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Spawning Locations within and among Tributaries Influence Flannelmouth Sucker Offspring Experience

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Abstract

Migratory fishes often spawn across broad spatial scales to limit intraspecific interactions among mature and immature individuals, leading to long-distance movements of both adults and offspring. Thus, offspring are potentially exposed to a range of environmental conditions throughout their development that affect growth, survival, and recruitment. Migratory suckers (family Catostomidae) can be used to test spatial variation in early life stage experiences for iteroparous fishes. We use the Flannelmouth Sucker *Catostomus latipinnis*, a fish that is endemic to the American Southwest, to illustrate how larval and juvenile stages are affected by the distance of upstream spawning migration in tributaries that vary in flow regime and habitat availability (i.e., perennial versus intermittent streams). Remote detection of PIT-tagged migrating adults indicated that spawning and larval rearing sites were distributed over 32 km within McElmo Creek, a perennial tributary to the San Juan River, Utah. Physical sampling of an upstream intermittent tributary, the Mancos River, New Mexico showed that spawning adults—and then larvae—were restricted to within 1 km of the main-stem river. Quantile regression demonstrated recruitment of larvae to the juvenile stage was significantly (i.e., up to 2 weeks) faster in more upstream reaches of the perennial tributary, potentially due to more constant thermal regimes. Spatial differences in animal community structure at sites with larval Flannelmouth Sucker indicated that the potential for predation and competition was greatest in upstream reaches. Small, rare, and even intermittent tributaries concentrate spawning activity that dictates larval sucker experiences. Conserving, maintaining, and enhancing connectivity via flows synchronized with spawning and rearing are critical steps to protect migratory suckers in arid environments.

Migration is a globally ubiquitous feature of the animal kingdom that is defined as “the geographic [link] of individuals and populations between one life cycle stage and another” (Webster et al. 2002:76) and often involves reproduction (Salomonsen 1955; Bauer et al. 2016). Even so, a general dichotomy between terrestrial (i.e., mammals, birds, and certain amphibians) and fish (and certain reptile) migrations is the degree of parental care provided after migration or birth (e.g., Winemiller and Rose 1992;

Farmer 2000; Webb et al. 2002; Jonsen et al. 2006). Many mammal and bird migrations must benefit adults, their offspring, and populations via site selection according to resource availability that accommodates individuals of various life stages (Post and Forchhammer 2008; Bauer et al. 2016). Alternatively, freshwater fish migrations, while often evolutionarily honed to promote fitness, invoke a “spray-and-pray” approach at terminal habitats where, after spawning, adults die (e.g., Pacific salmon

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Oncorhynchus spp.) or leave immediately and the offspring (or embryos)—along with their population's future—remain (Lucas and Baras 2001; McIntyre et al. 2016). Consequently, responses by early life stages and population dynamics of migratory fishes are strongly dependent on spawning site selection that can variably affect growth, survival, and recruitment of offspring.

Responses of freshwater fishes to heterogeneity in freshwater river networks include spatially structured cohorts of early life stages (Foldvik et al. 2010), populations (Salisbury et al. 2016; Spurgeon et al. 2018), processes such as spawning (Torgersen et al. 1999), and communities (Osborne and Wiley 1992; Fernandes et al. 2004). This spatial structuring is particularly important for species with complex life cycles that rely on different habitats according to life cycle stage, thus contributing to their inter- and intraspecific interactions, such as predation, competition, and density (Borcard et al. 2004; Falke and Fausch 2010). For example, juvenile semelparous and iteroparous fish in coastal and inland river networks are influenced by spatial variation among habitats according to longitudinal distance upstream, temperature, flow patterns, or spawning location (Marschall et al. 2011; Roni et al. 2012; Falke et al. 2013; Lopes et al. 2019). Moreover, corridors connecting spatially structured populations have been compromised by dams or diversions, leading to diminished survival of juveniles or failure to access spawning habitats by adults (Marschall et al. 2011; Lopes et al. 2019). This suggests that connectivity and increased available river habitat can benefit spatially structured populations.

Suckers (Catostomidae) provide a useful model to explore how complex migratory life histories exploit heterogeneous freshwater habitats to promote offspring survival through increased growth. Many catostomid species are large bodied and long-lived and make annual spawning migrations. For example, suckers place offspring in a range of habitats via individual variation in spawning migrations that can occur between or within main-stem and tributary habitats of varying flow regimes (Weiss et al. 1998; Bunt and Cooke 2001; Catalano and Bozek 2015), between lakes or reservoirs and tributaries (Olson and Scidmore 1963; Cooperman and Markle 2003; Childress and McIntyre 2015; Albrecht et al. 2018), and within lakes (Burdick et al. 2015) or reservoirs (Albrecht et al. 2010). Many species contribute to ecosystem functions such as nutrient cycling (Childress et al. 2014; Childress and McIntyre 2015), are highly imperiled (Cooke et al. 2005), and can exhibit population-level migratory homing behavior (Olson and Scidmore 1963; Werner and Lannoo 1994; Neely et al. 2009). In the Colorado River basin, the endemic Flannelmouth Sucker *Catostomus latipinnis* is known for its annual migrations from main-stem habitats in the Grand Canyon (Weiss et al. 1998), San Juan River (Cathcart et al. 2015, 2018), and upper Colorado River

(Fraser et al. 2017) into tributaries where, once there, they may swim over 30 km upstream to spawning grounds. Despite an understanding of their migratory patterns and conservation need, many suckers, including the Flannelmouth Sucker, have not been well studied relative to spatial and environmental drivers of populations—especially early life stages in field settings (Fraser et al. 2019; Hookey-Underwood et al. 2019). Given the limited availability of tributary habitats, testing the effects of variation in tributary conditions on offspring experience is a crucial next step in identifying habitat needs and understanding population processes of migratory sucker species in arid landscapes.

We formed four hypotheses to test our overarching objective to determine whether rearing habitat experienced by larval Flannelmouth Sucker was dependent on migration distance in two tributaries that vary in flow regime (i.e., perennial flow versus intermittency) and habitat upstream from a main-stem river. First, we hypothesized that the intermittent stream would have restricted spawning and rearing habitat compared to the perennial stream. Second, we hypothesized that downstream habitats would have earlier hatch dates (potentially from earlier arriving and earlier spawning adults) and larvae with larger sizes at age than upstream locations due to warmer water temperatures closer to the main-stem river. Accordingly, we hypothesized that larvae in downstream reaches would recruit to the juvenile stage at younger ages. Third, we hypothesized that differences in size at age between sampling periods would be largest during earlier sampling periods, as larval growth rates would be highest at first but decrease as they age. Fourth, we hypothesized that the distributions of larval Flannelmouth Sucker and their potential competitors or predators (i.e., native and nonnative fishes, amphibians, crustaceans, and insects that share habitats with larval Flannelmouth Sucker) would seasonally co-occur with a more diverse community at upstream reaches depending on longitudinal differences in habitat or environmental conditions. We based this prediction on prior work in our study system, which showed that seasonal fish communities in tributaries differed according to distance from the main-stem river and had increased diversity at the upstream-most reach (Cathcart et al. 2015), as well as studies that implicated nonnative animals in the declines of Southwest native fishes through interactions such as predation on larval fish (e.g., Ruppert et al. 1993; Brandenburg and Gido 1999; Mueller et al. 2006). To test our four hypotheses, we first measured the abundance and distribution of spawning adults via remote monitoring of tagged individuals in the perennial tributary and physical sampling in the intermittent tributary. We then sought to quantify the postemergence size at age of larval stages, critical periods of recruitment to the juvenile stage, and community associations of larval Flannelmouth

Sucker relative to spatial variation in rearing habitats distributed upstream from a main-stem river.

METHODS

Target species.—The Flannelmouth Sucker has declined throughout its range, but compared to other regional endemics it has relatively stable populations throughout approximately half of its historical range in the Colorado River basin (Budy et al. 2015). The spring migrations of Flannelmouth Sucker are characterized by the annual homing of adults to tributaries, where they spawn during base flow conditions prior to snowmelt runoff flows of the main-stem rivers (Cathcart et al. 2018). Apparent threats to the persistence or resilience of Flannelmouth Sucker populations include hybridization with White Sucker *Catostomus commersonii* (McDonald et al. 2008); altered stream connectivity from water development, such as dams or irrigation-mediated dewatering (Chart and Bergersen 1992); and competition with or predation by nonnative animals (Marsh and Douglas 1997; Carpenter 2005).

Study area.—The San Juan River basin encompasses a watershed over 99,000 km² across portions of Colorado, New Mexico, Arizona, and Utah. Tributaries are rare (about 1 for every 60 km of the San Juan River) and often intermittent. Two tributaries with the ability to support or attract fish in the San Juan River basin are McElmo Creek (perennial) and the now-intermittent Mancos River (Figure 1). McElmo Creek drains 1,818 km² in Colorado and Utah and includes one small perennial tributary (Yellow Jacket

Creek) that joins near the border of the two states about 32 km upstream from the San Juan River. A U.S. Geological Survey (USGS) gauge (09372000) is located upstream of our study reaches in McElmo Creek. This system is only perennial due to irrigation runoff and has a base flow of about 0.57 m³/s (Cathcart et al. 2015). McElmo Creek enters the San Juan River near Aneth, Utah, about 34 km downstream of the Mancos River mouth. The Mancos River drains over 2,075 km² and was likely perennial historically but is now often disconnected due to the approximately 50 diversions and reservoirs created since 1876 that capture or repurpose over 4,900 hectare-meters of water per year (Stacey 2007). We established intermittency based on ground-truths linked to USGS gauge data in 2015; connectivity between the Mancos and San Juan rivers is maintained when Mancos River flows exceed 0.28 m³/s at USGS gauge 09371000.

In 2015, we sampled 10 sites within five distinct geomorphic reaches across the two study streams. We classified nine McElmo Creek sites into four distinct geomorphological reaches of the tributary system based on differences illustrated by Cathcart et al. (2015): the mouth (0–0.3 km upstream of the San Juan River); floodplain (1.7–7.1 km upstream); oilfield canyon (24–27 km upstream); and headwater tributary confluence zone, where Yellow Jacket Creek enters McElmo Creek (32–32.6 km upstream). Extensive upstream migrations of adult Flannelmouth Sucker—and thus our sampling—were restricted by intermittency in the Mancos River. Although we sampled over 1 km of the Mancos River upstream from the San Juan River (and

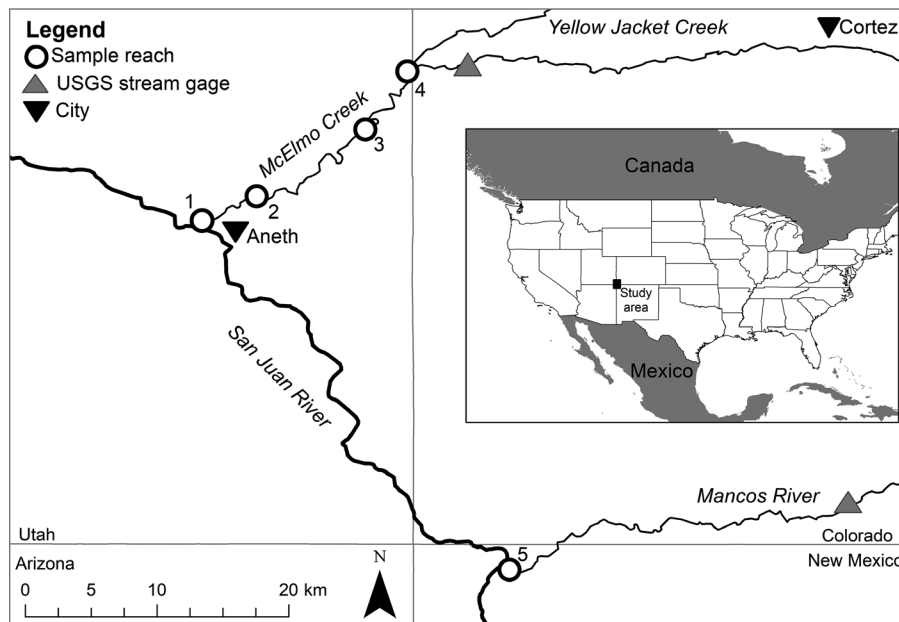


FIGURE 1. Study area map, showing the reaches sampled for larval Flannelmouth Sucker in McElmo Creek (1 = mouth; 2 = floodplain; 3 = oilfield canyon; 4 = headwater) and the Mancos River (5). Locations of U.S. Geological Survey (USGS) stream gauges are also shown.

found ripe adult Flannelmouth Sucker 0.2–1.06 km upstream), larval fish were only found in three pools between 0.2 and 0.4 km upstream from the San Juan River confluence. These pools were located upstream of two riffles (each exceeding 30 m) that separated the confluence zone (low-velocity, fine-substrate backwater habitat) from typical stream habitat (higher velocity habitat with coarser substrates).

Spawning locations.—Adult Flannelmouth Sucker (>300 mm) had been PIT-tagged previously in McElmo Creek and the San Juan River as well as detected at their confluence with a permanent stationary antenna (Cathcart et al. 2015, 2018). In 2015, we added eight additional PIT antennas distributed throughout the creek according to sites within the distinct reaches. Migration data were collected from February 2 to April 10, 2015, although most of the upstream migration had finished by March 26. Data used were restricted to remotely detected adults that were tagged prior to 2015; this was done to avoid potential bias from including locations of physically captured fish that, due to variation in spawning condition (i.e., presence or absence of freely flowing gametes), had not yet chosen their spawning site. Overall, the number of tagged fish was 2,645 adults exceeding 300 mm TL at tagging. Tagged fish smaller than 300 mm were excluded due to possible sexual immaturity. We identified the upstream-most antenna at which each individual fish was detected, signifying that their spawning site was at or upstream of that location. Because three antennas in the headwater reach were separated by less than 100 m, we pooled their detections.

The Mancos River reach was remote, lacked prior tagging efforts, and intermittent, so we determined that physical sampling would suffice to establish adult spawning distribution in its wetted reach. We used backpack electrofishing (Smith-Root LR-24 electrofisher) with two netters to sample adult Flannelmouth Sucker (>300 mm TL) in pool habitats. On March 9, 2015, we established a sampling reach from the upstream end of the first riffle separating the Mancos River from the confluence zone with the San Juan River to the upstream terminus where intermittency began and adult fish were assumed to not be upstream. This reach included 10 pools. We sampled four times from early March to early May to determine adult spawn timing and seasonal abundance.

Larval sampling, hatch dates, and size at age.—We sampled for larval (<25-mm) and juvenile (>25-mm) Flannelmouth Sucker at 10–19-d intervals in McElmo Creek and the Mancos River between April 10 and June 27, 2015. McElmo Creek samples were taken in 1 d, with the Mancos River being sampled either 1 d before or 1 d after McElmo Creek. Sampling was conducted via seine (1.5 × 2.0 m; 0.3-mm mesh). Seining was performed by one person in hauls averaging about 1 m wide × 2 m long. Sampling at a site was completed once either 15–30 larvae or

juveniles were captured or 10 hauls were achieved. For ease of identification and measurements, all larval or juvenile Flannelmouth Sucker used in size-at-age analysis were fixed in 10% formalin except on the date of first larval captures, when subsamples from each stream were preserved in 95% ethanol to age the otoliths for hatching dates. Larval and early juvenile fish samples were then identified in a laboratory to species and ontogenetic stage and were measured to determine SL. Ontogenetic stage classification followed Snyder and Muth (2004) and included protolarvae (no fin rays; yolk was present or absent); flexion mesolarvae (first caudal fin rays were apparent; yolk was present or absent); postflexion mesolarvae (full complement of caudal fin rays was present); metalarvae (caudal, dorsal, and anal fins all had the full complement of rays); and juveniles (the fin fold was completely absorbed between the pelvic fins and vent).

Establishing reach-specific hatch dates provided a standardized age to test for spatial structure in size at age among geomorphic reaches. Otolith daily growth rings were used to estimate hatch dates from a subsample of around 10 larval Flannelmouth Sucker first collected at each reach. Lapillus otoliths were removed, set in cyanoacrylate glue on microscope slides, immersed in mineral oil, and aged (d) by one reader with a light microscope at 40× magnification. We generated a reach-specific hatch date by using the modal hatch date for each reach.

To test whether the days to recruit from hatching to the juvenile stage differed according to spatial position, we used quantile regression to analyze differences in SL at age of formalin-preserved Flannelmouth Sucker across reaches using the *quantreg* package in R version 3.5.0 (R Development Core Team 2008). We used the 90th quantile regression to test our first (compare size at age among reaches, estimate the time it took for larvae to recruit to the juvenile stage) and second (critical periods of growth) hypotheses. We chose the 90th quantile to represent a reach's growth potential because it can capture the fastest growing fish, whereas the mean might be skewed by the influence of late-spawning adults or slow-growing larvae. We made two guiding assumptions: (1) hatch dates found from April 21 samples were representative of the reach and (2) no movement of larval Flannelmouth Sucker occurred among reaches in McElmo Creek. We used the 90th quantile to first compare size at age among reaches across the entire sampling period and then size at age within sampling periods to determine critical growth periods (indicated by among- and within-reach quantile slopes that differed from each other through time). To test responses for significant differences among each reach, we used 90% confidence intervals generated by the default rank inversion process in the *quantreg* package (Tarr 2012). We interpreted reaches to be significantly different at an age when the 90th quantiles diverged enough for

their confidence intervals to not overlap. From the slopes, we established reach-specific recruitment time as the period (d) it took for individuals to surpass 25 mm SL, a threshold that reduces predation and enhances survival of southwestern sucker species (Bestgen 2008). To compare growth potential to a central tendency of size at age within and among reaches, we compared 90th quantiles to the median quantile slopes per reach and calculated median SL per reach per sampling period along with a median-specific error metric (2.5× the median absolute deviation; Leys et al. 2013).

Longitudinal patterns of habitat and communities.—We tested our fourth hypothesis by analyzing whether longitudinal differences in physical habitat, water temperature, and community members (e.g., co-occurring aquatic animals that may interact with larval sucker) influenced the experience of early life stage Flannemouth Sucker in McElmo Creek. All organisms sampled during larval Flannemouth Sucker seining, including immature forms of aquatic insects (e.g., Odonata) and crayfish, were identified to the lowest possible taxonomic level and released. Larval and juvenile Flannemouth Sucker catch determined effort; thus, the abundance of overlapping species was potentially biased by the variable effort. Furthermore, a larval seine sampling a fixed area is less likely to capture some animals (e.g., large-bodied, highly mobile fishes) that may be able to outmaneuver the net or that may not continuously share habitats with larval fish. However, in the desert Southwest, several small-bodied aquatic species have been implicated in negative responses by larval native fishes that are sensitive to predation or competition. Our field sampling protocol expands on this hypothesis (typically tested under laboratory conditions) by including native community members that may also impart selective pressures on larval Flannemouth Sucker.

Data describing the catch of larval Flannemouth Sucker and the co-occurring community were integrated with environmental variables. Habitat measurements were taken in mid-March, when 10 cross-channel transects equally spaced over 300 m of stream were performed to characterize the reach, including wetted width (m), channel depth (cm; maximum and mean), water velocity, and substrate size. Substrates were ranked on a modified Wentworth scale ranging from 0 to 7 (where 0 = silt, 1 = sandy silt, 2 = sand, 3 = small gravel, 4 = large gravel, 5 = cobble, 6 = boulder, and 7 = bedrock). Within each transect, marginal habitats along banks ($n = 2$ per transect) were measured since they may serve as low-velocity habitats and retain larvae better than mid-channel habitats. Marginal velocity and depths were measured ($n = 20$ points per reach). Flow data were gathered from the McElmo Creek USGS gauge to obtain mean daily flow for the 10–19-d period prior to larval and juvenile sampling events. Water temperature was recorded at each site in McElmo Creek

with a HOBO temperature logger (Onset, Bourne, Massachusetts) that recorded every 15 min between early February and July 27 to encompass spawning, incubation, hatching, and growth. Loggers were placed at each antenna, but we only report data from the upstream-most logger in each reach. We collected the mean, maximum, minimum, and variation (the difference between the maximum and minimum) in daily water temperatures to illustrate or test concurrent environmental conditions with sucker rearing. The water temperature logger deployed in Mancos Creek malfunctioned in mid-March, and no data were available for further analysis at that reach.

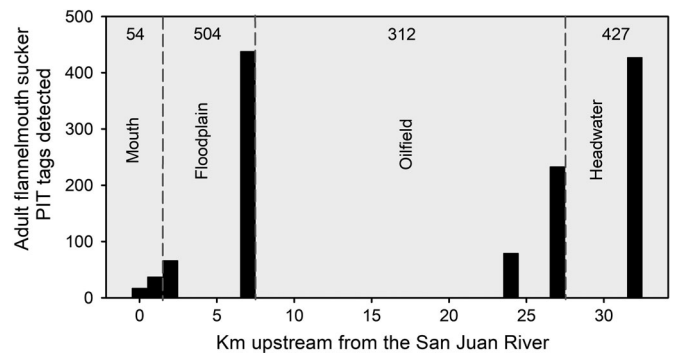


FIGURE 2. Passive integrated transponder (PIT) antenna detections of 1,297 PIT-tagged adult Flannemouth Sucker in McElmo Creek during 2015. Detected fish were tagged as adults (>300 mm TL) in 2012–2014. Numbers correspond to the total number of individuals detected per reach. Numbers should be interpreted as the count of fish that swam to or upstream of the given antenna but were not detected any further upstream.

TABLE 1. Captures of adult Flannemouth Sucker in the Mancos River across four backpack electrofishing sampling events that straddled peak spawning activities in 2015. The March 27 event was the only event during which spawning was observed. An asterisk indicates that the Mancos River was not connected to the San Juan River during the sampling event. Pool numbers in bold italics indicate where larvae and associated organisms were sampled.

Pool	Distance (km)	Mar 6	Mar 27	Apr 22*	May 9*
1	0.21	1	18	30	1
2	0.28	4	12	13	6
3	0.35	2	9	1	2
4	0.41	0	11	0	0
5	0.45	0	32	0	0
6	0.56	0	0	12	0
7	0.65	0	0	0	0
8	0.77	0	0	27	3
9	1.01	0	50	14	1
10	1.06	0	4	0	1
Total	1.06	7	136	97	14

To evaluate potential interactions within larval Flannemouth Sucker habitats, we used canonical correspondence analysis (CCA) to characterize spatial distributions and co-occurrence of species in habitats sampled for early life stages of Flannemouth Sucker in McElmo Creek (*vegan* package version 2.5-2 in R version 3.5.0; R Development Core Team 2008). We linked log-transformed ($\log x + 1$) taxon counts with physical habitat measurements taken in March and water condition (e.g., flow and temperature) data measured throughout the sampling time frame. As

Flannemouth Sucker were targeted for fixed sample sizes of 15–30 larvae or juveniles per site (30–60 per reach) and CCA is based on proportional abundances by preserving chi-square distance between samples, we assumed that other animals caught with larval Flannemouth Sucker would be the most likely to interact with them. Because we only measured physical habitat once, we assumed that changes in flow over time would not drastically alter the relative differences in physical habitat (substrates, widths, velocity [margin and maximum], and depths [mean

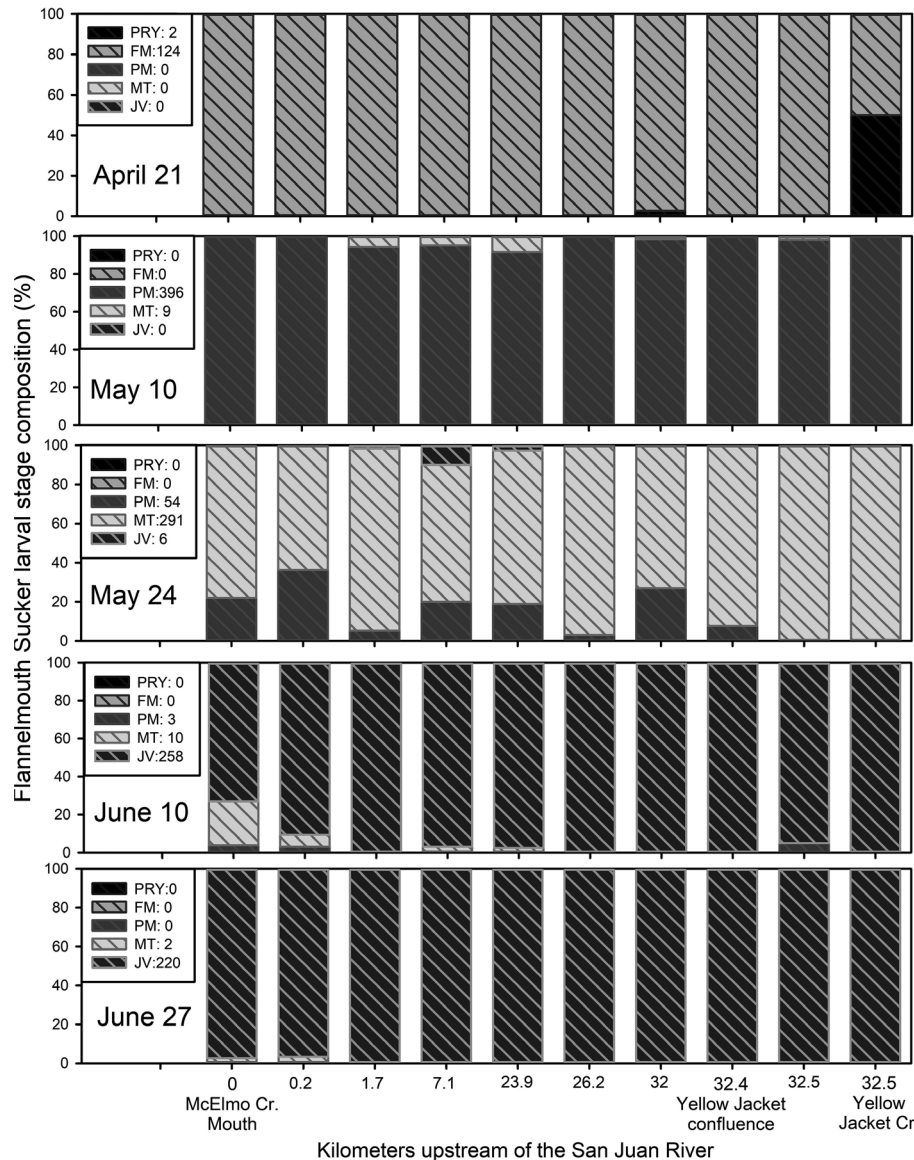


FIGURE 3. Weekly (2015) ontogenetic stage composition of Flannemouth Sucker at sites in McElmo Creek based on distance upstream from the San Juan River. Stage designations are as follows and were informed by Snyder and Muth (2004): protolarvae (PRY; yolk was still present, and no fin rays were apparent); flexion mesolarvae (FM; first caudal fin rays were apparent); postflexion mesolarvae (PM; full complement of caudal fin rays was present); metalarvae (MT; caudal, dorsal, and anal fins all had the full complement of rays); and juveniles (JV; the fin fold was completely absorbed).

margin, mean main channel, and maximum main channel]) to prevent misinterpretation across reaches. We then used the mean discharge (m³/s) from the preceding period between seining along with data on the mean, minimum, maximum, and variation in daily temperature to address environmental impacts on larval distribution and ontogenetic stages. We used variance inflation factors (VIFs) to test for multicollinearity, and we culled variables until the final model only used variables with a VIF less than 10. Permuted ANOVA (999 permutations) tested the significance of CCA axes and habitat variables (Anderson 2001).

RESULTS

Spawning Locations

In McElmo Creek, 1,297 individual adult Flannemouth Sucker were detected across all antennas (Figure 2).

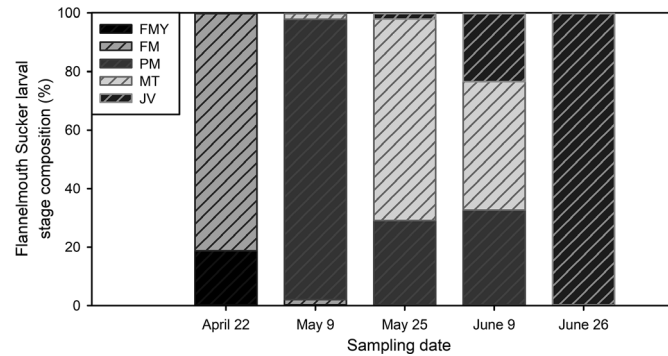


FIGURE 4. Weekly (2015) ontogenetic stage composition of Flannemouth Sucker at the Mancos River site. Stage designations are as follows and were informed by Snyder and Muth (2004): flexion mesolarvae (FM [or FMY if yolk was present]; first caudal fin rays were apparent); postflexion mesolarvae (PM; full complement of caudal fin rays was present); metalarvae (MT; caudal, dorsal, and anal fins all had the full complement of rays); and juveniles (JV; the fin fold was completely absorbed between the pelvic fins and the vent).

Of these, 120 swam less than 3 km upstream, 517 swam between 7 and 23 km upstream, and 660 (51%) swam 27 km or more upstream. One-third of the total number of detected adults ($n = 427$) swam at least 32.4 km to the confluence of McElmo and Yellow Jacket creeks.

In the Mancos River, the abundance of adult Flannemouth Sucker captured via electrofishing indicated that peak spawning occurred around March 27 (Table 1). Adults were distributed as far as the 10th pool upstream (1.06 km), but the majority (60%) were within 0.45 km of the San Juan River during this peak spawn sampling event. The later sampling events occurred during periods of intermittency and showed lower abundance yet still a broad distribution across the 10 pools within the wetted reach.

Larval Sampling, Hatch Dates, and Size at Age

We captured 1,375 larval and juvenile Flannemouth Sucker from McElmo Creek for analyses. No Flannemouth Sucker larvae were captured until April 21 in McElmo Creek and April 22 in the Mancos River. Larvae captured across McElmo Creek reaches generally showed a congruent progression in developmental stages between each sample until the juvenile stage was reached on June 10 (Figure 3). In the Mancos River, 274 larval Flannemouth Sucker were sampled, but three of the five sampling events had mixed composition among two or more larval stages (Figure 4). Hatch dates ranged from April 2 to 7 in McElmo Creek (mouth: number of individuals aged from otoliths = 11; floodplain: $n = 12$; oilfield: $n = 11$; headwater: $n = 17$) and from April 6 to 11 in the Mancos River ($n = 8$) and were latest at the headwater reach of McElmo Creek and the Mancos River (Table 2). Juvenile fish were the most prevalent stage throughout McElmo Creek by June 10 but did not dominate a Mancos River sample until June 26.

As determined by 90th quantile regression, larvae captured at the mouths of McElmo Creek and the Mancos River had the slowest growth rates and recruitment to the juvenile stage, which was nearly 2 weeks later than that

TABLE 2. Hatch dates (in 2015) and slope coefficients for size at age and recruitment metrics of larval Flannemouth Sucker from distinct geomorphic reaches in McElmo Creek and the mouth of the Mancos River. Recruit time indicates the number of days for larvae to reach the juvenile stage (25 mm SL). Regression equations indicate the change in SL (mm; y) with age (d; x).

Stream	Reach	Hatch date range	Modal hatch date	90th quantile		50th quantile	
				SL by age	Recruit time	SL by age	Recruit time
McElmo	Mouth	Apr 2–6	Apr 3	$y = 0.287x + 9.03$	56	$y = 0.254x + 7.599$	66
	Floodplain	Apr 1–7	Apr 2	$y = 0.336x + 8.32$	50	$y = 0.309x + 5.490$	63
	Oilfield	Apr 3–7	Apr 4	$y = 0.329x + 9.21$	48	$y = 0.296x + 7.268$	60
	Headwater	Apr 5–7	Apr 7	$y = 0.384x + 8.44$	43	$y = 0.357x + 6.218$	53
Mancos	Mouth	Apr 6–11	Apr 7	$y = 0.283x + 10.05$	54	$y = 0.218x + 9.432$	71

observed at the upstream-most headwater reach in McElmo Creek (Figure 5). Flannelmouth Sucker at the headwater reach of McElmo Creek had a significantly larger size at age through time relative to all other reaches, and the age when significant differences occurred between sites became progressively younger moving downstream (Table 3). The age at significantly different slopes of the 90th quantile between headwater and oilfield reaches was 49d compared to 21d for the headwater and floodplain reaches or 13d for the headwater and mouth reaches.

When we compared median quantiles for size at age among groups, the difference in time to the juvenile stage was even more disparate between the headwater reach in McElmo Creek and the mouth reaches of McElmo Creek (16-d difference) and the Mancos River (27-d difference). Critical “growth” periods inferred through interval-specific 90th quantile regression showed that all McElmo Creek sites had the steepest slopes between size at age of sampling events 3 (May 10) and 4 (May 24) compared to the Mancos River larvae, which exhibited the greatest

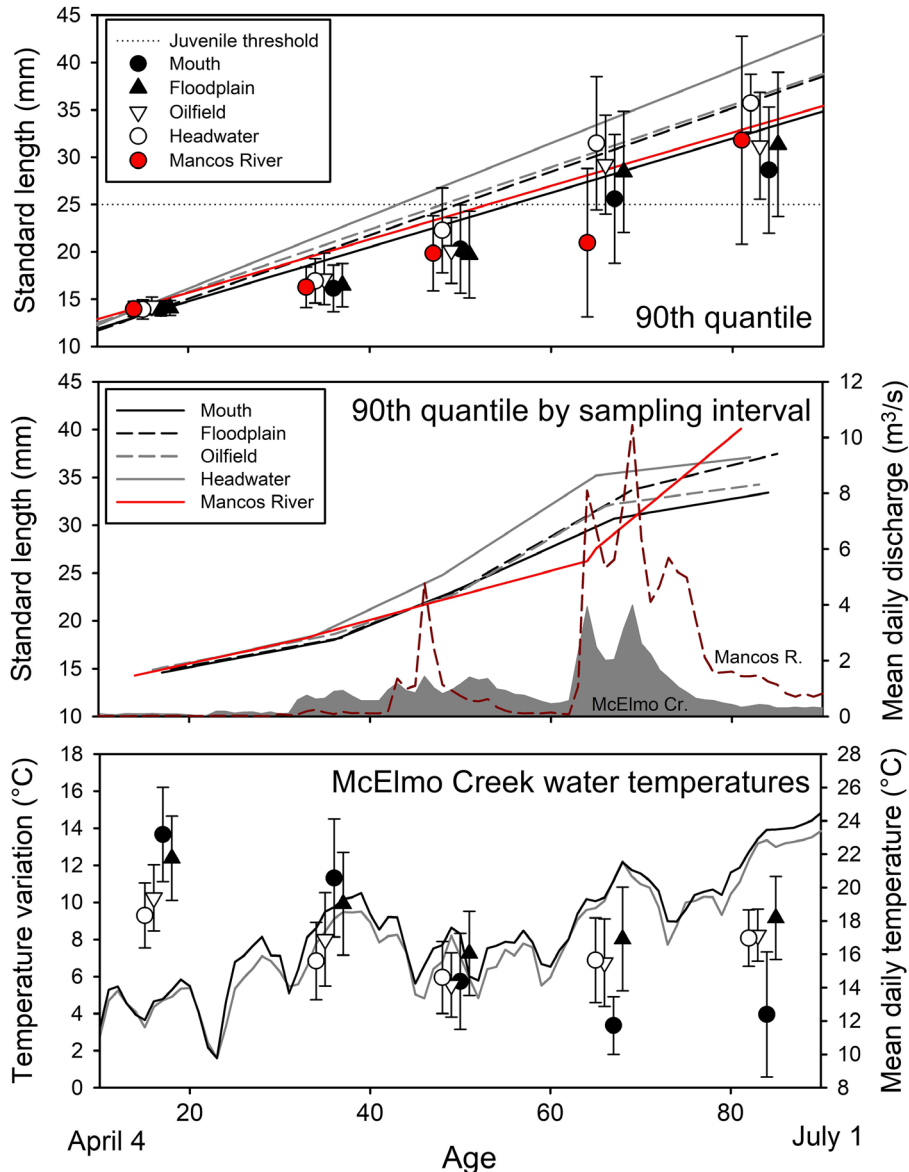


FIGURE 5. Ninetieth quantile regressions of SL (mm) versus age (d) for larval Flannelmouth Sucker sampled from McElmo Creek (4 reaches) and the Mancos River (1 reach) across all sampling periods in 2015 (top panel; with median SLs represented by symbols [± 2.5 median absolute deviation]). The middle panel presents the 90th quantile regressions according to each sampling period interval (also showing discharge from each study stream). The bottom panel indicates daily variation in water temperature (symbols) and mean daily water temperature from the mouth (black line) and headwater (gray line) reaches of McElmo Creek.

TABLE 3. Pairwise comparisons of 90th quantile slopes for early life stage Flannemouth Sucker SL (mm) versus age (d; see Table 2) between reaches in McElmo Creek and the Mancos River. Significantly different 90th quantile slopes are indicated by the number of days where slopes and their 90% confidence intervals separated. Nonsignificant differences are indicated by "NS."

Reach	Floodplain	Oilfield	Headwater	Mancos River
Mouth	58	44	13	NS
Floodplain		NS	21	NS
Oilfield			49	NS
Headwater				31

increases in size at age between samples 4 (May 25) and 5 (June 10).

Longitudinal Patterns of Habitat and Communities

We captured 2,750 animals while seining for larval fish in McElmo Creek and 442 animals in the Mancos River. Flannemouth Sucker comprised 50% of the McElmo Creek sample and 62% of the Mancos River catch. McElmo Creek had 12 species of fish (6 of which were native) in addition to immature nonnative American bullfrogs *Lithobates catesbeianus*, immature dragonflies (Odonata), and nonnative virile crayfish *Orconectes virilis* (Table 4). The Mancos River had nine species of fish (5 of which were native) in addition to native Woodhouse's toad *Anaxyrus woodhousii* and nonnative virile crayfish (Table 5).

After adjusting the model to cull multicollinear variables that had VIFs exceeding 10, two significant CCA axes were found, representing the proportional abundance of animals to Flannemouth Sucker in relation to physical habitat features (Figure 6). The final model included substrate ($P=0.012$), mean water velocity ($P=0.004$), maximum depth ($P=0.357$), maximum temperature ($P=0.001$), temperature variation ($P=0.001$), and reach or distance upstream from the San Juan River ($P=0.191$). The first CCA axis (51% of the variation; $P=0.001$) represented a gradient in water temperature variation where more positive values were related to samples collected earlier in time. Water temperature variation was greater in early periods and then diminished with time. Flannemouth Sucker early life stages were arranged along this axis from flexion mesolarvae (more positive) to juvenile (more negative). The second CCA axis (21% of the variation; $P=0.006$) represented a spatial gradient where more negative values indicated greater distance upstream from the San Juan River and followed vectors also associated with longitudinal distance, such as water velocity. Additionally, the second CCA axis was associated with a diversity gradient whereby Flannemouth Sucker in more

upstream reaches occurred among a greater diversity of animals as time went on (i.e., especially in the last two sampling events), including nonnative virile crayfish, nonnative American bullfrog tadpoles, dragonfly (Odonata) larvae, Roundtail Chub, and Speckled Dace.

DISCUSSION

The experiences of larval and juvenile Flannemouth Sucker varied according to spatially and temporally structured environmental and community patterns within and among study streams. In McElmo Creek, these experiences were made possible by a large population of spawning adults distributed throughout the system, with a tendency toward upstream habitats. Conversely, the diminished and intermittent flow at the Mancos River limited spawning and rearing habitat. Thus, our hypothesis that the intermittent stream would have restricted spawning and rearing habitat was supported by the lack of flows in the Mancos River compared to the perennial McElmo Creek. However, our general hypothesis that downstream reaches would have larger size at age and faster recruitment was not supported by our analyses. The upstream-most site in McElmo Creek had the largest size at age of larval Flannemouth Sucker despite hatching the latest compared to reaches that were most proximate to main-stem habitats; the mouth of McElmo Creek and the Mancos River reach had the smallest sizes at age across time. Quantile regression slopes suggested that larvae in the headwater reach overcame delayed hatching and recruited to the juvenile stage faster than those in any other reach.

Despite our attempt to separate reaches as much as possible, drifting larvae may have accumulated at downstream sites or even come from main-stem spawning events at the McElmo Creek mouth reach, thereby influencing the results. Greater composition of earlier ontogenetic stages at more downstream sites in McElmo Creek (e.g., the May 24 and June 10, 2015, samples) could be evidence of drift. Robinson et al. (1998) postulated that Flannemouth Sucker larvae (at stages prior to metalarvae) could drift at least 8.5 km in the Little Colorado River (a stream with base flow conditions 10× greater than those at McElmo Creek). Even though this suggests that distances between some of our reaches (i.e., the mouth and headwater reaches) would satisfy the assumption of no movement among reaches, especially at earlier sampling periods, postemergent drift should be considered as a relevant yet variable process in larval sucker life histories (i.e., Childress et al. 2016). As such, one alternative explanation for our findings is that patterns in Flannemouth Sucker arose from larger, more developed individuals being able to maintain a more upstream position in the network over time. Quantifying drift rates via drift

TABLE 4. Total animals captured per site during larval Flannemouth Sucker seining (in 2015) in the McElmo Creek system relative to distance (km) upstream from the San Juan River. Kilometer 32.4 is the confluence of Yellow Jacket Creek with McElmo Creek. Kilometer 32.6 is Yellow Jacket Creek. "Age 0" indicates larval and juvenile fish, typically smaller than 60 mm for suckers; "SA" indicates subadult fish, specifically where suckers *Catostomus* spp. had sizes greater than 80 mm but less than the size at maturity for the species based on observation in McElmo Creek (Bluehead Sucker *C. discobolus* < 185 mm; Flannemouth Sucker < 300 mm); and "AD" indicates adult fish. Asterisks denote nonnative animals.

Species/organism	Mouth		Floodplain		Oilfield		Headwater				Total	%
	km 0	km 0.2	km 1.7	km 7.1	km 23.9	km 27	km 32	km 32.4	km 32.5	km 32.6		
White Sucker <i>Catostomus commersonii</i> * (age 0)	0	1	0	0	0	0	0	1	0	1	3	0.1
Bluehead Sucker <i>Catostomus discobolus</i> (age 0)	4	10	0	0	0	0	3	0	3	1	21	0.8
Bluehead Sucker (SA)	0	0	0	0	0	1	1	0	1	1	4	0.1
Flannemouth Sucker <i>Catostomus latipinnis</i> (age 0)	165	173	153	157	171	154	180	74	133	15	1,375	50.0
Protolarvae	0	0	0	0	0	0	1	0	0	1	2	
Flexion mesolarvae	10	7	5	10	10	13	35	12	21	1	124	
Postflexion mesolarvae	53	84	37	48	40	42	68	25	54	2	453	
Metalarvae	46	24	56	31	33	32	28	24	34	4	312	
Juvenile	56	58	55	68	88	67	48	13	24	7	484	
Flannemouth Sucker (SA)	0	0	5	0	1	2	0	0	1	1	10	0.4
Red Shiner <i>Cyprinella lutrensis</i> * (age 0)	5	14	0	0	0	0	0	0	0	0	19	0.7
Red Shiner* (AD)	27	279	77	68	176	103	66	125	56	29	1,006	36.6
Western Mosquitofish <i>Gambusia affinis</i> * (AD)	0	1	0	0	0	0	0	0	0	0	1	0.0
Roundtail Chub <i>Gila robusta</i>	0	0	0	0	1	4	2	3	6	3	19	0.7
Channel Catfish <i>Ictalurus punctatus</i> * (AD)	0	0	0	0	0	0	1	0	0	0	1	0.0
American bullfrog <i>Lithobates catesbeianus</i> * (tadpole)	0	0	0	0	2	14	10	3	2	4	35	1.3
Largemouth Bass <i>Micropterus salmoides</i> * (SA)	0	2	1	0	0	0	0	0	0	0	3	0.1
Odonata spp. (immature)	0	0	1	1	1	1	0	0	0	0	4	0.1
Virile crayfish <i>Orconectes virilis</i> *	2	3	5	2	9	9	16	6	15	48	115	4.2
Fathead Minnow <i>Pimephales promelas</i> * (AD)	1	0	0	0	3	1	1	1	1	0	8	0.3
Colorado Pikeminnow <i>Ptychocheilus lucius</i> (SA)	0	0	1	0	0	0	0	0	0	0	1	0.0
Speckled Dace <i>Rhinichthys osculus</i> (age 0)	0	0	1	0	2	12	7	3	1	3	29	1.1
Speckled Dace (AD)	0	0	8	1	20	23	12	8	11	6	89	3.2
Razorback Sucker <i>Xyrauchen texanus</i> (age 0)	0	5	2	0	0	0	0	0	0	0	7	0.3
Total (15 taxa)											2,750	

nets throughout known spawning areas as well as determining swimming performance of early life stage sucker across various flow scenarios would help to alleviate some concerns of our study (sensu Ward et al. 2002). Additionally, comparative studies of main-stem and

tributary spawning groups would more accurately test the relative importance of these habitats for larval and juvenile Flannemouth Sucker. Main-stem and tributary habitats have been shown to exhibit asynchronously timed spawning and larval hatching conditions for

TABLE 5. Total animals captured in the Mancos River relative to sampling date in 2015. Percentages are only relative to larval seine samples ($n = 442$ animals) and do not include electrofishing. Daggers (†) by dates indicate when pools were sampled with both a larval seine and electrofishing; electrofished animals are indicated in bold. Electrofishing captures from pool 2 were only reported since all larval Flannemouth Sucker sampled on April 22 or May 9 came from that pool. Asterisks denote nonnative animals. Adult (AD) and subadult (SA) life stages are indicated when possible.

Species/organism	Apr 22†	May 9†	May 25	Jun 9	Jun 26	Total	%
White Sucker* (larvae)	0	1	0	3	0	4	1
Bluehead Sucker (larvae)	0	0	0	5	1	6	1
Flannemouth Sucker (larvae)	48	48	48	98	32	274	62
Flexion mesolarvae with yolk	9	0	0	0	0	9	2
Flexion mesolarvae	39	1	0	0	0	40	9
Postflexion mesolarvae	0	46	14	32	0	92	21
Metalarvae	0	1	33	43	0	77	17
Juvenile	0	0	1	23	32	56	13
Flannemouth Sucker (SA)	0	5	0	0	0	5	
Flannemouth Sucker (AD)	13	6	0	0	0	19	
Red Shiner*	0	0	5	33	21	59	13
Red Shiner* (AD)	9	0	2	0	1	12	3
Roundtail Chub (AD)	0	2	0	0	0	2	
Hybrid sucker* (larvae)	0	0	0	2	0	2	<1
Hybrid sucker* (AD)	1	0	0	0	0	1	
Largemouth Bass*	0	0	0	0	1	1	<1
Fathead Minnow*	0	0	0	0	3	3	1
Speckled Dace (AD)	1	1	0	0	0	2	
Speckled Dace (larvae)	0	0	0	0	1	1	<1
Colorado Pikeminnow (SA)	0	0	0	0	2	2	<1
Virile crayfish*	0	0	0	0	70	70	16
Woodhouse's toad <i>Anaxyrus woodhousii</i> (tadpole)	0	0	9	0	0	9	2
Total (11 species)	48	49	53	141	58	471	100

Flannemouth Sucker in the upper Colorado River basin (Fraser et al. 2019).

Identifying critical periods of drastic increases in size at age among two sample periods highlighted that growth was not synchronized between streams but was consistent across reaches in McElmo Creek. These findings did not support our hypothesis but might be explained in a few ways. First, size responded strongly to a critical threshold where larvae were large enough to consume abundant food (sensu Nunn et al. 2012). Second, size at age in McElmo Creek responded positively to a stable environment characterized by less variable temperature, a metric to which faster growth in suckers is attributed (Vondracek et al. 1982). Third, size at age in the Mancos River responded positively and rapidly to enhanced flows from spring rains that produced better rearing conditions than isolated pools—a potential mechanism that deserves further scrutiny among contemporary studies of intermittent systems and their communities (Hwan and Carlson 2016).

Although larval seining may have failed to capture co-occurring large-bodied fishes that could escape our gear, results showed that larval Flannemouth Sucker were exposed to different communities of native and nonnative

animals that could result in predation and competition; Red Shiner were ubiquitous in McElmo Creek. It is possible that larval Flannemouth Sucker are an abundant prey source or weak competitor early in the season, but the timing of emergence (and early life stages, such as flexion mesolarvae through metalarvae) is desynchronized with greater prevalence of multiple predators or competitors. This phenological mismatch could be important for the recruitment of larval Flannemouth Sucker as well as for resilience to invasion, predation pressures, and climate (Miller-Rushing et al. 2010). Invasive virile crayfish and American bullfrog tadpoles are demonstrably strong consumers and predators within aquatic food webs (Schiesari et al. 2009; Ficetola et al. 2012); both species prey upon sucker eggs and larvae (Mueller et al. 2006), and invasive virile crayfish can diminish the growth of juvenile Flannemouth Sucker through competition (Carpenter 2005). Dragonfly larvae and other fishes can also act as strong organizational forces in communities and food webs by eating larval fishes, including suckers (Power 1990; Horn et al. 1994; Crumrine and Crowley 2003; Carpenter and Mueller 2008). Indeed, the activity and prevalence of some of these potential predators or competitors apparently

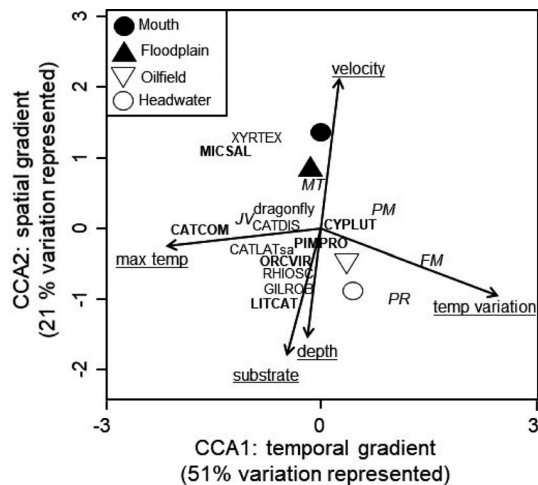


FIGURE 6. Canonical correspondence analysis (CCA) of larval and juvenile Flannemouth Sucker relative to the aquatic community sampled during larval surveys in 2015. Reach centroids are represented by symbols. Vectors (arrows; underlined text) indicate that larger diameter substrates occurred upstream (negative CCA axis 2 [CCA2] values), stable temperatures (temp) occurred earlier (positive CCA axis 1 [CCA1] values), and water velocity was slowest downstream (positive CCA2 values). Bold text indicates nonnative animals: virile crayfish (ORCVIR), American bullfrog (LITCAT), Fathead Minnow (PIMPRO), Red Shiner (CYPLUT), White Sucker (CATCOM), and Largemouth Bass (MICSAL). Nonbold text indicates native animals: subadult Flannemouth Sucker (CATLAT_{sa}), Roundtail Chub (GILROB), Bluehead Sucker (CATDIS), Razorback Sucker (XYRTEX), and Speckled Dace (RHIOSC). Flannemouth Sucker larval and juvenile stages are shown in italicized two-letter codes and were designated as follows (Snyder and Muth 2004): protolarvae (PR), flexion mesolarvae (FM), postflexion mesolarvae (PM), metalarvae (MT), and juveniles (JV).

peak in warmer months, especially for virile crayfish (Lewis 2001) and Speckled Dace (Cathcart et al. 2015). Although some negative community interactions may be mitigated by the early hatching of larval Flannemouth Sucker, ordination analysis and community sampling results illustrated the importance of the reach in which larvae were spawned. Specifically, larvae in the oilfield canyon or headwater reaches may have productive growing habitats with stable thermal regimes, yet they must eventually contend with a diverse assembly of native and non-native competitors or predators (i.e., higher proportional abundance of American bullfrogs, virile crayfish, Speckled Dace, and Roundtail Chub). In contrast, larvae in downstream reaches experience more dynamic thermal regimes that could retard growth and lead to less diverse assemblages, including species with lower proportional abundance yet potentially exerting pressure from competition (i.e., larval Bluehead Sucker) or predation (i.e., Largemouth Bass). Overlap with nonnative animals may be a greater threat to larval Flannemouth Sucker than overlap with native fishes since members of native communities limit competitive interactions by partitioning resources

and maintaining higher growth (Greger and Deacon 1988; Childs et al. 1998; Carpenter 2005). Therefore, the experience of Flannemouth Sucker offspring appears to depend on spatial variation in habitat conditions, such as distance upstream or temperature, yet a community context must be considered as associated species may also exert different pressures.

Spatial variation in larval Flannemouth Sucker rearing habitat, like the spatially discrete habitat types of other animals (birds, mammals, amphibians, and other fishes), illustrates the implications of reproductive migrations for fulfilling life cycles of populations (Pope et al. 2000; Brotons et al. 2005; Post and Forchhammer 2008; Falke and Fausch 2010). Although some sucker migrations have been well documented, the ecological tradeoffs that larvae may experience from adult spawning site selection are largely unknown. Due to conservation actions broadly targeting catostomids, including several endangered species, a more thorough understanding of both early life histories and long-term population processes (i.e., adult recruitment) could aid in managing populations dependent on spatially variable habitats through a changing climate (Cooke et al. 2005; Fraser et al. 2019). Because of relatively widespread ranges that present conditions requiring the use of drastically different habitats (even within an endemic species, such as Flannemouth Sucker), the biocomplexity of migratory species may manifest in localized adaptations to the spatial variation of spawning and rearing habitats (Hilborn et al. 2003). Long-term research linking distinct migratory corridors (i.e., antennas and weirs) to rearing habitats (i.e., larval sampling) across many years would help to alleviate the limited temporal scale of this study and would provide a more accurate representation of how annual cohorts of long-lived migratory fishes with low rates of adult recruitment respond to dynamic riverscape processes, such as intermittency (Geen et al. 1966; Hooley-Underwood et al. 2019). For example, if seasonal community assemblage and water temperature are strongly tied to flow patterns, larval sucker growth and recruitment could be variably affected across years by tributary flow and spawning migration timing. The complex ecology of migratory species like the Flannemouth Sucker, which exploit tributary and main-stem habitats containing thermally complex and dynamic flow conditions for spawning and larval experiences, may enhance their resiliency to anthropogenic and climatic perturbations. Ultimately, this biocomplexity could explain how the aggregate Colorado River basin population of this species has maintained a relatively high proportion of its range.

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