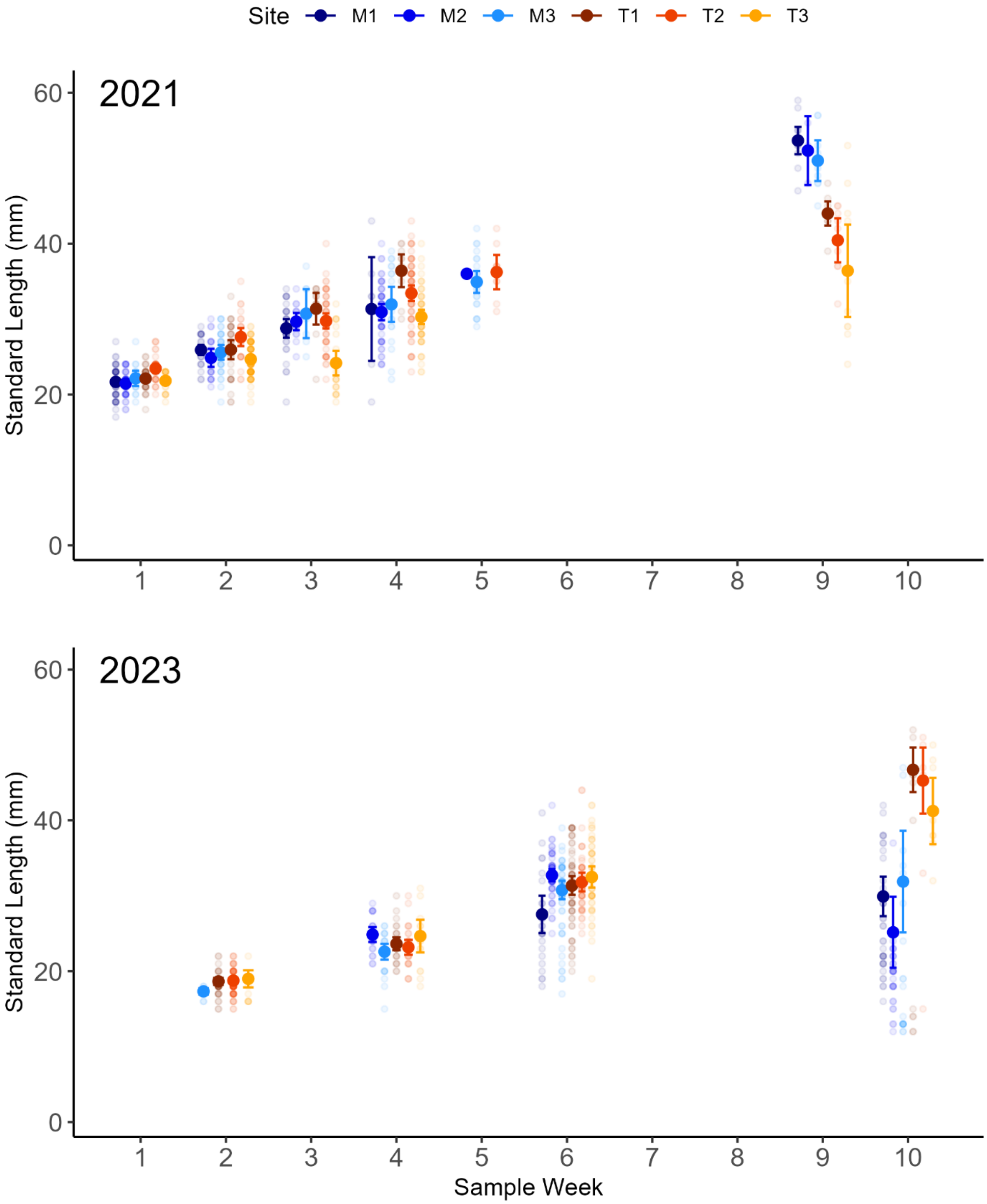

Figure 4.3. Comparison of juvenile flannelmouth suckers (*Catostomus latipinnis*) lengths from fish captured during periodic seining of McElmo Creek (warm colors) and the San Juan River (blues). Solid points show mean length for each site and bars indicate 95% confidence intervals. Individual measurements are indicated as transparent points. Sample week 1 corresponds to the last week of May.

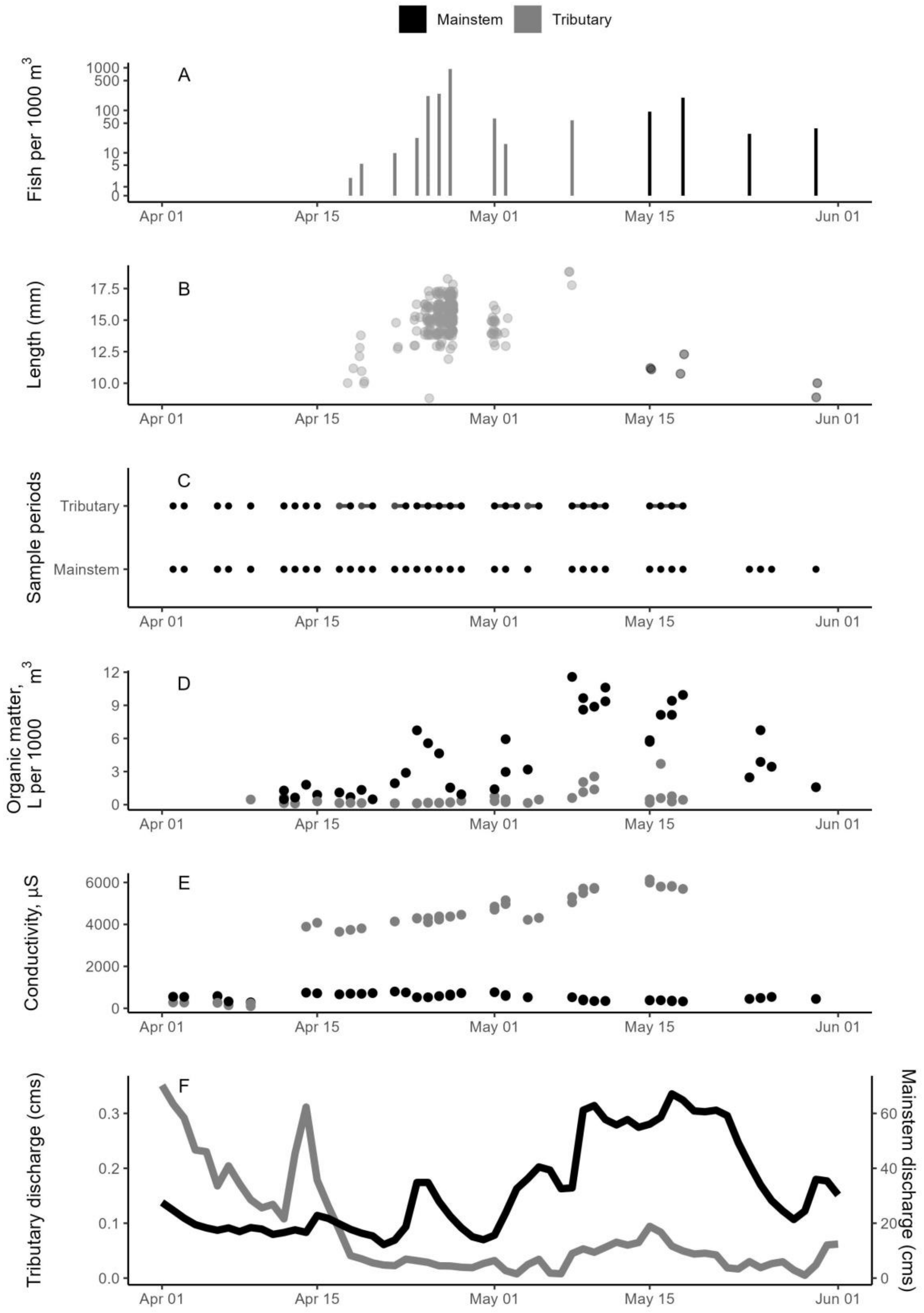

Figure 4.4. Fish and environmental data from drift sampling in 2022. Black indicates data from the San Juan River, grey indicates data from McElmo Creek. A) Number of larval fish captured

per 1000 m^3 of water filtered. B) Total length of larval fish captured in drift nets. C) The timing of drift sampling events. Bars between points indicate multi-hour drift net sets. D) The amount of organic matter captured in drift nets. Values were not recorded for the first four sampling events. E) Conductivity of stream measured at the beginning of drift net deployment. F) Mean daily discharge of McElmo Creek (U.S. Geological Survey (USGS) gaging station 09372000) and the San Juan River (USGS gaging station 09379500) during the study period.

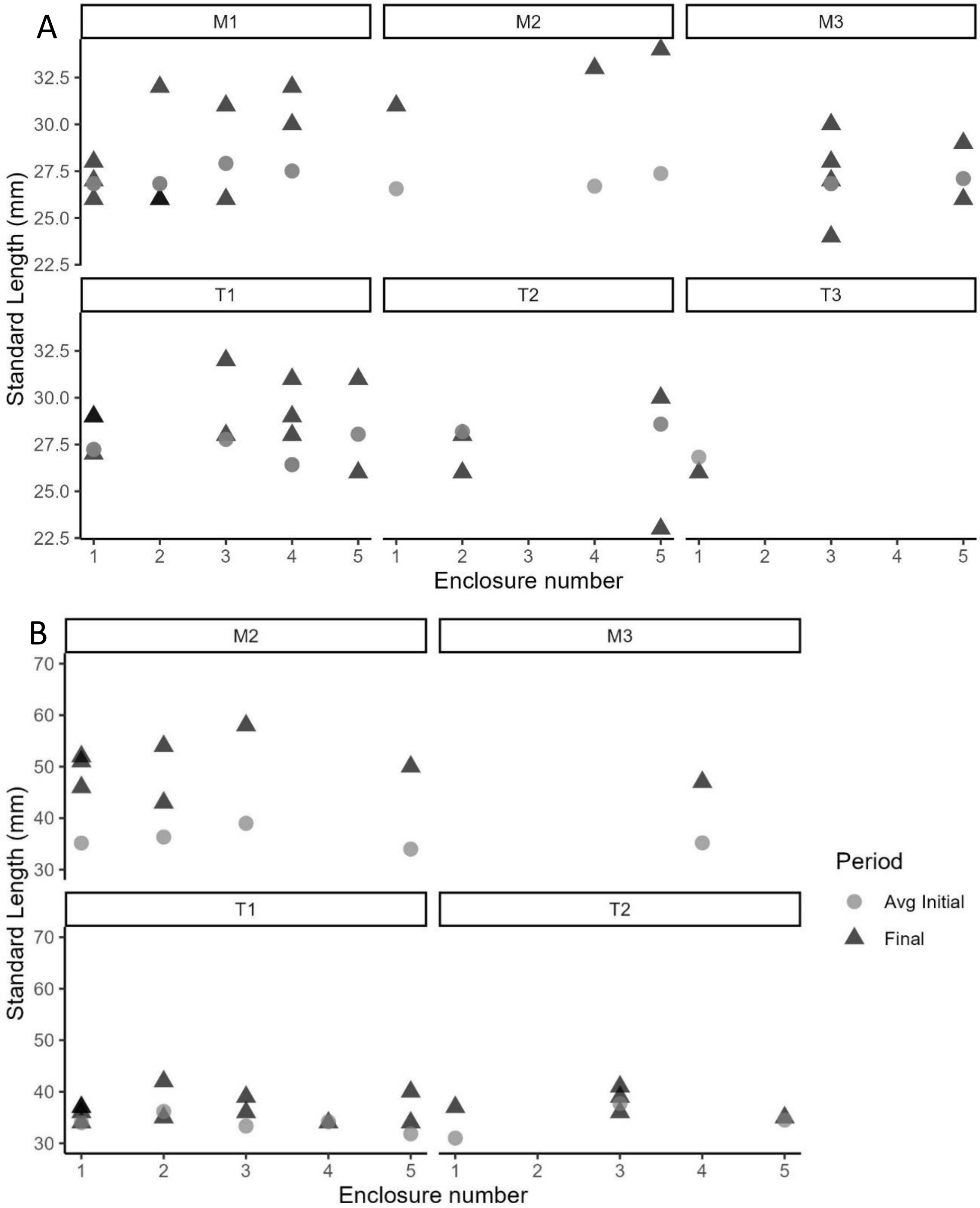

Figure 4.5. Comparison of average initial (grey circle) and final (black triangle) standard length (mm) of surviving fish in the enclosure experiment during A) 2021 and B) 2023. Sites are indicated on the top of each quadrant with mainstem on the top and tributary sites on the bottom. All enclosures at site M3 besides enclosure 4 in 2023 were excluded in survival calculations due to a drying event.

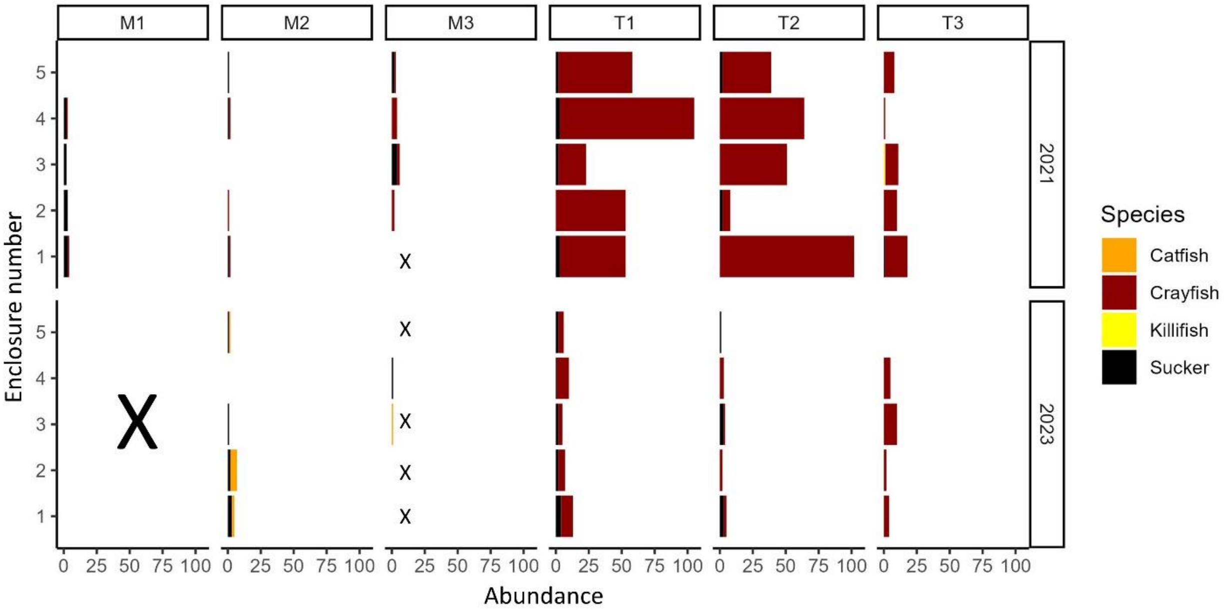

Figure 4.6. Number of macroconsumers present in enclosures at the end of the experiment. Large "X" indicates that site M1 was not initiated in 2023. Small "x" indicates individual enclosures that were lost (2021) or from which survival of flannelmouth sucker (*Catostomus latipinnis*) could not be assessed due to a drying event in the middle of the experiment.

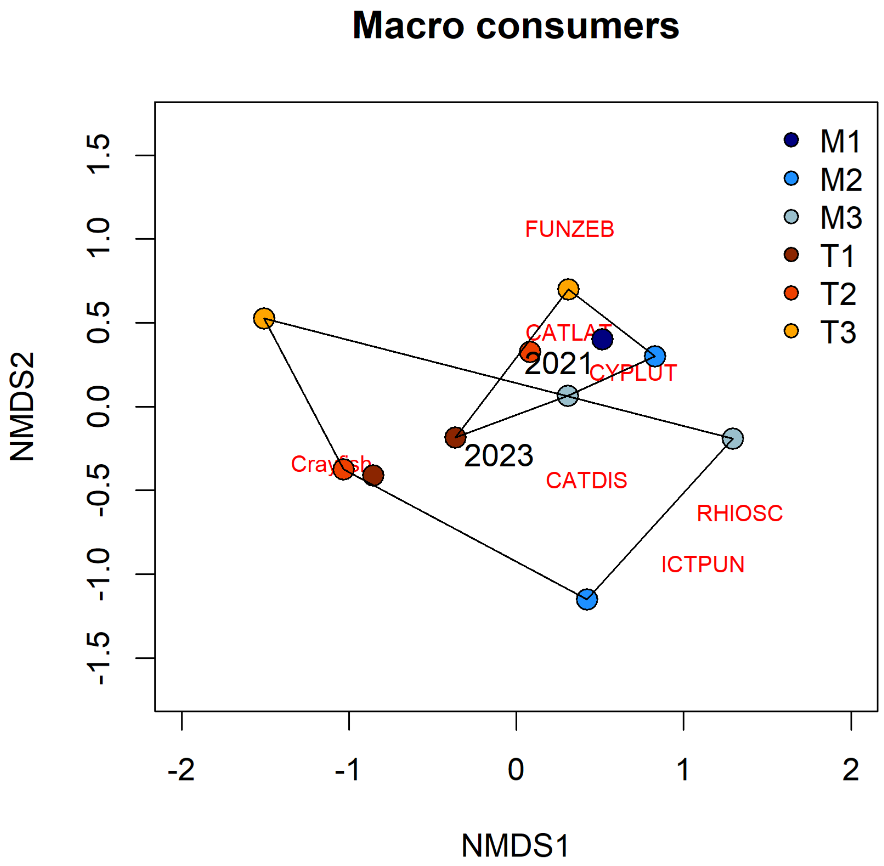

Figure 4.7. Nonmetric multidimensional scaling plot of macroconsumer assemblage sampled at each mainstem (M) and tributary (T) site at the conclusion of the enclosure experiment. Stress = 0.08. Species loadings are indicated by species code: *Catostomus discobolus* (CATDIS), *Catostomus latipinnis* (CATLAT), *Cyprinella lutrensis* (CYPLUT), *Fundulus zebrinus* (FUNZEB), *Ictalurus punctatus* (ICTPUN), and *Rhinichthys osculus* (RHIOSC).

Chapter 5 – Conclusions

Characterizing migration patterns of flannelmouth suckers (*Catostomus latipinnis*) adds to the growing literature regarding the ecology of this Colorado River basin native. Tributary use by spawning flannelmouth sucker has been documented throughout the basin (Weiss et al. 1998; Robinson and Childs 2001; Bower et al. 2008; Cathcart et al. 2015; Fraser et al. 2017; Hooley-Underwood et al. 2019) with varying emphases on habitat, timing, juvenile response, and community. While other works have compared flannelmouth suckers genetically across the basin (Douglas et al. 2003), this is the first study comparing timing and environmental cues for migration across the basin (Chapter 2). Leveraging long-term data allows us to recognize migration patterns and identify potential threats to this life history strategy. Previous studies examining flannelmouth sucker tributary fidelity were limited to three years and estimated lower levels of site fidelity (Fraser et al. 2017; Hooley-Underwood et al. 2019). Use of Cormack-Jolly-Seber models with 10 years of data provides a more robust picture of annual migrations and site fidelity to McElmo Creek (Chapter 3). My attempt at comparing the experience of early life stage fish using both observational and experimental data suggested that interannual variation and the interactions with non-natives influence the success of young of year. Enclosures of young-of-year fish can be difficult to maintain as this life stage has high rates of mortality, but the method used in Chapter 4 allowed us to compare growth of fish contained in one habitat. In Chapters 3 and 4, I focused on McElmo Creek as a tributary of the San Juan River, but additional work will be required to see if our results extend to other tributary systems. Other systems likely have features, such as nearby cooler hypolimnetic releases (Robinson and Childs 2001) or fewer non-natives, that could increase the value of tributary spawning. Conversely, water development in tributaries could lead to the extirpation of flannelmouth sucker (Budy et al. 2015). These features could also drive site fidelity in other systems.

The partial migration of flannelmouth sucker to tributaries for spawning provides an additional case study of the four properties of tributaries (habitat diversity, connectivity, ecological asynchrony, and density dependent processes) identified by Bouska et al. (2023) that support populations of large-river fish. Chapter 2 discussed ecological asynchrony and connectivity as timing of migration was cued by a combination of mainstem and tributary temperature and discharge. Chapter 3 addressed density-dependent processes in the number of fish that return year-after-year together to the tributary. This chapter also highlighted the importance of connectivity making other tributaries available for spawning in wetter years and discontinuity in the system eliminating individuals from the spawning population once they have gone downstream of barriers. Chapter 4 investigated the variation in habitat between McElmo Creek and its mainstem, with juvenile sucker growth being impacted by the density of non-natives, and the asynchrony of spawning time between tributary and mainstem habitats. Connectivity is fundamental for this reproductive strategy of migrating to tributaries for spawning, but the other three properties of habitat diversity, ecological asynchrony, and density-dependent processes are the components that make migration for adults worthwhile. Human alterations that degrade any of these could jeopardize partial migration as a bet-hedging strategy.

Accounting for tributaries may serve as a useful component of conservation plans (Pracheil et al. 2013; Laub et al. 2018; Bouska et al. 2023), but only if further water development is limited (Budy et al. 2015). Human modifications such as water extraction, dam construction, and introduction of non-native species has decreased channel and habitat heterogeneity (Ward and Stanford 1995; Rahel 2002). Ironically, discharge in both McElmo Creek and Roubideau

Creek (Chapter 2) is augmented by irrigation returns that increase the duration of flow during the year. The future of water distribution in the Colorado River basin is unknown with ongoing climate and political issues (Wheeler et al. 2022), and the strain between the need of water for people and water for fish increases (Gido et al. 2023).

The groundwork provided by Cathcart et al. (2015, 2018, 2019) and the research presented here together can help inform management actions and future research. Chapters 2 and 3 would not have been possible without the infrastructure constructed for previous studies and the maintenance of PIT tag antenna arrays since that time. Continued monitoring of tagged individuals throughout the basin and exploration of the data collected by these antenna arrays will contribute to a better understanding of flannelmouth sucker movement and reproductive ecology. Movement between tributary and mainstem habitats is relatively easy to measure by placing an antenna array at the confluence, but more work is needed to quantify the spawning patterns of flannelmouth sucker within the mainstem. The genetic consequences of tributary spawning are another area for further exploration. High site fidelity may or may not lead to a genetically distinct group of tributary spawners, but flannelmouth spawning in tributaries are much less likely to hybridize with razorback sucker (*Xyrauchen texanus*) as few are present in the tributary during that time of year (Cathcart et al. 2015). The importance of sucker hybridization is an ongoing discussion in Colorado River basin (Wolters et al. 2019; Bangs et al. 2020; Schwemm et al. 2020). The temporary movement of thousands of large fish into a tributary may have important ecosystem effects. Additional research into nutrient dynamics (Childress et al. 2014) and scrutiny of the impacts of crayfish in McElmo Creek will provide a clearer picture of the impact of flannelmouth sucker on ecosystem processes.

This dissertation focuses on a species that is not federally listed and is historically viewed as non-charismatic with no economic value (Budy et al. 2015). Few people wax poetic about flannelmouth sucker (but see (Cathcart 2018) and fish migration research has historically been dominated by a focus on salmonids. However, there is a push to include more diverse native species in fish management and conservation plans (Rypel et al. 2021). Desert fish are subject to many stressors that act synergistically, and the severity of those synergisms are likely to increase in the future as water shortages increase, coupled with shifts in regional to global climate (Gido et al. 2023). Research conducted before species are threatened is needed for rapid decision-making regarding conservation actions. Too often we wait until a species is endangered to study it. A quick search of Google Scholar indicates twice as many results for the federally endangered "razorback sucker" as "flannelmouth sucker". Research on flannelmouth sucker can provide a useful comparison for sympatric species without natural recruitment (Pennock et al. 2019) but cannot act as a surrogate. By recognizing the intrinsic value of each species and the interconnectedness of life on Earth, we can make more informed decisions about conservation, management, and research moving forward.

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