MULTI-SCALE DISTRIBUTIONS AND MOVEMENTS OF FISH COMMUNITIES IN TRIBUTARIES TO THE SAN JUAN RIVER

by

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Abstract

Recognizing habitat needs of fishes across space and time is increasingly important for managing altered stream networks, such as in the Colorado River basin. Recent work on warm-water fishes suggest they might benefit from access to tributaries and their confluences. Fish movements or distributions within tributaries relative to distance from mainstem confluences in two streams with different network types (linear versus dendritic) were investigated in the San Juan River basin, USA. Upstream distance from the San Juan River resulted in species declines (Chaco Wash, linear network) or turnover (McElmo Creek, dendritic network). McElmo Creek movement patterns were likely attributed to spring spawning migrations of flannelmouth sucker (*Catostomus latipinnis*), spawning aggregations of razorback sucker (*Xyrauchen texanus*), foraging or refuge seeking by Colorado pikeminnow (*Ptychocheilus lucius*), and monsoon-related movements for channel catfish (*Ictalurus punctatus*) and razorback sucker. Razorback sucker and Colorado pikeminnow dominated movements at Chaco Wash, suggesting this backwater-like tributary supplied thermal or current refuge, foraging habitat, or both. Within McElmo Creek, a second study explored the importance of confluences by characterizing habitat use and movements of fishes at the junction of McElmo and Yellow Jacket creeks. Native fish dominated the confluence community composition. The reach downstream of the confluence had consistently higher abundances, species richness, and more frequent detections of tagged fishes relative to upstream reaches. Movement behaviors inferred by detection frequency of tagged fish among reaches surrounding the confluence differed among species. Small flannelmouth sucker (< 300 mm) and roundtail chub (*Gila robusta*) were commonly detected in Yellow Jacket Creek whereas large flannelmouth sucker (> 300 mm), bluehead sucker (*C. discobolus*), and channel catfish used McElmo Creek reaches. Monsoons increased McElmo Creek discharge which triggered upstream movements of channel catfish and displaced large flannelmouth sucker and bluehead sucker. Monsoons increased movements between McElmo and Yellow Jacket creeks by roundtail chub, small flannelmouth sucker, and black bullhead (*Ameiurus melas*). Combined, these two field studies emphasized using links between patterns and processes of tributary fish communities. Conservation, rehabilitation, and maintenance of connectivity and habitat heterogeneity at confluence zones likely can be a localized management strategy with expansive ecosystem effects.

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Dedication

This work of science is dedicated to my parents for keeping me active, fueling my passion for fish, patience, and support over the years (and watching the dog). I appreciate my mom for encouraging my creativity, humor, literacy, and scientific endeavor. I am grateful to my dad for taking me fishing. The brook trout, creek chubs, white suckers, and common shiners that we caught formed a sense of wonder toward fish that quickly transformed into an enthusiastic pursuit of a fish biology career. To my brother for providing the excitement, friendship, and generally good role model a younger brother needs. My grandma has been the best pen pal I could ask for, even from such an exotic location as northern Minnesota, and without her and her positive perspectives, the past decade away from home would not have been as comfortable.

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Preface

Chapter one is written with common fish species names in the style of the American Fisheries Society writing guide.

Chapter 1 - Fish community distributions and movements in two tributaries of the San Juan River, New Mexico and Utah, USA

Abstract

Recognizing how stream fish communities – and their habitats – can differ across space and time relative to network position (i.e., mainstem versus tributary habitats) is increasingly important for managing complex river networks where freshwater systems are highly altered, such as in the Colorado River basin. We studied patterns (community composition) and processes (movement) that shape species abundances and distributions in two tributary systems of the San Juan River, Utah and New Mexico. Results show upstream distance away from the San Juan River is a strong driver of community patterns whether through species richness declines (Chaco Wash) or species turnover (McElmo Creek). Likewise, habitat gradients (i.e., depths, substrate, and widths) were also affected by proximity to the San Juan River. Movement patterns at McElmo Creek varied by species but generally were associated with spring spawning migrations (Flannelmouth Sucker *Catostomus latipinnis*, Razorback Sucker *Xyrauchen texanus*), exploratory movements (Colorado Pikeminnow *Ptychocheilus lucius*), and monsoon flooding (Channel Catfish *Ictalurus punctatus,* Razorback Sucker). Movements at Chaco Wash were dominated by endangered Razorback Sucker and Colorado Pikeminnow suggesting this habitat supplies useful habitat, forage, or both. Acknowledging the utility of these peripheral habitats relative to the mainstem can more broadly incorporate the spatiotemporal dynamics of native and nonnative fish communities into basin-wide management actions.

Introduction

Recent studies have reported occurrences of "big river" endangered species in smaller tributary systems in the American Southwest, sparking an interest in the role of these habitats in stream networks (Wick et al. 1991; Bottcher et al. 2013; Fresques et al. 2013). Tributary habitat use by fishes is dependent on the permanence of water (ephemeral or perennial), size of the tributary, and also the location of confluences on the mainstem river network (Osborne and Wiley 1992; Datry et al. 2014). Incorporating these systems into research and management can expand our knowledge of the spatial distribution of species of conservation interest by including habitats that might support critical life history stages of fishes (Schlosser 1991; Fausch et al. 2002).

The Colorado River Basin (CRB) is a highly modified stream network that supports relic populations of endemic fishes in the midst of massive water development projects, habitat alteration, and species introductions (Minckley and Deacon 1968; Poff et al. 1997). Despite widespread alterations, much of the endemic fish community persists through natural or artificial means such as stocking and augmentation programs (Zelasko et al. 2010). Alterations exist throughout the major sub-basins in the Upper Colorado River Basin: the San Juan, Duchesne, Yampa, Green, Gunnison, and White rivers (Bottcher et al. 2013). Nonetheless, stream networks within these sub-basins continue to be regarded as key native fish habitats that maintain migratory routes (Irving and Modde 2000), meet life stage specific needs (i.e., spawning, refuge, feeding; Childs et al. 1998; Robinson et al. 1998; Weiss et al. 1998), and allow for population conservation (Bestgen et al. 2007).

The Colorado River and its major sub-basins have been intensively monitored largely due to the presence of federally endangered and threatened species but critical information on life history dynamics continue to be discovered. For example, Razorback Sucker (*Xyrauchen texanus*) were recently reported to successfully spawn in the White River, UT and passive integrated transponder (PIT) tag studies identified movements of endangered Bonytail Chub (*Gila elegans*), Colorado Pikeminnow (*Ptychocheilus lucius*), and Razorback Sucker, with some movements exceeding 500 km (Bottcher et al. 2013; Webber et al. 2013; Travis Francis, pers. comm United States Fish and Wildlife Service). Mainstem rivers within these sub-basins account for a large proportion of critical habitat but undesignated habitats, including small tributaries, are also used by sensitive and endangered native fishes (Bezzerides and Bestgen 2002; Finney 2006; Compton et al. 2008). Our overarching objective of this study was to investigate fish community dynamics of small tributary networks (i.e., streams with <10% of mainstem discharge that can vary in the configuration of channels whether linear streams comprised of one channel or branching networks made of multiple joined channels) in the San Juan River basin within mainstem reaches that are designated critical habitat for endangered Colorado Pikeminnow and Razorback Sucker. We combined systematic sampling of two tributaries over spatial and temporal gradients with a PIT tagging study to quantify movements between tributary and mainstem habitats.

Even though there have been several studies exploring the San Juan River fish community dynamics (i.e., Gido et al. 1997; Propst and Gido 2004; Franssen and Durst 2013), explicit consideration of the role of tributary habitats on fish distributions has been limited to a data review (Miller and Rees 2000) and a study at the Mancos River confluence and adult Colorado Pikeminnow spawning movements (Ryden and Ahlm 1996). Miller and Rees (2000) suggested tributaries exhibited compositional changes from native to nonnative fish communities due to alterations while acknowledging historically-limited data exist for many tributaries. Small tributaries generally remain overlooked, probably because of small size, remoteness, and political boundaries, yet they can still provide habitat allowing persistence of native fishes

(Clarkson et al. 2012; Pool et al. 2013). Fresques et al. (2013) provided the first published record of Colorado Pikeminnow in McElmo Creek, a small tributary of the San Juan River, but other species' use of the tributary networks relative to the mainstem San Juan River remain poorly documented. Increasing numbers of studies throughout the upper Colorado River Basin documenting the use of smaller tributary habitats by endangered species and species of special concern suggests that these systems might have important conservation value (Wick et al. 1991; Webber et al. 2012; Bottcher et al. 2013).

Specific objectives of this study were to link seasonal distributions, abundances, stream geomorphology, and movement of the fishes in two small, but mainly perennial, tributaries to distance away from the San Juan River. Dispersal and habitat limitations have been implicated in the patterns of fish community composition and species abundance relative to position in stream and reservoir networks (i.e., proximity to confluences or different habitats; Osborne and Wiley 1992; Benda et al. 2004; Falke and Gido 2006; Thornbrugh and Gido 2010). Thus, we hypothesized that distance from the mainstem San Juan River would best explain community structure gradients whereby species more indicative of mainstem communities will blend with tributary communities near the San Juan River and the farthest away communities will be composed of tributary-associated species. Further, we hypothesized the habitats will display gradients where wetted widths will decrease and depths increase with increasing distance from the mainstem San Juan River. We also hypothesized that species would differ in their annual timing and frequency of movements into and within these tributaries associated with spawning migrations and other critical processes related to season and environmental changes in temperature and discharge.

Methods

Study Area

The San Juan River is a main tributary to the Colorado River and drains 99,200 km^2 from its headwaters in southwest Colorado in addition to Utah, Arizona, and New Mexico before entering Lake Powell 365 stream kilometers (skm) downstream of Navajo Dam (Franssen and Durst 2013). Navajo Dam impounded the San Juan River in 1962, inundated 56 skm upstream, and has partly modified flow and temperature regimes downstream in the 288 skm of river before entering Lake Powell (Ryden and Ahlm 1996; Franssen and Durst 2013). The Animas River, which drains 2823 km^2 and lacks a major mainstem impoundment, enters the San Juan River at Farmington, NM and maintains a partially natural flow regime with increases in discharge during spring snowmelt and summer monsoons although withdrawals and depletions have greatly reduced annual volume (USGS gage 9363500).

Two small tributaries within the San Juan River Basin that have been understudied, but might provide habitat for native and nonnative fishes include McElmo Creek and Chaco Wash (Figure 1). McElmo Creek flows through Colorado and Utah before confluencing with the San Juan River near Aneth, UT. The McElmo Creek watershed drains 1818 km^2 from headwaters in Colorado then downstream through the Navajo Nation (Utah) to the confluence with the San Juan River at SJR skm 163 (Navajo Nation Environmental Protection Agency 2012). McElmo Creek has one perennial tributary; Yellow Jacket Creek, which enters McElmo Creek at the Colorado-Utah border, approximately 32 skm upstream of the San Juan River. McElmo Creek was historically an intermittent stream, but irrigation and water development stemming from the creation of McPhee Reservoir in 1986 effectively transformed it to a perennial system by diverting water from the Dolores River basin to the McElmo Creek watershed (Fresques et al.

2013). Riparian vegetation is dominated by Russian olive (*Elaeagnus angustifolia)* but also includes saltcedar (*Tamarisk* spp.), willow (*Salix* spp.) and rarely, eastern cottonwood (*Populus deltoides)*. Land use practices include agriculture; oil and natural gas development; and grazing. Chaco Wash drains an area of 11,396 km^2 to the confluence of the San Juan River east of Shiprock, NM at skm 243.5 (Figure 1). Chaco Wash has perennial flow only downstream of the outlet from an off channel reservoir called Morgan Lake, upstream from the San Juan River approximately 6 skm. Morgan Lake was created in 1961 and is the site of a coal-burning power plant that diverts San Juan River water to cool the generators. Flows in summer 2012 maintained connectivity throughout the year whereas in 2013, flows were disconnected upstream of the study reach. Riparian vegetation is similar to McElmo Creek and is dominated by Russian olive but also has saltcedar and willow. Land use along Chaco Wash is primarily sheep and cattle grazing.

Fish Sampling

To characterize spatial and seasonal variation in fish communities, McElmo Creek was sampled in June and October of 2012 and March, May, and November of 2013 at five sites representing a longitudinal gradient away from the mainstem San Juan River as well as for ease of access because of the remoteness of locations (Figure 1). All sampling dates occurred when McElmo Creek discharge was near base flow with good visibility (mean daily discharge < 0.57 m^3/s). At each site, single-pass backpack electrofishing with two netters sampled fixed-distance reaches of 300 m. At the confluence with the San Juan River we sampled with three seine hauls (approximately 10 -20 m) using a bag seine (6.1 x 1.22 m, 1.69 mm mesh) in addition to the single pass electrofishing. All fish were identified, measured, and released.

In Chaco Wash, seasonal fish sampling at the confluence and six consecutive riffle and pool habitats upstream of the confluence occurred in June, July, August, and October of 2012 and then in March, June, August, and November of 2013. Three seine hauls using the bag seine were conducted at the confluence of Chaco Wash and the San Juan River. Due to extremely high turbidity, coarse substrates, and high conductivity, we chased fishes with a backpack electrofisher downstream through the riffle and approximately 20 m downstream into a bag seine located in the pool. Pool sizes varied considerably so we standardized area sampled to the smallest pool habitat length (pool 6, 20.7 m).

Habitat Sampling

To estimate spatial variation in habitat, wetted width was measured at ten equally spaced transects at each site where each transect then were used to characterize depths and substrate using a modified Wentworth scale (0 – silt, 1- sand, 2 – gravel, 3 – cobble, 4 – boulder, 5 – bedrock). Habitat measurements were taken on all dates corresponding with fish sampling. The distance of sites from the San Juan River was based on a combination of high resolution NHD data (1:24,000/1:12,000 scale) and digital elevation models (10 m resolution) measurements from satellite images using ArcGIS V10.0 mapping software. Water temperatures and discharge from McElmo Creek and the San Juan River were collected to identify environmental triggers of fish movement and resulting patterns of abundances and distributions. Water temperature was recorded every 30 min from Chaco Wash. Water temperature at McElmo Creek was monitored from 8 October 2012 through 4 August 2013 at 30 min intervals. Water temperature collection ended in August 2013 because of a flood event that dislodged the temperature logger. Daily discharge was collected by United States Geological Survey streamflow stations in McElmo Creek and the San Juan River (Figure 1). Each Chaco Wash site was characterized by measuring the pool and riffle lengths, distance from the San Juan River, mean and maximum depths, wetted widths, and substrate size based on a modified Wentworth scale at 10 equally spaced intervals across two transects per pool or riffle. A temperature logger was deployed 22 June 2012 and recorded temperature at 1 h intervals until July 17, 2013. Habitat measurements at Chaco Wash were taken in June and October of 2012 and then in March and June 2013.

Movement Study

To identify movement of fish into tributaries, all fishes greater than 115 mm total length – besides Speckled Dace (*Rhinichthys osculus*), White Sucker (*Catostomus commersonii*) and White Sucker hybrids - were implanted with a 12 mm (134.2 kHz) full duplex Passive Integrated Transponder (PIT) tag. Speckled Dace were not included due to their primarily small size (<100 mm) and shorter life spans relative to large bodied fishes. Opportunistic tagging of fishes outside of seasonally sampled sites occurred throughout McElmo and Yellow Jacket creeks as well as in several reaches of the San Juan River between May 2012 and November 2013. Additionally, stocked Colorado Pikeminnow and Razorback Sucker in the mainstem were tagged by state (Utah Division of Wildlife Resources and New Mexico Fish and Wildlife) and federal agencies (United States Fish and Wildlife Service) and other native fishes in the McElmo Creek basin were tagged by Colorado Parks and Wildlife prior to and during the study period. To evaluate movement of fishes into and out of McElmo Creek, we installed a PIT tag antenna array that spanned the width of McElmo Creek on 2 May 2012 approximately 150 m upstream from the confluence with the San Juan River. This five antenna array had a “pass-over” design where antennas were anchored flat to the streambed (i.e., underwater) and fish are assumed to track the streambed as they move. Detection ranges were tested occasionally throughout the study period and ranged from 10-51 cm. Detection data for this study ended 31 January 2014. Some, but not all, antennas were disabled during disturbance events in January (ice flows) and October (monsoonal flooding) 2013. As such, directional data are not presented here.

We deployed a portable PIT antenna (3.05 x 0.76 m) in Chaco Wash 27 m upstream from the confluence with the San Juan River from 6 June 2013 to 17 July 2013. This antenna was installed with a "pass-through" design where the antenna is situated vertically along the long side of the antenna and can detect movement through a cross-section of the water column. Additionally, we installed block nets between the stream bank and the sides of the antenna to direct fish movement through the antenna. Detection ranges were tested during weekly battery changes and varied from 13-46 cm. This antenna was destroyed after a flooding event occurred during the beginning of the seasonal monsoon season on 17 July 2013.

Data Analysis

We analyzed spatiotemporal variation in fish community structure of McElmo Creek and Chaco Wash using canonical correspondence analysis (CCA; vegan package version 2.0-10 in R version 3.0.3; R Development Core Team 2008). Species count data were objects or dependent variables. To remove the influence of extreme values, counts were either $\log_{10}(x + 1)$ transformed or rare species were removed (i.e., species that occurred at 2 or fewer sites sampled in McElmo Creek or species that comprised less than 2% of the total sample in Chaco Wash). Because the first axis generally explained those spatial gradients and the greatest amount of variation in community structure, we only interpreted this axis. Habitat variables included distance from confluence with San Juan River, wetted width, mean depth, maximum depth, and substrate scores and were not transformed after visual inspection of the distribution of values. Multicollinearity was assessed for all environmental variables via variance inflation factors (VIF) and redundant variables were removed if VIFs were >10. The first two CCA axes were analyzed with permuted ANOVA and ordination interpretation since little variation was explained if additional axes were included.

Results

Habitat

For both streams, wetted widths decreased with upstream distance from the mainstem. Substrate size increased with upstream distance in Chaco Wash but generally remained consistently sized in McElmo Creek (Figure 1.2). Mean depth decreased with upstream distance in Chaco Wash but increased in McElmo Creek. The wider 95% confidence intervals of habitat metrics in Chaco Wash compared to McElmo Creek reflects the flashy, occasionally intermittent nature of Chaco Wash relative to the more perennial nature of McElmo Creek.

The San Juan River has much greater flow than McElmo Creek, with some synchronization in discharge between the two systems (Figure A.1). Flow spikes associated with the monsoon season occurred in 2012 and 2013 in both systems but spring releases simulating runoff from snowmelt were only present in May and June in the San Juan River while McElmo Creek had constant low flow. The thermal regime was warmer in McElmo Creek compared to Chaco Wash and had greater variability between daily minimum and daily maximum temperatures (Figure A.2).

Fish Sampling

McElmo Creek and Chaco Wash both had fish communities of 13 species and McElmo Creek also had native hybrid suckers *C. discobolus x C. latipinnis* (Table 1.1; Table 1.2). Roundtail Chub (*G. robusta*) was absent from Chaco Wash collections while Green Sunfish (*Lepomis cyanellus*) was absent from McElmo Creek samples. One Razorback Sucker was collected from each tributary at the sites closest to the San Juan River. In November 2013 sampling at Chaco Wash, 112 Colorado Pikeminnow (< 90 mm TL) were collected; however since this was immediately after annual stocking of age-0 fish, only the 10 fish greater than 90 mm were retained for further analysis. Two sites in Chaco Wash produced fishless samples; site 3 from July 2012 and site 5 from June 2013.

Mean species richness in McElmo Creek and Chaco Wash was highest at sites closest to the San Juan River (Figure 1.3). Mean species richness decreased on a scale of hundreds of meters in Chaco Wash whereas McElmo Creek richness exhibited higher richness nearest to the confluences of the San Juan River (most downstream site), decreased at middle sites and increased again near the confluence with Yellow Jacket Creek (most upstream site). Overall, McElmo Creek maintained higher richness across all sites relative to Chaco Wash.

Flannelmouth Sucker (*Catostomus latipinnis*) and Speckled Dace had consistently high abundance throughout McElmo Creek whereas Roundtail Chub and Bluehead Sucker (*C. discobolus*) had increasing abundance with distance from the San Juan River (Figure 1.4). Colorado Pikeminnow were distributed throughout the system at lower abundance, but had highest abundance near the downstream confluence with the mainstem and upstream confluence with Yellow Jacket Creek. Nonnative Channel Catfish (*Ictalurus punctatus*) and Red Shiner (*Cyprinella lutrensis*) had similar abundance patterns as Colorado Pikeminnow, reflecting higher abundances near confluences. Black Bullhead (*Ameiurus melas*) had highest abundance in sites closest to the San Juan River and was altogether absent in the two most upstream sites.

Flannelmouth Sucker, Speckled Dace, Colorado Pikeminnow and Bluehead Sucker had relatively constant abundances throughout Chaco Wash (Figure 1.5). Channel Catfish decreased in abundance with greater proximity from the San Juan River, although they were present throughout Chaco Wash. In contrast to McElmo Creek, Black Bullhead abundance increased upstream in Chaco Wash relative to the low abundance at the confluence with the San Juan River. Red Shiner abundances declined with increasing distance upstream from the San Juan River confluence. Swarms of young-of-the-year Black Bullhead and adult Speckled Dace in breeding coloration were both found in upstream habitats of Chaco Wash suggesting they might fulfill complete life histories in the stream.

Fish Habitat Associations

Canonical Correspondence Analysis (CCA) illustrated associations between fish community structure and measured environmental variables. For McElmo Creek, no habitat variables had VIFs >10, thus all were included in the analysis. However, Chaco Wash had two variables (mean wetted width and mean depth) with VIFs > 10 and were excluded from the analysis. Biplots indicated that the McElmo Creek fish community transitioned from a blended native and nonnative community nearest to the San Juan River to a native fish oriented community in the upstream sites largely influenced by Roundtail Chub and Bluehead Sucker (Figure 1.6). Spatial distribution of McElmo Creek sites relative to the San Juan River explained the majority of the variation on CCA axis 1, and this axis was found to be highly significant (*p-value* < 0.005). An ANOVA of habitat variables found distance from the San Juan River to be the most, and only, significant variable explaining community structure among the sites ranging from 0 – 32 km away from the San Juan River (*p-value* < 0.001). The second axis accounted for temporal variation in fish communities and habitat variables but was only marginally significant (*p-value* < 0.1). Channel Catfish were the only species best explained by the second axis, owing largely to their higher abundances during autumn sampling. With the exception of site four in May 2013, all May and autumn sampling dates in McElmo Creek were negatively loaded on the second axis.

Chaco Wash sites exhibited high temporal variations in reference to habitat scores but the fish community was explained with both spatial proximity to the San Juan River. Axis 1 was marginally significant based on an ANOVA of axis scores (*p-value* < 0.1). Channel Catfish were the species most closely associated with maximum depths (Figure 1.7). Black Bullhead were the species most closely associated with distance from the San Juan River compared to the distributions of Speckled Dace, Red Shiner, and Flannelmouth Sucker. Colorado Pikeminnow and Bluehead Sucker had similar positions along an intermediate gradient between depth and distance from the San Juan River. A temporal gradient was unclear at Chaco Wash but habitats at sites were seasonally variable in depth and usually more associated to the second axis at Chaco Wash. Flannelmouth Sucker and Speckled Dace had limited associations to either axis due to stream network-wide ranges and higher abundances.

Fish Movement

We detected a total of 1,586 fishes representing 8 species and 1 native hybrid (*C. discobolus* x *C. latipinnis*) at the McElmo Creek PIT antenna array, with Flannelmouth Sucker, Channel Catfish, Razorback Sucker, and Colorado Pikeminnow comprising over 98% of the detections (Table 1.3). Flannelmouth Sucker were detected in high abundance (hundreds of individuals) in late March and early April 2013 (Figure 1.8). Channel Catfish were detected both years where peak abundance involving over a hundred individual fish occurred in early summer through autumn. Razorback Sucker were detected during spring (especially May for both years with over 40 individuals were detected each year) and also in autumn 2012 (November especially) but not as many as in autumn 2013. Colorado Pikeminnow were detected at relatively low abundance (<10 individuals per month) throughout the year but highest abundances occurred from late summer through December in both years. We detected a total of 135 fishes representing 6 species at the portable PIT antenna stationed in Chaco Wash during 2013, with Razorback Sucker and Colorado Pikeminnow accounting for over 89% of the detections (Table 1.4). Razorback Sucker detections of multiple individuals peaked around 10 June and 12 July 2013 while Colorado Pikeminnow had consistent detections of fewer individuals throughout the antenna deployment (Figure 1.9).

Discussion

Fish communities in both McElmo Creek and Chaco Wash included six and five native species, respectively, but the distribution differed between the two systems. Chaco Wash is a linearly structured stream with diminishing habitat and species richness upstream, whereas McElmo Creek is a branching network with an upstream tributary (Yellow Jacket Creek) that resulted in species turnover moving upstream from the San Juan River. Differences in community patterns could also arise due to more extreme flow variability across all sites in Chaco Wash. The confluences with the San Juan River structure the fish communities at both McElmo Creek and Chaco Wash but Yellow Jacket Creek boosted diversity and abundances by providing an upstream confluence zone in McElmo Creek.

The patterns of increased diversity and increased abundance of certain species at McElmo Creek sites adjacent to confluences (Site 1 and Site 5) highlight potentially important habitat in these areas. For example, headwater species like Roundtail Chub and Bluehead Sucker were most abundant nearest to Yellow Jacket Creek and Razorback Sucker, a big-river specialist, occurred at the San Juan River confluences in both systems. The use of confluence zones by nonnative species also differed between the linearly configured Chaco Wash compared to the dendritic McElmo Creek. For example, Black Bullhead and Red Shiner were most abundant near confluence zones in McElmo Creek but only Red Shiner was more associated to the confluence in Chaco Wash. This pattern is consistent with previous work that found Black Bullhead were more apt to colonize upstream habitats in a flashy stream (Fausch and Bramblett 1991). Channel Catfish in McElmo Creek were more likely to be found throughout the stream in autumn, reflective of behavior attributed to increased habitat connectivity provided by higher regional monsoonal flows (Figure A.1). In McElmo Creek, co-occurrence of fishes at the confluence with the San Juan River during various times of the year may lead to negative interactions through competitive or predatory interactions between the nonnative and native fishes (Gido and Propst 1999; Brandenburg and Gido 1999; Ryden and Smith 2002; Compton et al. 2008). Also, the apparent overlap of Colorado Pikeminnow with Red Shiner and Fathead Minnow at the McElmo Creek confluence with the San Juan River could be driven by dependence of Colorado Pikeminnow on nonnative forage with implications on San Juan River food web dynamics (Gido et al. 2006; Franssen and Durst 2013; Walsworth et al. 2013).

Upstream of pool one, Chaco Wash is a flashy, harsh, intermittent stream, yet it might be relevant to basin-wide fish management objectives considering native species including Colorado Pikeminnow colonize upstream pools. PIT antenna data from the confluence zone, which is a stable, backwater-like habitat, indicated frequent use by several species, primarily endangered fishes. While this is partly an artifact of our sampling design (i.e., fewer fishes were tagged in upstream San Juan River habitats or Chaco Wash compared to in and around McElmo Creek) and temporally limited to one season, the data show a high frequency of use of this habitat suggesting it might offer foraging habitat, thermal refuge, and respite from the higher velocity of the San Juan River (Figure A.2; Fresques et al. 2013). Backwater habitats are relatively rare in the San Juan River and Chaco Wash may represent one of the few stable backwater systems able to constantly support fish use (Bliesner et al. 2009). The confluence area also supported higher abundance of juvenile fishes including Speckled Dace, Flannelmouth Sucker, and Bluehead Sucker. The tributary habitat upstream of the confluence offers harsh, variable, and highly turbid environments that likely prohibit the successful completion of many life history strategies for native and nonnative fish alike. While not presented here, based on observations, Black Bullhead, Red Shiner, and Speckled Dace are the only species that were observed in spawning condition upstream in Chaco Wash.

Movement of fishes corresponded to environmental cues related to spawning (i.e., hydrograph and temperature requirements), predictable weather activity (monsoon season), and flow regime. Razorback Sucker movements peaked during the ascending limb of the San Juan River hydrograph that coincided with the descending limb of the McElmo Creek hydrograph when water temperatures were within the range of spawning conditions 9-17 C in both stream systems and confirms findings of Tyus and Karp (1990). Colorado Pikeminnow had consistent detections at McElmo Creek throughout the year but appeared to become more frequent in late autumn and winter, which is associated with seasonal downstream migrations to more suitable overwintering habitat potentially from warmer water (Durst and Franssen 2014). Year-round detections of Colorado Pikeminnow may reflect transient individuals actively foraging or seeking more desirable thermal and flow regimes relative to the steep flow gradient of the San Juan River (Fresques et al. 2013). Although Colorado Pikeminnow are indeed using the McElmo Creek stream network, there needs to be more substantial investigation into the potential benefits fish gain by using these tributary systems since a potential recruitment bottleneck is occurring for stocked fish (Durst and Franssen 2014). Accordingly, conservation strategies should only consider these habitats if they enhance probability of achieving target conservation goals (i.e., promote recruitment to adulthood). Likewise, Colorado Pikeminnow use of Chaco Wash confluence habitats and upstream pools suggest an upstream oriented behavior of subadult fish potentially driven by similar foraging and refuge seeking. Flannelmouth Sucker detections showed the most dramatic movement associated with spawning during spring where fish from the San Juan River moved upstream into McElmo Creek. These detections were coincident with March sampling that collected ripe, tuberculated males and gravid or expressing females in large schools. It is remarkable that a large-bodied species from the San Juan River like Flannelmouth Sucker uses McElmo Creek to spawn in massive numbers yet similarly large-bodied Razorback Sucker have not adapted the tributary-spawning trait, suggesting they are an obligatory mainstem species. The predictable Flannelmouth Sucker spawning event likely has cascading effects on the fish community and stream ecosystem, especially for downstream predators that presumably forage on drifting larval suckers (Childress et al. 2014). Channel Catfish appear to have multiple movement strategies ranging from limited exploratory movements around the confluence of McElmo Creek with the San Juan to stream network wide forays over 30 km upstream into McElmo Creek. This might reflect opportunistic use of tributary habitats that is coincident with the presence of spawning and young-of-the-year sucker (<100 mm) species from April to July and then high monsoon-driven flows in autumn. For example, Razorback Sucker spawning occurs on a gravel bar near the mouth of McElmo Creek (Ryden 2001) and this activity along with the presence of expressed eggs and recently hatched Flannelmouth Sucker larva drifting out of McElmo Creek could attract Channel Catfish. Other studies have shown Channel Catfish movements are associated with rainfall and increased discharge (Wendel and Kelsch 1999). Likewise, other studies have shown movements often associate to tributary habitats along large rivers (Dames et al. 1989; Newcomb 1989).

Unlike Flannelmouth Sucker and Channel Catfish, distributions of Roundtail Chub and Bluehead Sucker were restricted to upstream habitats in the McElmo Creek tributary network. This corroborates the paucity of detections at the antenna station near the mouth of McElmo Creek. Lack of Bluehead Sucker detections in McElmo Creek can be partially explained by their abundance in the San Juan River which is highest in upstream reaches (Franssen and Durst 2013). Very low detections of Roundtail Chub at the PIT antenna station near the mouth of McElmo Creek can be explained by several factors, including historical alterations and habitat loss in the San Juan River network but also is probably attributed to upstream stocking in McElmo and Yellow Jacket creeks in Colorado (Miller and Rees 2000). Between 2005 and 2013, the McElmo Creek system has received annual autumn stockings of over 96,200 young-of-the-year Roundtail Chub (mean annual total length 39– 73 mm; Fresques et al. 2013; Colorado Parks and Wildlife, unpublished data). Channel Catfish are known to predate upon other stocked species (Marsh and Brooks 1989) and appear to access upstream reaches of McElmo Creek after monsoon seasons in late summer into autumn. Roundtail chub stocking in upstream habitats may overlap with Channel Catfish movements into these areas, despite the considerable distance from the mainstem San Juan River. Spring stocking of age-1 Roundtail Chub may be desirable to avoid unintended loss of stocked native fish to Channel Catfish. Also, stocking at more downstream locations may potentially expand their McElmo Creek distribution or at least provide a better understanding of habitat limitations within the network. The upstream-oriented habitat use of Bluehead Sucker and Roundtail Chub in McElmo Creek is indicative of more abundant preferred habitat including deep pools at the most upstream site (Bower et al. 2008).

Including tributaries in management frameworks can identify potential negative factors and aid conservation of endangered and native fishes throughout different habitats and seasons.

For example, our results highlight the potential for including San Juan River tributaries and their confluence zones in removal efforts to control Channel Catfish that are potentially having a competitive and predatory influence on native fishes (Franssen and Durst 2013). Predictable, seasonal movements, such as those observed in our study provide a reasonable basis for including tributary habitats in targeted removal efforts. Mechanical control could involve weirs near PIT antenna station or physical removal with electrofishing or seining throughout the stream, especially during spring and after high flow events. Removal efforts in tributaries would expand on main channel efforts that may miss fishes seeking refuge in these laterally connected systems (Franssen et al. 2014). Our results also might help inform efforts to stock native fishes in these systems. Lastly, our study illustrated how PIT tag antenna increase the number of recapture events of tagged fishes relative to physical sampling, and the continuous collection of data that can be linked to local stream gages or temperature loggers. PIT tag antennas can be cost prohibitive and spatially limited in their habitat monitoring but are valuable tools that can be tailored to specific questions regarding habitat use, especially at junctions that confluence zones provide. PIT tag antennas also allow data collection during times where it is difficult to sample (i.e., night, winter, etc.)

This study highlights an alternative to longstanding perspectives toward water development in the American Southwest. Dams and diversions are often associated with deleterious effects on native fishes by serving as sources for nonnative species, fragmenting habitats, and altering natural thermal and flow regimes (Clarkson and Childs 2000; Compton et al. 2008). However, in these study systems, water development created habitats that now support several native and nonnative species. McElmo Creek flows increased because of the 1986 construction of McPhee Reservoir in the Dolores River basin that allowed for water to be transported across watersheds and ultimately led to McElmo Creek receiving more perennial flow within the tributary network including Yellow Jacket Creek (Fresques et al. 2013). While not to the same spatial extent, Chaco Wash flows and water presence probably became more persistent with the 1961 construction of the off channel Morgan Lake which is used to cool generators of the coal powered Four Corners Power Plant. We do not advocate for further development but simply acknowledge that these systems that support fish communities likely would be very different and less productive without the regional water development. Additionally, due to water depletions in other smaller tributaries within the San Juan River basin (i.e., La Plata River, Mancos River), the McElmo Creek fish community may function similarly to historically perennial tributaries that have undergone declines in native fish communities (Miller and Rees 2000).

Tributary networks within the Colorado River Basin offer habitats suitable for incorporating increasingly broad fish community studies. The San Juan River has few perennial tributaries adjacent to the middle reaches of the mainstem, so the ones that do exist (McElmo Creek) offer unique habitat in this river network. Tributary habitats and associated use by the fish community will vary over space and time, necessitating active sampling to validate the extent of use across seasons. As research expands to include smaller tributaries into future planning of the Colorado River Basin and other arid river networks it is likely other habitats will similarly require incorporation into a rigorous study, including transient or temporary confluence habitats like ephemeral washes, intermittent stream reaches between perennial water, and billabongs (Benda et al. 2004; Kiffney et al. 2006; Datry et al. 2014). Conservation of fishes and aquatic environments in arid regions will benefit with more exhaustive research into the exchange of species and populations among perennial and ephemeral systems. Combining movement and different flow regimes into comparative studies will likely continue to shed light into habitat use of systems that have been extensively modified in the past and are expected to change in the future.

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Figures and Tables

Figure 1.1 Map of the study area, sites, United States Geological Survey stream gages, and water bodies or structures within the San Juan River (SJR) basin, U.S.A.

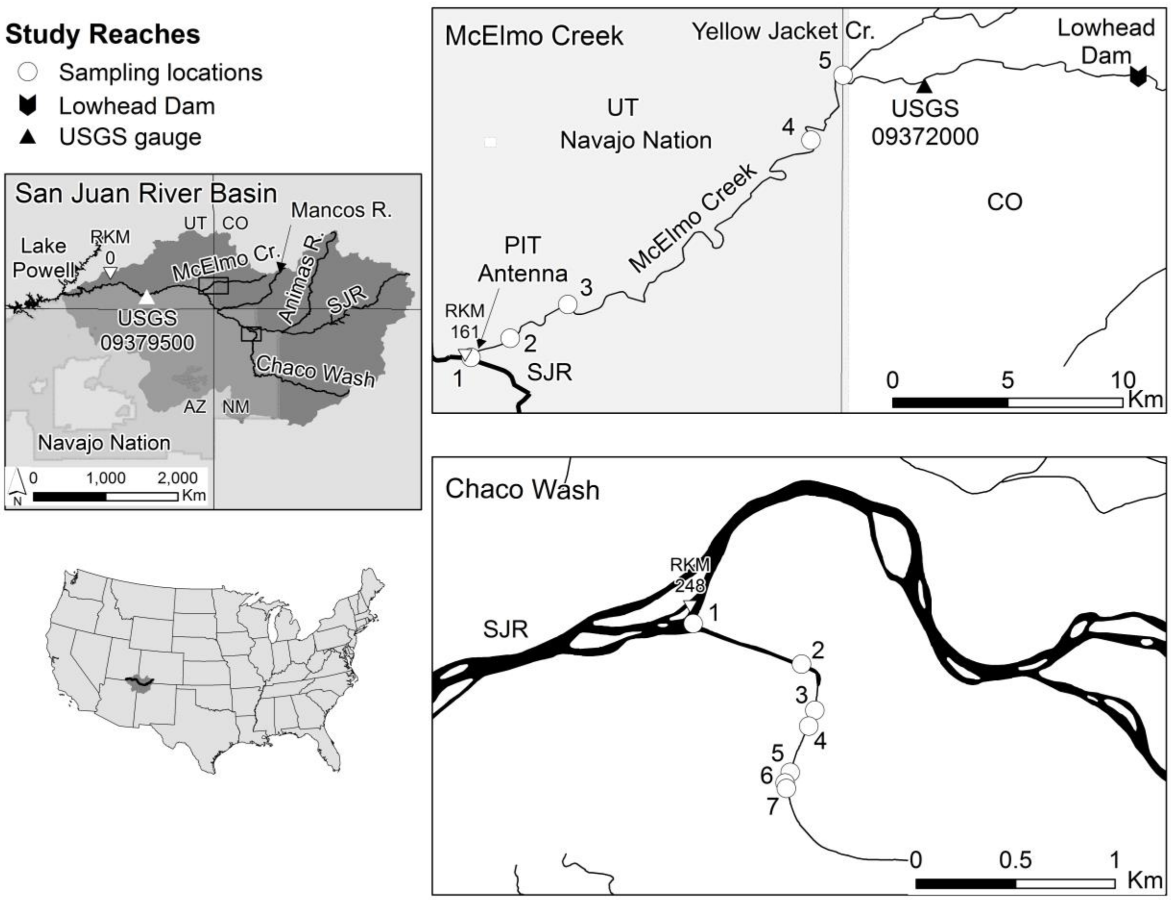

Figure 1.2 Mean wetted width (m), mean depth (cm), and modified Wentworth substrate scores relative to distance from the confluence with the San Juan River in McElmo Creek, UT (left panels) measured at five seasonally sampled sites in 2012 (May and October) and 2013 (March, June, and November). The same metrics were measured in Chaco Wash, NM at seven seasonally sampled habitats measured in 2012 (June and October) and 2013 (March and June). 95% confidence intervals are shown by error bars.

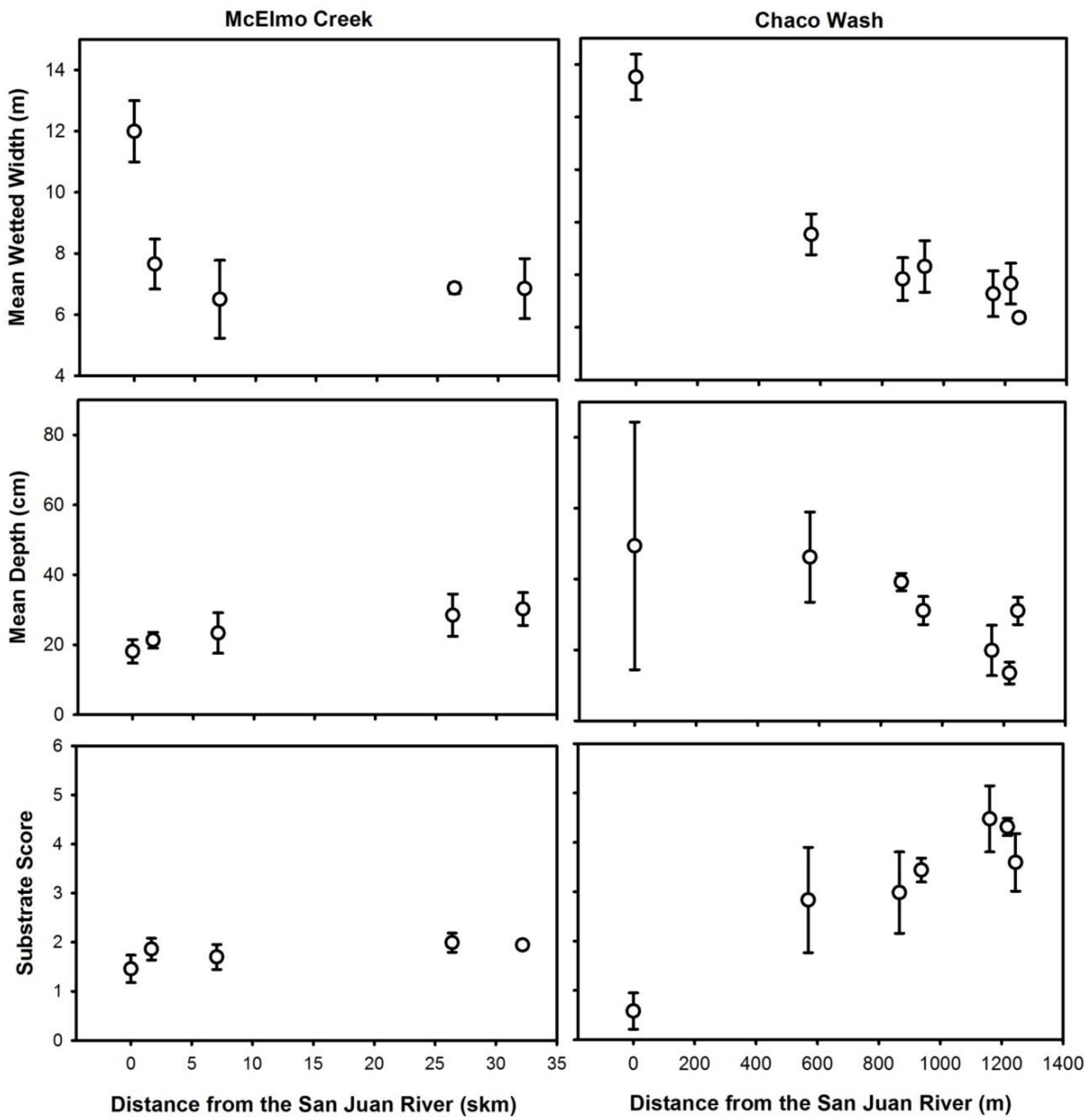

Figure 1.3 Comparison of species richness as a function of upstream distance in kilometers (km) in McElmo Creek, UT and Chaco Wash, NM from their respective confluences with the San Juan River. 95% confidence intervals are shown. McElmo Creek had 5 sites upstream of the confluence with 5 sampling events in 2012 (June and October) and 2013 (March, May, November). Chaco Wash had 7 sites at and upstream of the confluence sampled 8 times

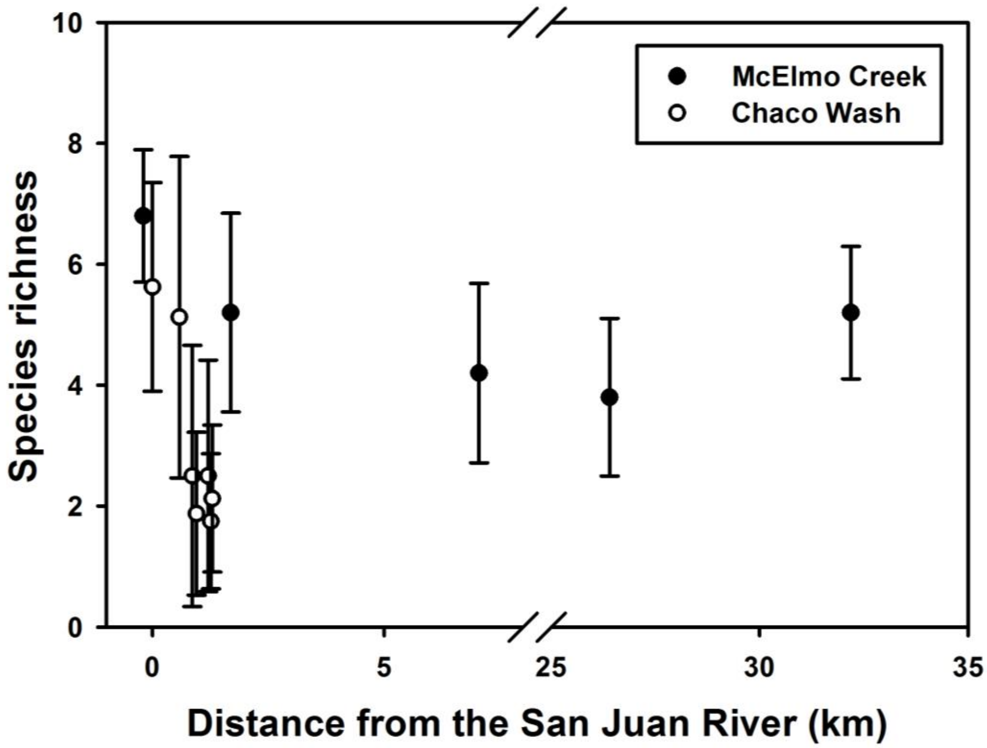

Figure 1.4 Native and nonnative species densities (number per 100 m²) with 95% confidence intervals and distributions upstream of the confluence in kilometers (km) with the San Juan River for eight frequently encountered species in McElmo Creek, Utah based on five sites sampled seasonally in 2012 (June and October) and 2013 (March, May, November).

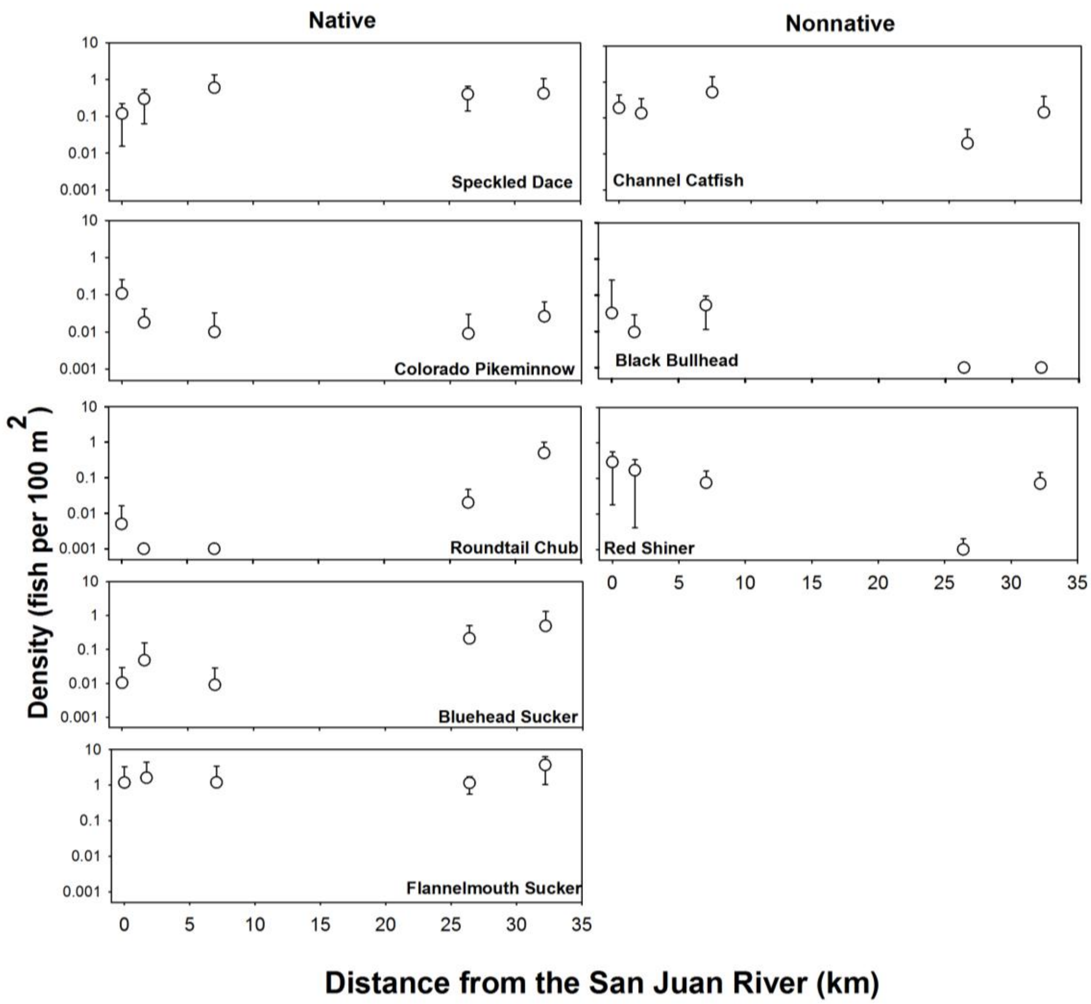

Figure 1.5 Native and nonnative species densities (number per 100 m²) with 95% confidence intervals for frequently encountered native (left panels) and nonnative fish species (right panels) sampled at 7 sites distributed in Chaco Wash, New Mexico upstream from the confluence with the San Juan River during 8 events from 2012 (June, July, August, and October) and 2013 (March, June, August, November).

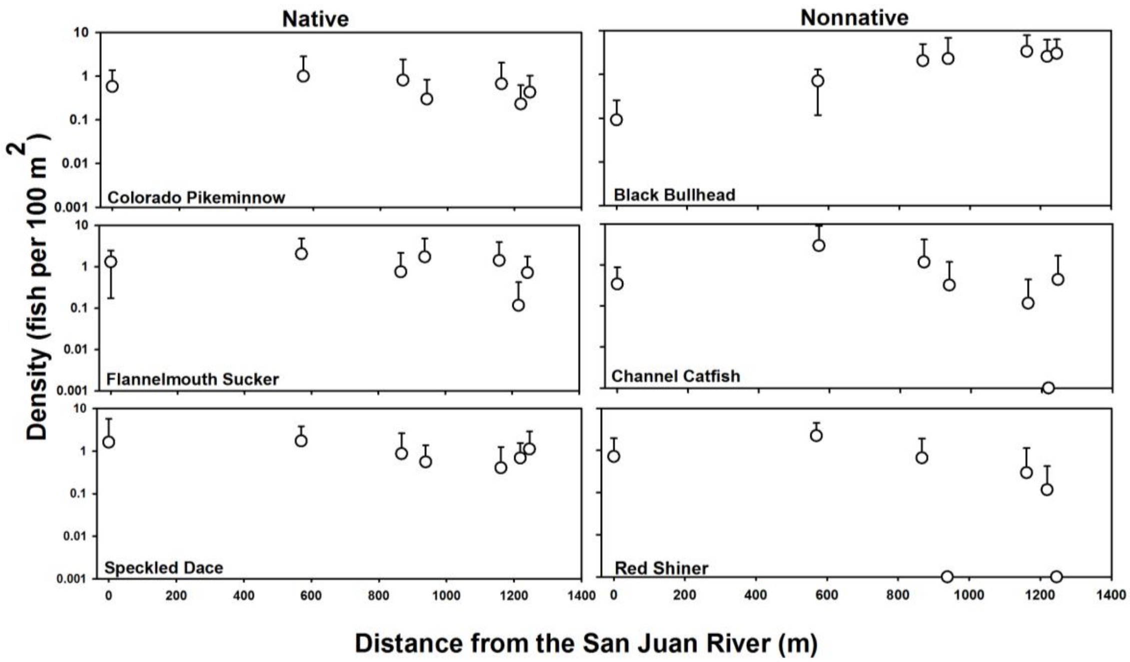

Figure 1.6 Canonical correspondence analysis (CCA) of fish species constrained by site and stream morphometry across sites sampled seasonally in McElmo Creek, UT in June and October 2012, and March, June, and November 2013. CCA axis 1 (x-axis) was associated with upstream distance from the San Juan River. CCA axis 2 (y-axis) was associated with temporal variation in habitats. Native fish are in italics and nonnative fish are in bold letters.

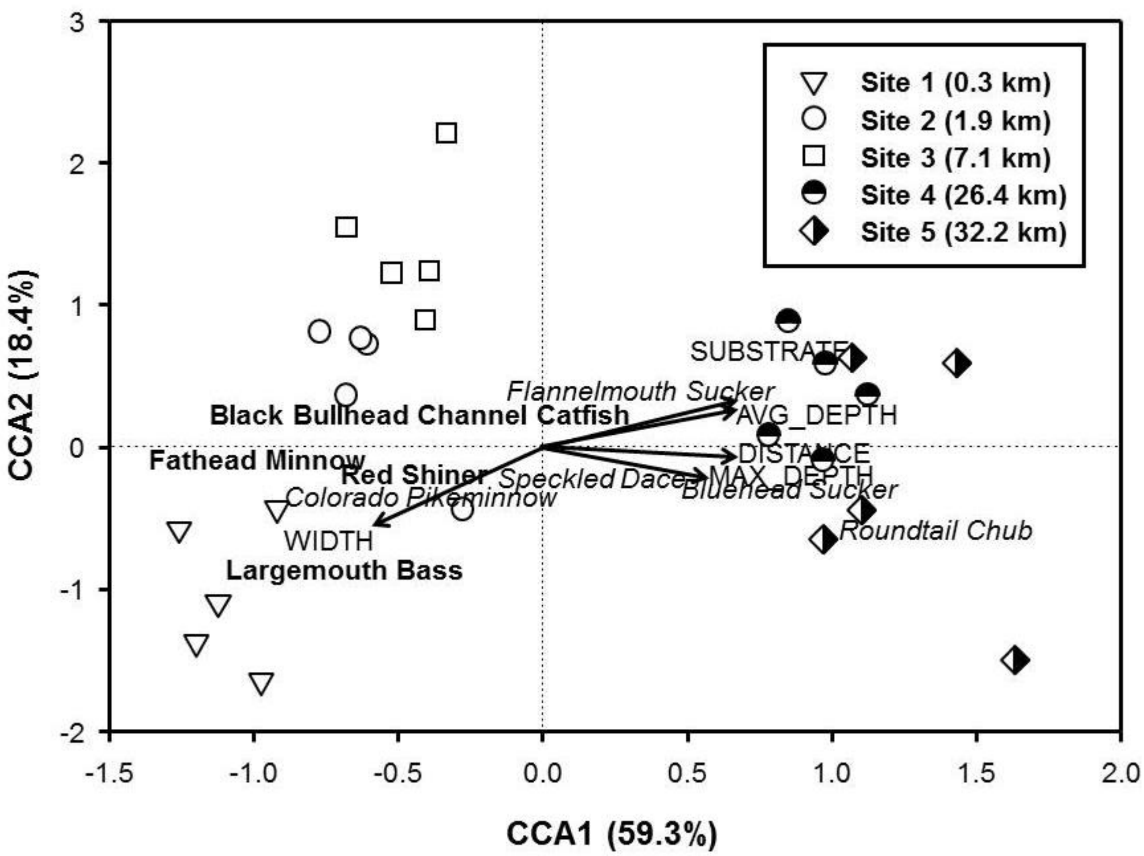

Figure 1.7 Canonical correspondence analysis (CCA) of fish species constrained by site and stream morphometry across sites sampled seasonally in Chaco Wash in June and October 2012, and March and June 2013. CCA axis 1 (x-axis) was associated with upstream distance from the San Juan River. CCA axis 2 (y-axis) was associated with temporal variation in habitats. Native fish are in italics and nonnative fish are in bold letters.

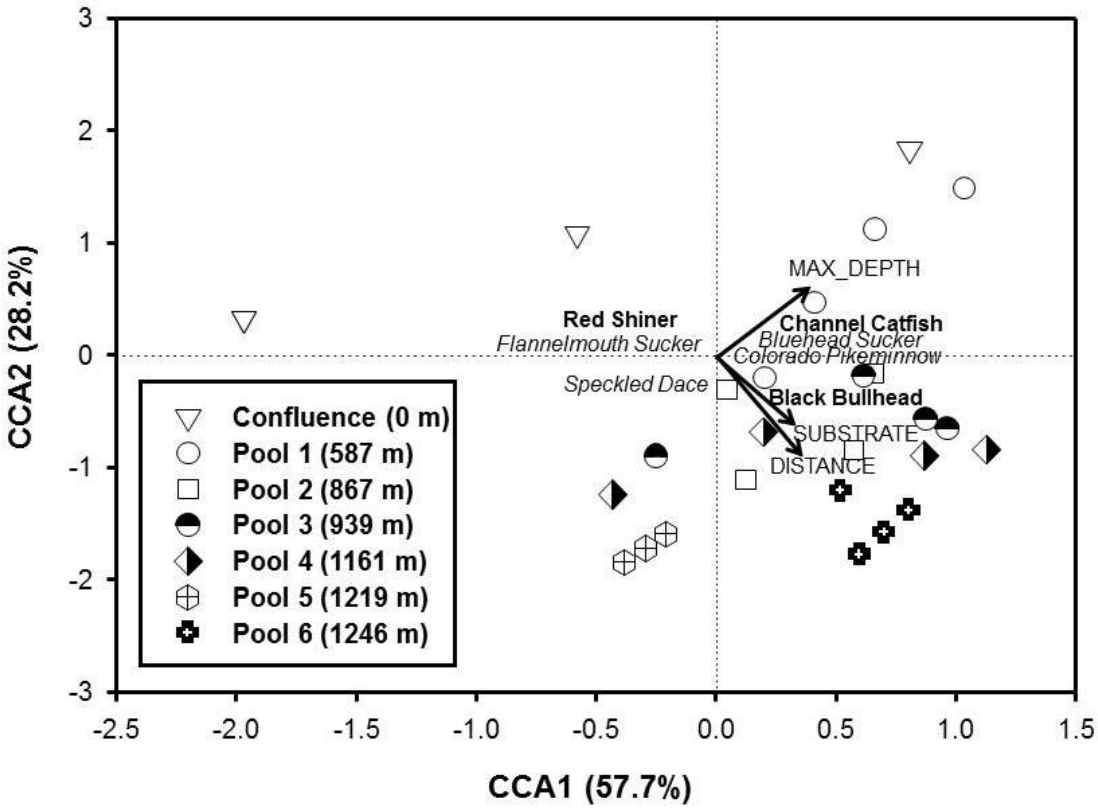

Figure 1.8 Unique monthly detections of Passive Integrated Transponder (PIT) tagged Flannelmouth Sucker (*Catostomus latipinnis*), Channel Catfish (*Ictalurus punctatus*), Razorback Sucker (*Xyrauchen texanus*) and Colorado Pikeminnow (*Ptychocheilus lucius*) at a PIT antenna array in McElmo Creek, Utah 150 meters upstream from the confluence with the San Juan River between 2 May 2012 and 31 January 2014. Mean daily discharge for the San Juan River (USGS gage 9379500, Bluff, Utah) is shown as reference.

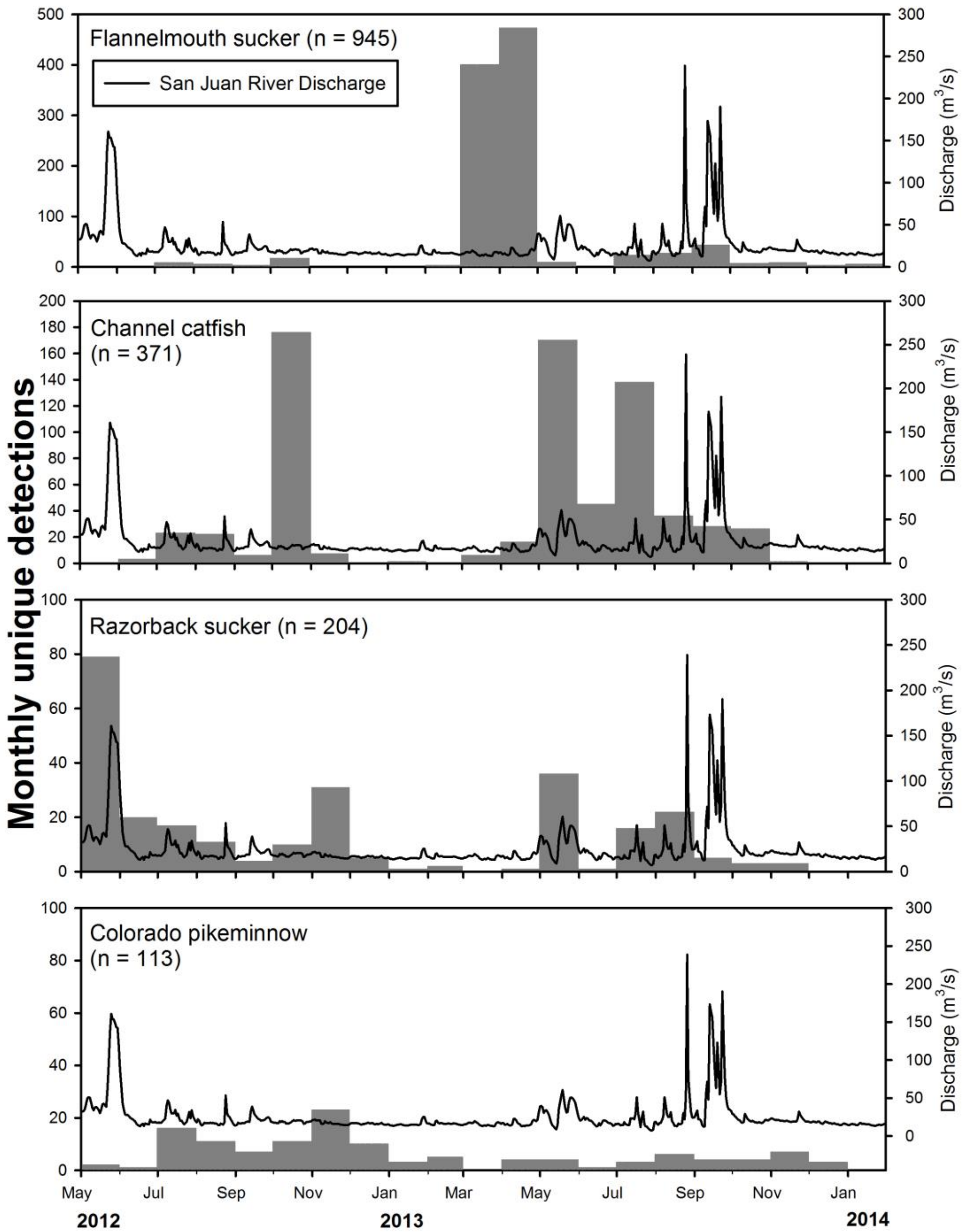

Figure 1.9 Daily unique detections of Passive Integrated Transponder (PIT) tagged endangered Colorado Pikeminnow (*Ptychocheilus lucius*) and endangered Razorback Sucker (*Xyrauchen texanus*) between June 7 and July 17, 2013 at a PIT antenna station in Chaco Wash, New Mexico 27 meters upstream of the confluence with the San Juan River.

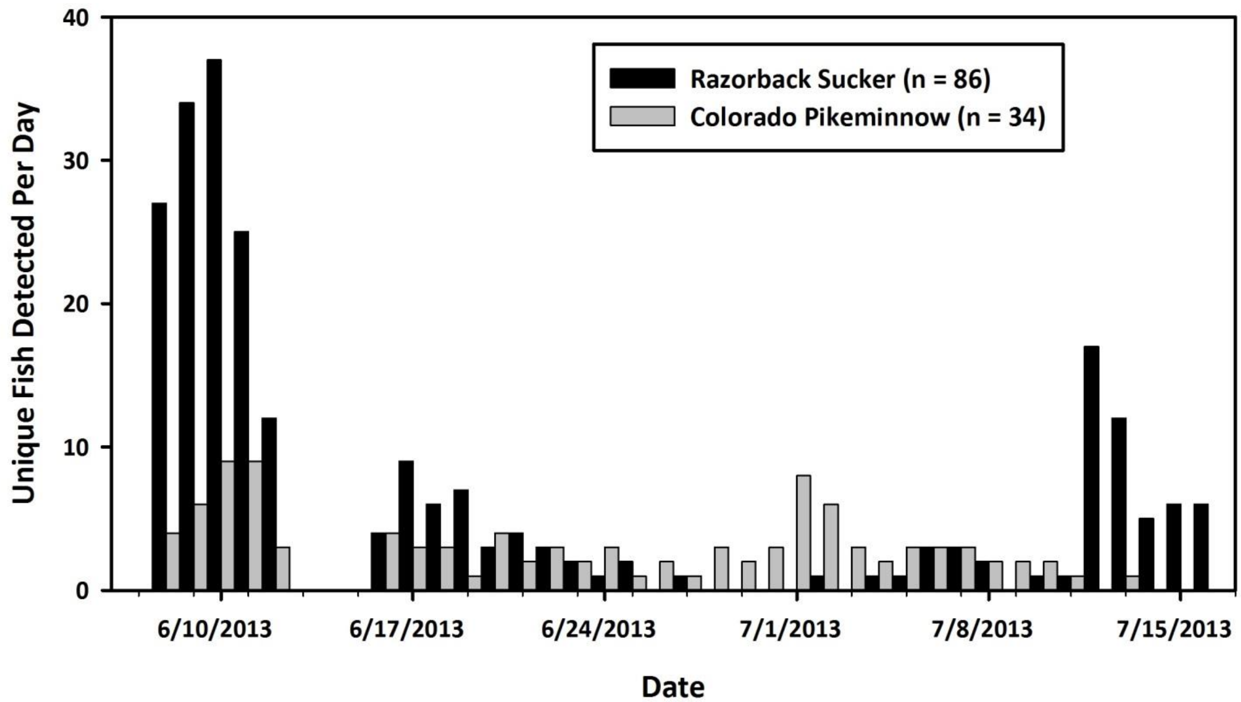

Table 1.1 Fish community sampling summary for McElmo Creek across sites sampled upstream from the San Juan River in June and October 2012 and March, May, and November 2013. Nonnative species are in bold.

	Site Number and Distance from San Juan River (km)					
	1	**2**	**3**	**4**	**5**	
Species	**0.3**	**1.9**	**7.05**	**26.4**	**32.2**	**Total**
Flannelmouth Sucker *Catostomus latipinnis*	200	194	127	117	346	984
Speckled Dace *Rhinichthys osculus*	22	32	48	41	38	181
Channel Catfish *Ictalurus punctatus*	35	14	49	2	16	116
Red Shiner *Cyprinella lutrensis*	50	20	6	0	7	83
Bluehead Sucker *Catostomus discobolus*	2	6	1	22	45	76
Roundtail Chub *Gila robusta*	1	0	0	2	50	53
Colorado Pikeminnow *Ptychocheilus lucius*	19	2	1	1	3	26
Fathead Minnow *Pimephales promelas*	11	2	0	0	0	13
Black Bullhead *Ameiurus melas*	6	1	5	0	0	12
Largemouth Bass *Micropterus salmoides*	6	1	0	0	0	7
Hybrid Sucker *C. latipinnis x C. discobolus*	0	0	0	0	3	3
Western Mosquitofish *Gambusia affinis*	2	0	0	0	0	2
Razorback Sucker *Xyrauchen texanus*	1	0	0	0	0	1
Common Carp *Cyprinus carpio*	0	1	0	0	0	1
Total	355	273	237	185	508	1558

Table 1.2 Fish community sampling summary for Chaco Wash, NM across 7 sites at and upstream of the confluence with the San Juan River during 2012 (June, July, August, October) and 2013 (March, June, August, November). Nonnative species are in bold.

	Site Number and Distance from the San Juan River (m)							
	1	**2**	**3**	**4**	**5**	**6**	**7**	
Species	**0**	**570**	**867**	**939**	**1161**	**1219**	**1246**	**Total**
Speckled Dace *Rhinichthys osculus*	110	22	9	5	3	6	8	163
Flannelmouth Sucker *Catostomus latipinnis*	81	26	7	16	12	1	5	148
Black Bullhead *Ameiurus melas*	6	9	22	23	33	22	22	137
Red Shiner *Cyprinella lutrensis*	47	28	7	0	2	1	0	85
Channel Catfish *Ictalurus punctatus*	16	34	11	3	1	0	3	68
Colorado Pikeminnow *Ptychocheilus lucius*	34	11	8	3	6	2	3	67
Bluehead Sucker *Catostomus discobolus*	8	9	2	10	3	3	1	36
Common Carp *Cyprinus carpio*	12	2	0	0	1	0	0	15
Fathead Minnow *Pimephales promelas*	11	1	0	0	0	0	0	12
Western Mosquitofish *Gambusia affinis*	4	3	0	0	2	0	0	9
Largemouth Bass *Micropterus salmoides*	1	5	0	0	1	0	0	7
Green Sunfish *Lepomis cyanellus*	0	2	0	0	0	0	1	3
Razorback Sucker *Xyrauchen texanus*	1	0	0	0	0	0	0	1
Total	331	152	66	60	64	35	43	751

Table 1.3 Detections of tagged fishes at the McElmo Creek, UT stationary Passive Integrated Transponder (PIT) antenna array between 2 May 2012 and 31 January 2014. Nonnative fishes are in bold.

Species	**Detected**
Flannelmouth Sucker (*Catostomus latipinnis*)	945
Channel Catfish (*Ictalurus punctatus*)	**355**
Razorback Sucker (*Xyrauchen texanus*)	150
Colorado Pikeminnow (*Ptychocheilus lucius*)	113
Black Bullhead (*Ameiurus melas*)	**10**
Bluehead Sucker (*Catostomus discobolus*)	7
Largemouth Bass (*Micropterus salmoides*)	**3**
Roundtail Chub (*Gila robusta*)	2
Hybrid Sucker (*C. discobolus x C. latipinnis*)	1
Total	1586

*16 Unknown detections are not included in total number

Table 1.4 Detections of tagged fishes at a portable Passive Integrated Transponder (PIT) tag Chaco Wash, NM between 7 June and 17 July 2013. Nonnative fishes are in bold.

Species	Detected
Razorback Sucker *Xyrauchen texanus*	86
Colorado Pikeminnow *Ptychocheilus lucius*	34
Flannelmouth Sucker *Catostomus latipinnis*	7
Black Bullhead *Ameiurus melas*	3
Channel Catfish *Ictalurus punctatus*	3
Common Carp *Cyprinus carpio*	2
Total	135

*7 Unknown tags detected not included in total

Chapter 2 - Habitat Use and Movement Behavior of Fishes at a Desert Stream Confluence Zone

Abstract

River confluence zones connect disparate habitats and support increased species diversity and life history strategies. The local "edge" effects of confluence zones have potentially more spatially expansive consequences for entire river network processes because they might inhibit or facilitate movement through the system. We studied the junction of two small streams in the San Juan River basin to characterize habitat use and movement behavior of fishes with respect to the confluence zone. The fish community in this area was comprised of > 90% native fishes. The reach downstream of the confluence had consistently higher abundances, diversity, and more frequent detections of tagged fish relative to upstream reaches. The confluence habitat on average contained the highest abundance and richness of all habitats sampled. Movement among habitats was significantly different among species and size classes. Small flannelmouth sucker (*Catostomus latipinnis;* < 300 mm) and roundtail chub (*Gila robusta*) were commonly detected in Yellow Jacket Creek whereas large flannelmouth sucker (> 300 mm), bluehead sucker (*C. discobolus*), and channel catfish (*Ictalurus punctatus*) primarily used McElmo Creek habitats. Movements differed according to McElmo Creek discharge where channel catfish appeared after the monsoon season began while other large-bodied fishes (flannelmouth sucker and bluehead sucker) were displaced. Monsoon events also triggered movements of roundtail chub, small flannelmouth sucker, and black bullhead (*Ameiurus melas*) between McElmo and Yellow Jacket creeks. These results suggest confluence zones maintain local diversity through increased habitat heterogeneity and regional diversity by providing movement corridors for different species and size classes of native fishes.

Introduction

One of the major challenges in understanding how the spatial structuring of fish communities arises comes from the complexity surrounding interactions among species with different life histories and adaptations to complementary habitats that exist within spatially variable stream networks (Schlosser 1995; Fausch et al. 2002; Fullerton et al. 2010). Neighborhood effects and landscape complementation are spatial processes responsible for maintaining diverse life history strategies within and among species (Dunning et al. 1992; Falke et al. 2013). Neighborhood effects arise when adjacent habitat conditions influence an organism (e.g., a fish in this study) within a given spatial scale (Addicott et al. 1987). Landscape complementation involves life-stage specific requirements that habitats meet for a particular species (e.g., one tributary offers adult fish habitat and another tributary is used by juveniles for rearing; Falke et al. 2013). These spatial processes ultimately govern complex, species-specific movement behaviors that can vary depending on age, size, disturbance, and interspecific interactions across a stream network (Skalski and Gilliam 2000; Gilliam and Fraser 2001; Young 2011). Thus, the interaction of stream network configuration and habitat arrangements is a major factor in habitat selection of species.

Confluences are ubiquitous stream network habitats that have been recognized as hotspots for physical and geomorphological processes including their largely downstream influence on channel morphology, sediments, and thermal regime (Benda et al. 2004). Diversity and abundance responses to confluence zones are less understood but can positively influence aquatic macroinvertebrates distributed around a stream junction (Rice et al. 2001). Responses are attributed to habitat heterogeneity because confluence zones represent discrete transitions that might join two similar-sized streams with similar habitat and water quality (and potentially function) or join streams with vastly different habitat and water quality (Rice et al. 2001).

Ecological processes of streams in and around confluence zones can also be influenced by the types of habitats being connected and spatial positioning of confluences relative to natural (e.g., mainstem rivers) or unnatural features (e.g., reservoirs) of the riverscape (Benda et al. 2004; Hitt and Angermeier 2008a; Hitt and Angermeier 2008b). For example, small streams connected to mainstem rivers (Thornbrugh and Gido 2010) or reservoirs (Falke and Gido 2006) often contain fish species indicative of those adjacent habitats. Falke and Gido (2006) noted the confluence between Great Plains streams and reservoirs supported higher diversity than adjacent stream reaches due to a blended community of reservoir and stream species. The spatial extent of those influences can be abrupt or extend several kilometers upstream (Hitt and Angermeier 2008a, Thornbrugh and Gido 2010). Despite the recognition of confluence zones as critical interfaces of geomorphological and ecological processes in a variety of branched networks, research emphasizing patterns of species behavior and habitat use surrounding these confluence zones is lacking (Fisher 1997; *sensu* Douglas and Douglas 2000).

The Colorado River basin is an iconic large stream network characterized by significant reductions in diversity of native fishes preceded by expansive alterations in mainstem and tributary habitats (Minckley and Deacon 1968; Douglas and Marsh 1998; Clarkson and Childs 2000; Pool et al. 2010). While major tributaries and mainstem habitats have been studied more rigorously, smaller tributaries are often overlooked because of remoteness, political boundaries, or simple lack of knowledge of their contributions to fish communities (Clarkson et al. 2012; Pool et al. 2013). There has been some work to include small tributaries into Colorado River management initiatives (Wick et al. 1991; Bottcher et al. 2013; Fresques et al. 2013). Fish access these tributaries from large tributaries or mainstem habitats and confluence zones in mainstem and large tributary systems are thought to promote abundance of migratory native fish through landscape complementation (Douglas and Marsh 1998; Weiss et al. 1998; Douglas and Douglas 2000; Webber et al. 2013). Investigation into how small tributary confluence zones affect fish communities is relevant to management within the Colorado River network that often aims to simultaneously conserve imperiled native species and control nonnative fishes (Robinson et al. 1998; Bottcher et al. 2013).

We investigated multi-scale patterns of fish community structure and movement behaviors at and around a confluence joining two small tributaries in the San Juan River basin. The two primary objectives of this study were to characterize 1) fish diversity and abundances in habitats and reaches around the confluence zone and 2) movement behaviors among species and size-classes within and among reaches around the confluence zone. We hypothesized that 1) diversity and abundance would peak at and downstream of the confluence via increased habitat heterogeneity and habitat size and 2) movement among reaches would differ according to species and size-class but would generally be greatest downstream of the confluence due to movement into the confluence area but not farther upstream. Movement differences by species and size-class are likely due to different life history traits and differential accessibility to habitat types according to habitat features (i.e., ability to fulfill life history requirements, connectivity) and body size.

Methods

Study Area

McElmo Creek drains 1,818 km² in Colorado and Utah before emptying into the San Juan River near Aneth, UT approximately 163 river km (rkm) upstream of Lake Powell (Figure 2.1; Navajo Nation Environmental Protection Agency 2012). Yellow Jacket Creek is a perennial tributary to McElmo Creek flowing almost entirely within Colorado before entering McElmo Creek at the

Colorado-Utah border, approximately 32 rkm upstream of the San Juan River. The McElmo and Yellow Jacket confluence area is at an elevation of 1,475 m above sea level. McElmo Creek and Yellow Jacket Creek were historically an intermittent stream network, but irrigation and water development stemming from the creation of McPhee Reservoir in 1986 effectively transformed it to a perennial system by transporting Dolores River basin water into the McElmo and Yellow Jacket watersheds (Fresques et al. 2013). Riparian vegetation around the confluence is dominated by Russian olive *Elaeagnus angustifolia* but also includes saltcedar *Tamarisk* spp. and willow *Salix* spp. This study area was frequented by cattle and feral horses.

Characterizing Fish Community Structure, Habitat, and Movement

To identify spatial and temporal variation in fish community structure around the Yellow Jacket and McElmo creek confluence we sampled 17 habitats 10 times between June 2012 and June 2014 (Figure 2.1). Downstream of the confluence of McElmo and Yellow Jacket creeks, we sampled the first five pools. Upstream of the confluence, we sampled the first five pools in Yellow Jacket Creek and the first six pools in McElmo Creek. The confluence habitat was sampled individually and was considered as the pool or run extending to the first riffle upstream or downstream of the confluence of McElmo and Yellow Jacket creeks. Sampling occurred in 2012 (June, August, and October), 2013 (March, May, July, August, and November), and 2014 (March and June). Fish were sampled in each habitat with backpack electrofishing during low flow periods (base flow where mean daily discharge < 0.57 m^3/s) or by chasing fish into a bag seine with a backpack electrofisher (during monsoon season when late-summer rainstorms increased flows that exceeded base flows and turbidity reduced visibility). All fishes > 115 mm were tagged with a uniquely coded full-duplex Passive Integrated Transponder (PIT) tag (12.5 x 2.07 mm, 134.2 kHz, BioMark, Boise, Idaho). We tagged fishes throughout McElmo Creek and the San Juan River mainly between rkm 161 and 153 from 2012-2014, in addition to other tagging conducted by Colorado Parks and Wildlife in reaches upstream of our study between 2011-2014, and by the United States Fish and Wildlife Service who tagged endangered Colorado pikeminnow *Ptychocheilus lucius* and razorback sucker *Xyrauchen texanus* (Cathcart et al., in prep). Habitats were measured concurrent with fish sampling, except August 2012. We measured wetted widths, substrates and depths at two transects per individual pool habitat. Substrates and depths were measured at ten equally spaced points along the wetted width. Maximum pool depth was also measured and sought out if separate from the initial pool transect.

To monitor movement behaviors around the confluence area, three PIT antennas were deployed upstream (McElmo and Yellow Jacket creeks) or downstream (only McElmo Creek) of the first riffle separating reaches around the confluence from May 29 – August 2, 2013 (Figure 2.1, inset). Antenna dimensions in reaches upstream of the confluence were 1.52 x 0.76 m while the downstream antenna was 3.05 x 0.76 m (BioMark, Boise, Idaho). The antennas effectively served as boundaries between other adjacent habitats and reaches. Water temperature loggers were deployed June 2 in McElmo and Yellow Jacket creeks upstream of the confluence in 2013 to measure temperature every 30 min. The McElmo Creek temperature logger was dislodged during a monsoon event on July 23 and the Yellow Jacket Creek water temperature logger was stopped when antenna detections ended August 2. A water temperature logger was also deployed in the downstream reach of McElmo Creek but was lost during a high flow event in July 2013. McElmo Creek discharge was collected spanning the dates of antenna deployments by a USGS streamflow gage (09372000) upstream of the study area. While flood events in both creeks can exceed 7 m^3/s, Yellow Jacket Creek winter base flows are between 0.113-0.169 m^3/s whereas autumn (post-monsoon) flows are higher and range from 0.424-0.707 m^3/s (Fresques et al. 2013).

Data Analysis

Habitat and Reach Scales

Evaluating how species diversity and abundance vary at habitat (e.g., pool – run complex) and reach (i.e., series of 5-6 habitats) scales around a confluence was explored with four analyses. First, habitat (wetted width and maximum depths) and fish abundance and species richness at habitat scales were visually analyzed with respect to distance from the confluence using bubble plots overlaid on a spatially-explicit representation of the confluence zone. Species abundances were square-root transformed prior to plotting these data due to undo influence of a few extremely large abundance values. Flannelmouth sucker abundances were split into four size classes to identify ontogenetic changes in habitat use ranging from young-of-year to adult fish. In a second analysis, we ranked habitats based on their overall mean-richness to test whether the confluence habitat conformed to our hypothesis that it would have the highest diversity relative to other habitats. Thirdly, we performed unconstrained correspondence analysis (CA) to explore habitat scale variation in fish community structure using $\log_{10}$+1 transformed abundances across all sampling periods. Significant axes were determined with the Kaiser-Guttman criterion where nonsignificant axis are deemed as random. Finally, repeated measures analysis of variance (ANOVA; $\alpha = 0.05$) with time as the repeated factor was used to test whether species richness, log-transformed abundances, and habitat (wetted widths, maximum depths) differed among reaches surrounding the confluence (i.e., downstream and upstream in McElmo Creek, Yellow Jacket Creek) and the confluence habitat.

Movement Behavior

For movement analyses relevant to hypothesis two, all tagged fishes were analyzed by species except flannelmouth sucker which were grouped into two size classes, small (115 - 300 mm) and large (> 300 mm). Unique tags (individual fish) were enumerated and analyzed per species, per day and per antenna to determine frequency of habitat use (antenna) according to mean number of unique fish detected per day throughout the length of the antenna deployment and to determine movement behaviors of unique fish among antennas. To evaluate if movement behaviors differed among species, size classes and environmental cues we analyzed movement data collected by the PIT antennas in three ways. First, differences in the frequency of occurrence of PIT tagged fish identified from the three antennas around the confluence (Figure 2.1) was evaluated with ANOVA ($\alpha = 0.05$). Post hoc analyses with Tukey's HSD were used to test pairwise contrasts between habitats (antennas) for each species and size class. Secondly, we classified movement behaviors of each species and size class based on antenna detections through the use of Venn diagrams. These diagrams illustrated the seven possible movement behaviors of fishes through and around the confluence area: 1) restricted to upstream McElmo Creek 2) restricted movement at Yellow Jacket Creek 3) restricted movement downstream in McElmo Creek 4) movement between upstream McElmo and Yellow Jacket creeks 5) movement between upstream and downstream segments of McElmo Creek 6) movement between downstream McElmo Creek and Yellow Jacket Creek and 7) detections at all three antennas. Finally, to classify habitat (antenna) use for each species and size classes we used cluster analysis (R version 3.0.3) based on the proportion of detections among the seven possible habitat-use scenarios. Cluster distances were based on chi-square distances of the proportion of fishes exhibiting one of the seven movement behaviors and were restricted to fishes that had at least nine detections (Legendre and Legendre 1998). Complete agglomerative linkages were used for cluster analysis rather than single agglomerative linkages which are used more often to illustrate gradients (Borcard et al. 2011). All statistical analyses were performed in R. 3.0.3 (R Development Core Team 2008).

Results

Habitat Scale

Habitat metrics relative to distance and direction from the confluence illustrate the habitat-to-habitat variation in width, depth, and resulting richness (Figure 2.2). Generally, Yellow Jacket Creek habitats were much shallower and narrower than all McElmo Creek habitats but pools downstream from the confluence were relatively wider and deeper than upstream McElmo Creek habitats (Figure 2.2). We collected 2,073 individual fish representing 12 species and a *C. latipinnis* x *C. commersonii* hybrid (Table 2.1) over the course of 170 sampling events (17 habitats sampled 10 different months). One hundred and fifty-eight individuals were unidentified larval sucker species that were omitted from the analysis, leaving 1,915 individual fish available for analysis. Flannelmouth sucker and speckled dace (*Rhinichthys osculus*) were the most abundant large-bodied and small-bodied native fishes, respectively. Channel catfish and red shiner (*Cyprinella lutrensis*) were the most abundant large-bodied and small-bodied nonnative fishes, respectively. Over 90% of the individuals captured were native fishes (Table 2.2). Overall, the confluence habitat contained the highest total abundance (411 fishes), highest total diversity (12 species), and highest mean-richness ranking (3.4) across all sampling periods (Table 2.1; Figure 2.3). Three habitats in the McElmo Creek downstream reach (Tables 2.1 and 2.2) ranked in the top third of all samples (Figure 2.3). Habitats influenced species richness similarly to mean-richness rankings and also structured communities across two significant gradients as indicated by unconstrained CA: spatial (CA1 axis, 20% variation) and temporal (CA2 axis, 17% variation explained) (Figure 2.4). Thirty of the 170 samples were fishless with

83% of fishless samples occurring in upstream McElmo Creek or Yellow Jacket Creek reaches (Table 2.2).

Reach Scale

Mean daily temperatures from McElmo Creek and Yellow Jacket creek differed by an average of 0.6 C with McElmo Creek usually being warmer (Figure 2.5). Comparisons among reaches showed the highest mean richness occurred downstream of the confluence (Figure 2.6a) but based on ANOVA, no significant differences existed among reaches and the confluence habitat. ANOVA testing log-transformed total abundances among reaches was significant ($F_{3, 39} = 4.13$, $P = 0.013$). Post hoc analysis using Tukey's HSD found only Yellow Jacket Creek had significantly lower abundance than the downstream McElmo Reach ($P = 0.006$; Figure 2.6b).

Based on ANOVA, mean maximum depths were significantly different ($F_{3, 35} = 15.19$, $P < 0.001$) among reaches and the confluence habitat. Post hoc analysis with Tukey's HSD showed that only Yellow Jacket Creek was significantly shallower than the two McElmo Creek reaches (Figure 2.6c). Mean wetted widths were significantly different ($F_{3, 35} = 44.19$, $P < 0.001$) among reaches and the confluence habitat. Post hoc analysis with Tukey's HSD suggested McElmo Creek reaches and the confluence habitat were significantly wider than Yellow Jacket Creek and downstream McElmo Creek was significantly wider than upstream McElmo Creek but neither McElmo Creek reach was significantly different than the confluence habitat (Figure 2.6d).

Movement

Of the 2, 873 individuals from eight species tagged in the McElmo Creek network (including Yellow Jacket Creek but excluding San Juan River fishes), 594 representing all eight species were tagged within the confluence study area prior to the completion of this study in August 2013 (Table 2.3). The three antennas cumulatively detected 270 individual tags (seven species) during the 66 d antenna deployments. Detected fishes were from tagging events between 2011 and 2013 and were at-large an average of 92 days prior to first detection (Table 2.3; Figure B.1). Distance from where detected fishes were tagged included habitats within the study area (< 500 m) and as far away as in the San Juan River (> 32 rkm downstream). Based on a one-way ANOVA, movement behavior indicated by number of unique detections per day differed significantly among antennas ($F_{2, 65} = 61.28$, $P < 0.001$) and among species and size classes ($F_{5, 65} = 80.46$, $P < 0.001$). Post hoc comparisons of antenna use by the fish community indicated the McElmo Creek antennas received significantly higher mean daily unique detections relative to Yellow Jacket Creek (Table 2.4; Figure B.2). Accordingly, a post hoc analysis was performed with Tukey's HSD to test habitat use of each species or size class, allowed us to interpret different habitat affinities for species (Table 2.4). Small flannelmouth sucker (< 300 mm) mean daily unique detections at the downstream McElmo Creek antenna were significantly higher than the upstream reach of McElmo Creek, which was more frequently used than Yellow Jacket Creek. Large flannelmouth sucker (> 300 mm) detections in both McElmo Creek reaches did not differ but were significantly higher than the Yellow Jacket Creek reach. Roundtail chub (*Gila robusta*) detections in the upstream McElmo Creek reach were significantly higher than Yellow Jacket Creek, but was not significantly different from the downstream McElmo Creek antenna. Bluehead sucker (*C. discobolus*) detections in both McElmo Creek reaches were significantly higher than the Yellow Jacket reach but not significantly different from each other. Channel catfish detections in the upstream McElmo Creek reach were significantly higher than other reaches with the downstream McElmo Creek reach having significantly higher mean daily unique detections than Yellow Jacket Creek. Black bullhead (*Ameiurus melas*) mean daily unique detections among each reach were not significantly different.

Antenna detections varied according to species, size, and environmental cues like mean daily McElmo Creek discharge and connectivity (Figure 2.7). The monsoon season increased McElmo Creek daily discharge and was coincident with the arrival of channel catfish and a disappearance of large flannelmouth sucker and bluehead sucker. Monsoon season and higher discharge was also coincident with frequent use of Yellow Jacket Creek by small flannelmouth sucker and black bullhead. Roundtail chub used Yellow Jacket Creek consistently throughout the study, except for the ~15 d period in early July where low flow in Yellow Jacket Creek prevented connectivity with McElmo Creek. Visualizing movement behaviors of the tagged populations of fishes with Venn diagrams illustrated intra- and interspecific differences (Figure 2.8; Table 2.5). The majority of fishes (178 of 270 individuals) detected used the confluence zone to move among two or more habitats but had species-specific habitat use. Bluehead sucker and channel catfish occupied primarily McElmo Creek sections; roundtail chub and black bullhead regularly moved among all three antennas; and flannelmouth sucker exhibited the differential movements between small and large fish where fish under 300 mm moved into Yellow Jacket Creek (especially after monsoons began) and fish greater than 300 mm remained in McElmo Creek reaches (Figures 2.7 and 2.8). Cluster analysis generated with the proportions of the seven different movement strategies illustrated with the Venn diagrams identified three general movement behaviors of fishes around the McElmo and Yellow Jacket confluence (Table 2.5). Cluster 1 was restricted to channel catfish that displayed a largely upstream McElmo Creek signature. Cluster 2 was represented by large flannelmouth sucker (>300 mm) and bluehead sucker which exhibited movements among both upstream and downstream reaches of McElmo Creek. Cluster 3 included small flannelmouth sucker (< 300 mm), roundtail chub, and black bullhead which all moved regularly through the confluence to access all three reaches in McElmo Creek (upstream and downstream) and Yellow Jacket Creek (Figure 2.9).

Discussion

Habitat and Reach Scales

Our multi-scale observations tested patterns of abundance and diversity among individual habitats as well as reaches surrounding the McElmo Creek and Yellow Jacket Creek confluence. Patterns in overall abundance, diversity, and mean ranking of the 17 habitats were consistent with the prediction that confluence habitats support diversity hotspots at the local scale. The lack of significant difference in richness among reaches may be attributed to the high temporal variability among habitats within reaches as well as species turnover. While both the reach and habitat scales were associated with different patterns in diversity and distributions, habitats downstream of the confluence maintained higher diversity ranks and abundance relative to other habitats in upstream reaches, lending support to the claim that the confluence complements habitats downstream (Figure 2.3). The finer spatial resolution of habitat-scale measurements relative to reach scale measurements revealed greater variation in habitat properties. For example, variability in maximum pool depth was greater at and downstream of the confluence (Figure 2.6c). Variability in wetted widths was also greater downstream of the confluence although one outlier in McElmo Creek upstream of the confluence skews this relationship (Figure 2.6d). Species associations to habitats based on the first CA axis indicated smaller bodied fishes (i.e., fathead minnow, black bullhead, red shiner) were more associated to Yellow Jacket Creek habitats than larger bodied fishes (i.e., flannelmouth sucker and channel catfish) which had more negative first CA axis scores (Figure 2.4). The second significant CA axis is generally a temporal gradient in community structure but in this case, may require further analysis to support interpretations. For example, negative scores could indicate higher abundance in spring or early summer as seen in flannelmouth sucker which may be biased toward higher spring sample sizes. Species scores near zero are fish more likely caught in summer or fall (i.e., roundtail chub and channel catfish) and species with more positive scores have relatively expansive distributions across more seasons like red shiner and speckled dace.

Movement Behavior

Our second hypothesis that movement behaviors would differ according to species and size-class but movement would generally be greatest downstream of the confluence was partially supported by PIT tag detections. Whereas the grand mean number of daily unique detections throughout the duration of antenna deployments were generally lowest at the Yellow Jacket antenna (Table 2.4; Figure B.1), this pattern was not consistent among species and size-classes, suggesting movement behaviors among species are different. For example, no differences in detections among McElmo Creek reaches were observed for large flannelmouth suckers but small flannelmouth suckers were significantly different among all reaches. The different movement behaviors among flannelmouth sucker size classes may be due to a progressive recruitment of individuals throughout the system where larger fish (> 300 mm) recruit out of Yellow Jacket Creek (because of smaller, more shallow habitats) into McElmo Creek as subadult fish and ultimately to the mainstem San Juan River as adults (> 400 mm). These adult flannelmouth suckers return to McElmo Creek in the spring between February and March for spawning (Cathcart et al., in prep). Distributions of multiple size classes of flannelmouth sucker around the confluence corroborate ontogenetic changes in habitat use (Figure B.4) and are an example of how age-structured spatial distributions of stream fish populations arise from landscape complementation (Young 2011). These findings also support movement as a dynamic stream network process that can maintain the expansive distributions of flannelmouth sucker throughout mainstem, large tributary, and small streams in the altered Colorado River basin (Chart and Bergerson 1992; Douglas and Marsh 1998; Weiss et al. 1998; Compton et al. 2008).

Based on antenna detections, Yellow Jacket Creek habitat might provide refuge from high flows and facilitates the local persistence of roundtail chub, black bullhead, and small flannelmouth sucker (< 300 mm) during the monsoons (Table 2.4). Specifically, Yellow Jacket Creek antenna detections during the first 33 d averaged 2.7 unique detections per day, followed by only 1 individual (a small flannelmouth sucker) detected during the following 15 d span when connectivity with McElmo Creek was extremely low or absent. After the monsoons began on July 15 through August 2, daily fish detections averaged over 6.4 unique detections per day (Figure B.1). Booth et al. (2014) observed higher use of stream margins by suckers during floods suggesting these habitats provide refuge to high flow and displacement. The persistence of the small flannelmouth sucker, roundtail chub and black bullhead within our study area were also coincident to a sharp decline (potentially displacement) in McElmo Creek detections of large flannelmouth and bluehead suckers associated with increasing water level (Figure 2.6). Alternatively, mortality may have been mistaken as displacement of the two sucker species. For example, immediately after a spate in mid-July 2013, several untagged individuals (e.g., roundtail chub, flannelmouth sucker, bluehead sucker, speckled dace, channel catfish, and red shiner) were observed stranded and dead on the banks. Lack of bluehead sucker detections in Yellow Jacket Creek show a similar pattern of avoidance by smaller bluehead sucker (mean TL = 185 mm in this study) as Bower et al. (2008) who found that juveniles avoided ephemeral reaches, including an adjacent tributary, in Wyoming (Table 2.4). Webber et al. (2012) found bluehead sucker to have limited movements (< 15 km) in another tributary system (Weber River, UT) and our movement data also suggest they are less mobile exhibiting the least mean distance moved among species (470 m) and limited to McElmo Creek habitats (Table 2.4).

Roundtail chub and black bullhead exhibited similar movement behaviors among all three antennas except for the pre-monsoon season where roundtail chub were consistently using the Yellow Jacket Creek antenna and black bullhead were not. Roundtail chub use mainstem, tributary and ephemeral habitats with a wide range of observed movements ranging from meters to > 30 km throughout the Colorado River basin (Kaeding et al. 1990; Beyers et al. 2001; Compton et al. 2008). Our study shows that within a local spatial extent, the movement behavior pattern of roundtail chub involved movements among confluence-linked habitats throughout the duration of antenna deployments (Figures 2.7 and 2.8; Table 2.4). Sixty-eight percent of the roundtail chub detected used two or more antennas suggesting the confluence promotes neighborhood effects by connecting frequently traveled routes between reaches (Figure 2.8). Interestingly, while roundtail chub had higher habitat use at Yellow Jacket Creek relative to other species besides small flannelmouth sucker, no individual roundtail chub exhibited movement restricted to Yellow Jacket Creek (Table 2.4). Although black bullhead represented the least detected species (n = 9), they were detected at every antenna, with detections most frequent after the monsoon season began (Figure 2.7). The similarity in number of detections (n = 10) at a McElmo Creek PIT antenna array ~150 m upstream from the San Juan River suggest black bullhead are tributary generalists, able to colonize and occupy upstream tributary reaches or those adjacent to mainstem (Cathcart et al., in prep). Lack of pre-monsoon black bullhead detections could be due to restricted movements of fishes living upstream of the antenna in Yellow Jacket Creek.

Several channel catfish colonized the McElmo Creek and Yellow Jacket Creek confluence zone from downstream habitats and based on their far ranging movements, exhibit a switch from using the mainstem San Juan River to a smaller tributary during periods of elevated discharge, most often during monsoon season. Channel catfish had the farthest mean (> 10 km) and maximum distance (> 35 km) traveled between tagging location and first detection, suggesting that their initial locations were closer in proximity to the mainstem San Juan River relative to other species (Table 2.3). Determining exact movement behaviors was compromised for 2 d after a spate on July 23 that displaced the downstream McElmo Creek antenna, making it possible that the 14 channel catfish only detected at the upstream McElmo Creek antenna (Figure 2.8) swam past the disabled downstream antenna. Therefore, it is more likely that while they do represent their own cluster (upstream colonizers post-monsoon events), the observed upstream distribution (Figure 2.9) might be incorrect. While mainstem-tributary movements are not novel by channel catfish (e.g., Dames et al. 1989), their arrival represents a potential competitor and predator to native fishes (Marsh and Brooks 1989; Franssen and Durst 2013).

Network wide movements and distributions are also evident for Colorado pikeminnow since they were all originally stocked in the San Juan River. Colorado pikeminnow are stocked in the mainstem San Juan River (> 50 km upstream of the mouth of McElmo Creek, > 80 km away from the mouth of Yellow Jacket Creek) so their movements into tributaries are indeed expansive. Fresques et al. (2013) documented several Colorado pikeminnow upstream in Yellow Jacket Creek in 2007-10 in addition to the seven individuals we encountered. Regardless, there is no indication as to what their motivation is for occupying these upstream habitats or if any tributary preference exists. Colorado pikeminnow use other smaller tributary habitats elsewhere in the Colorado River basin suggesting this is not a unique behavior (Marsh et al. 1991; Wick et al. 1991; Bottcher et al. 2013). Longer duration of antenna deployments during autumn and winter (seasons with more frequently expected movements) would likely better our understanding of tributary use by Colorado pikeminnow. For example, Durst and Franssen (2014) showed a downstream movement pattern by Colorado pikeminnow in winter that could increase their chances of encountering, then entering McElmo Creek from the San Juan River. Some have speculated that tributary use from mainstem fish signifies an escape from potentially adverse conditions in the mainstem such as cooler thermal regimes or higher gradient flows (Fresques et al. 2013; Cathcart et al., in prep).

Movement behaviors may have resulted from other habitat characteristics of adjacent reaches that were not measured quantitatively such as turbidity, productivity, and chemistry. Turbidity was generally highest in Yellow Jacket Creek, clearest in the upstream reach of McElmo Creek, and intermediate downstream of the confluence in McElmo Creek. The only observed times during this study when McElmo Creek turbidity was greater or equal to Yellow Jacket Creek was during or after monsoon flows. Turbidity has well documented effects on feeding and hiding behaviors of fishes and could be responsible for the distributions and movements among reaches connected by confluences (Gradall and Swenson 1982; Braaten and Guy 1999; Leahy 2011). Water temperatures in both stream reaches declined with increased flows upon the arrival of higher flows from monsoon events (Figure 2.5). Turbidity, stream flow, and temperature are often correlated to each other and to fish movement and are likely contributors to patterns of species behavior (Albanese et al. 2004).

Implications

Our designation of a confluence zone was based on channel morphology but there was a notable gradient of fish community structure around this junction (Figure 2.4). However, strictly designating a confluence habitat within a framework of ecological neighborhoods (habitats or reaches) provided a relatively simple way to evaluate behaviors related to environmental cues and habitat characteristics at a local scale. Overall, we found the effects of spatial processes (neighborhood effects and landscape complementation) on movements are species specific. We differentiated species-specific movement behaviors that illustrated how fish interpret local confluence scales differently depending on species, their size, and environmental cues. These different interpretations were inferred from behaviors representing upstream colonization (channel catfish in McElmo Creek), refuge seeking or upstream movements into Yellow Jacket Creek (small flannelmouth sucker, roundtail chub, and black bullhead), and emigration out of the local study area (large flannelmouth sucker and bluehead sucker). We provided further evidence of how exchanges of fishes through confluence habitats are a dynamic force structuring southwestern USA fish communities (Booth et al. 2013; Booth et al. 2014). This study illustrated that recruitment of flannelmouth sucker may depend on lateral connectivity to small tributaries, roundtail chub persistence is facilitated by Yellow Jacket Creek, and introduced channel catfish make expansive movements from the mainstem San Juan River. Landscape complementation was reflected through the differences in movements between size classes of flannelmouth suckers at the reach scale. Neighborhood effects were evident through the majority of fish movement patterns (66%) that used the confluence zone to access two or more different reaches. Understanding these habitat requirements and movement behaviors of southwestern fishes enables managers to identify critical habitat needs of species and make informed decisions relative to native and nonnative fishes (Bezzerides and Bestgen 1997; Bottcher et al. 2013; Booth et al. 2014). Management initiatives can thus use confluence zones as focal areas to monitor and conserve spatial patterns of diversity, habitat heterogeneity, and dispersal across multiple scales

(Douglas and Douglas 2000). Future challenges of confluence movement designs include elucidating directionality and timing of species movements, comparing network position and confluence function of different watersheds, improving the delineation of confluence zones as functional habitats, and investigating whether these ecological hotspots and their associated species have any bearing on survival and population dynamics.

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Figures and Tables

Figure 2.1 Study area and conceptual design of 17 habitats sampled and three passive integrated transponder antennas stationed around the confluence of McElmo and Yellow Jacket creeks near the border of Colorado and Utah, U.S.A.

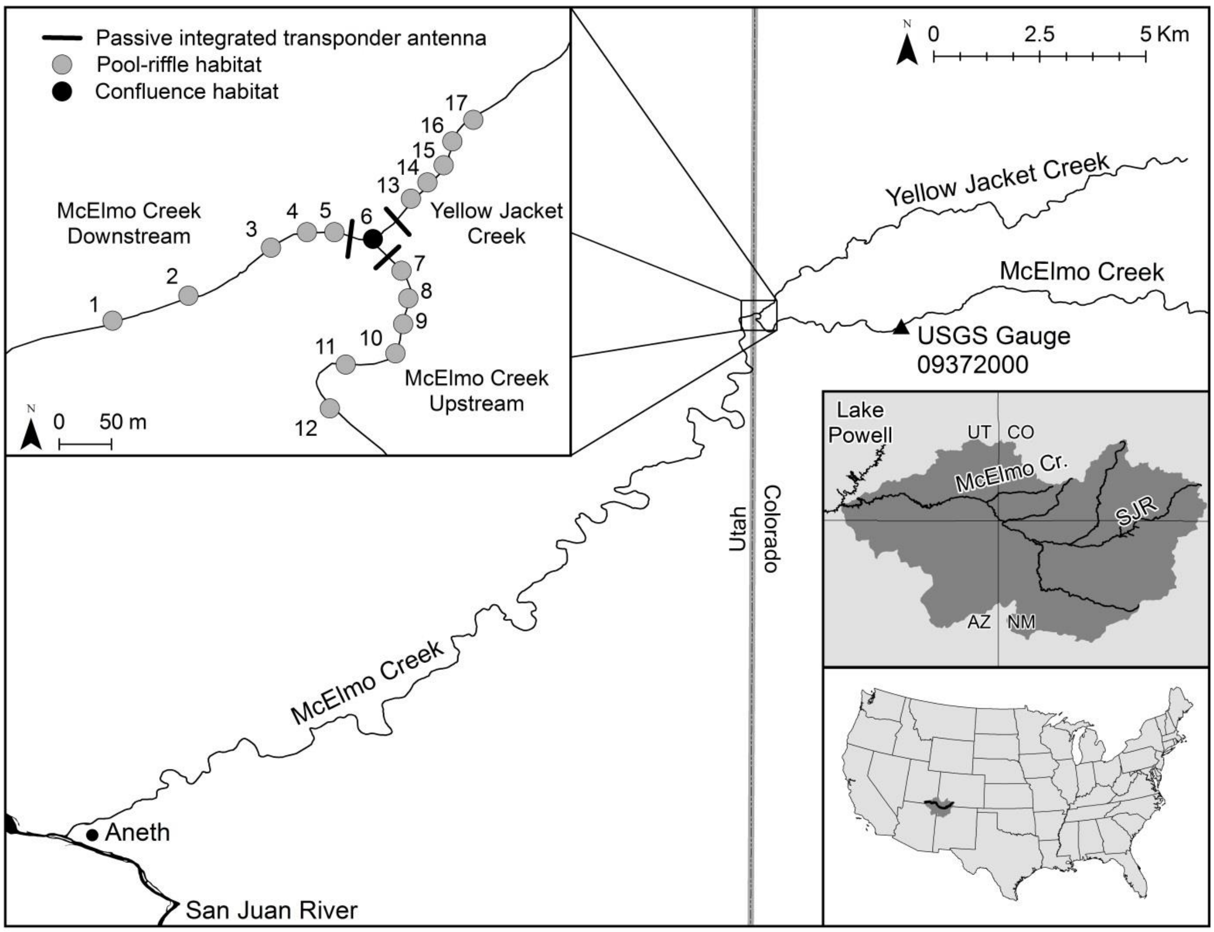


Figure 2.2 Species richness, mean wetted widths, and maximum depths with 95% confidence intervals of habitats relative to the confluence of McElmo and Yellow Jacket creeks near the border of Colorado and Utah, U.S.A. Habitats were sampled 10 times between June 2012 and June 2014.

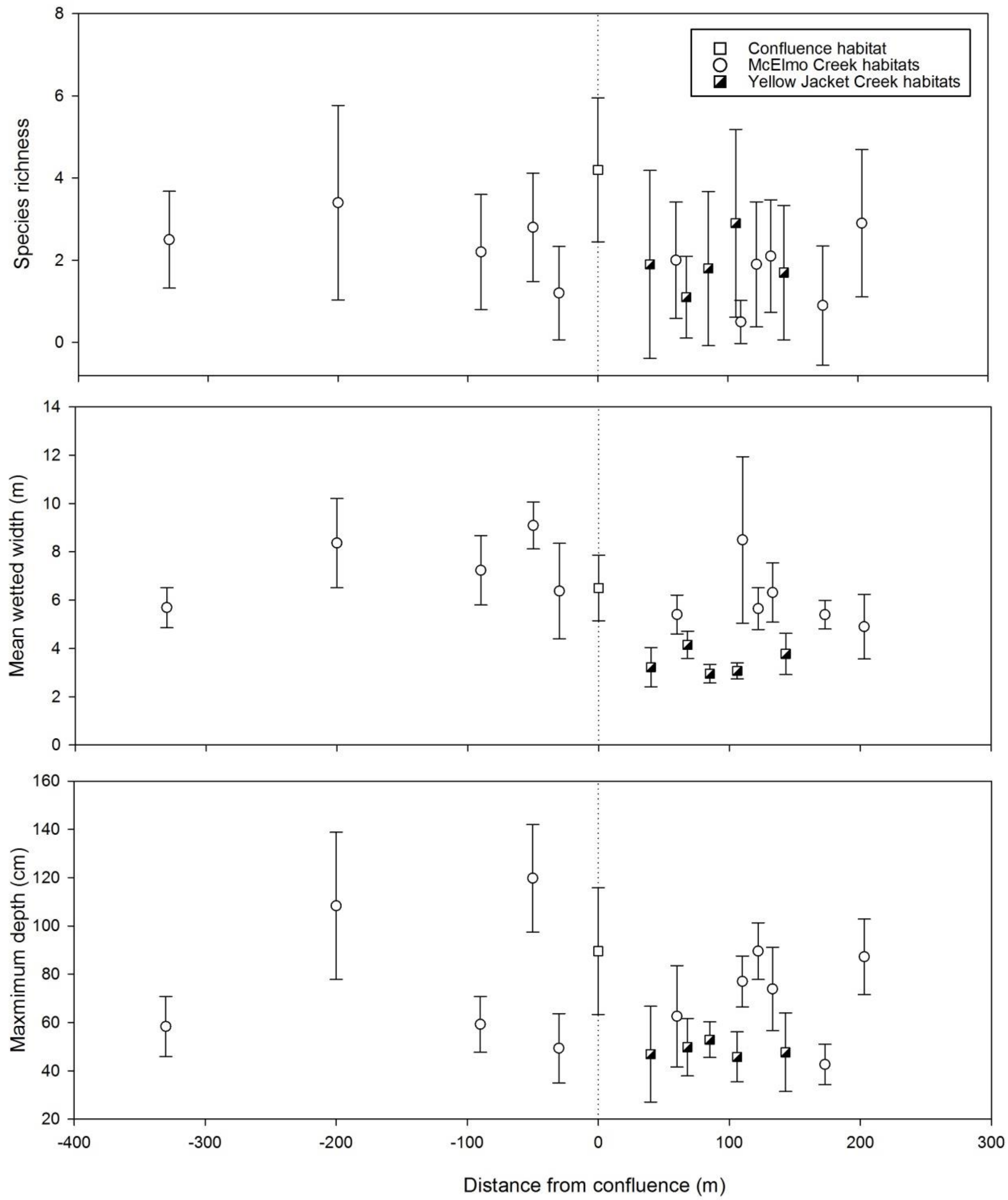


Figure 2.3 Mean rank of habitats with 95% confidence intervals at and around the confluence of McElmo and Yellow Jacket creeks based on species richness sampled 10 times at each habitat between June 2012 and June 2014.

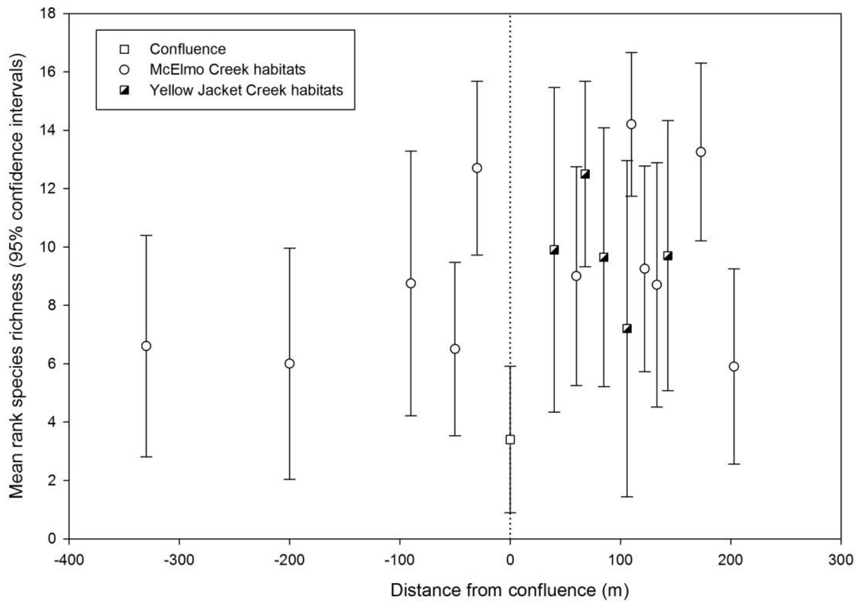


Figure 2.4. Mean species richness and correspondence analysis (CA) axes scores from habitats in and around the confluence of McElmo and Yellow Jacket Creeks, Utah. Data are based off 10 samples from 17 habitats between June 2012 and June 2014. To help interpret changes in community structure, weighted average species scores for each CA axis are plotted (horizontal grey lines) to the right of each panel. Species codes are as follows: black bullhead (AMEMEL); bluehead sucker (CATDIS); flannelmouth sucker (CATLAT); red shiner (CYPLUT); roundtail chub (GILROB); channel catfish (ICTPUN), fathead minnow (PIMPRO); and speckled dace (RHIOSC).

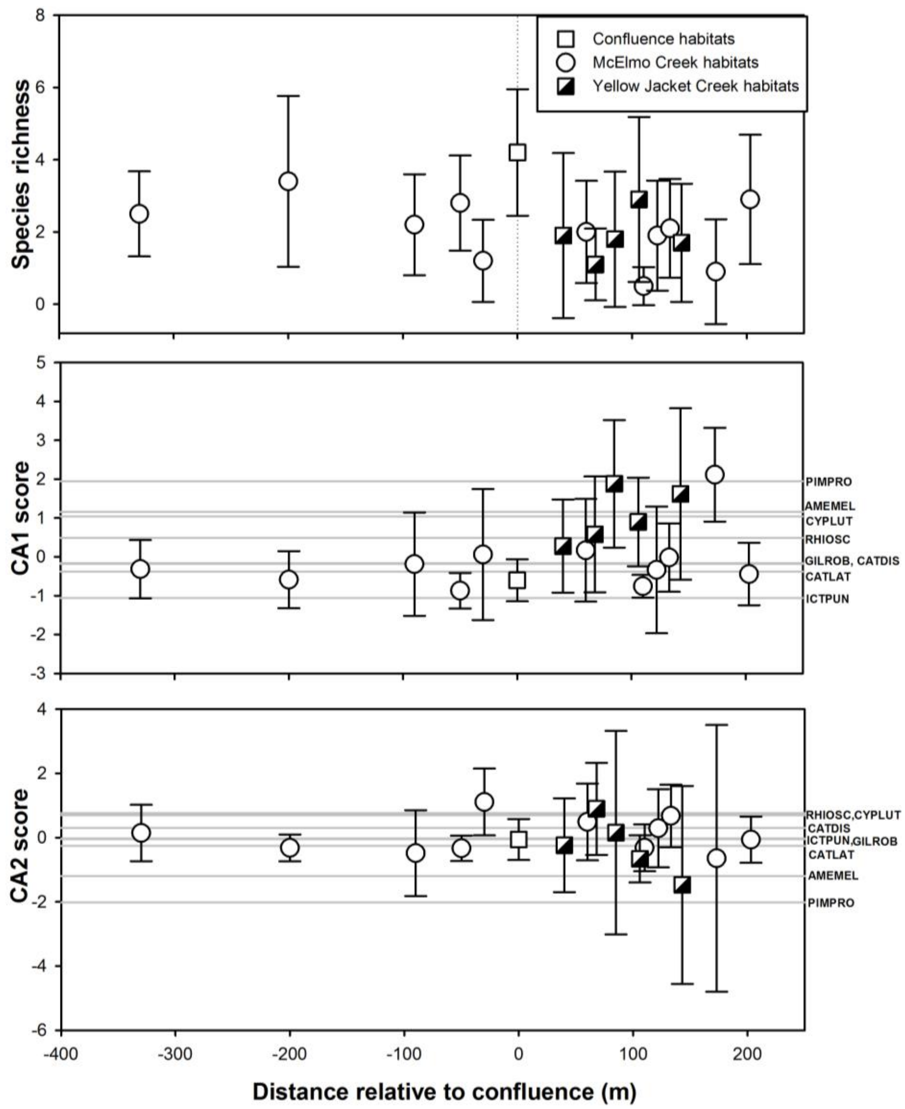


Figure 2.5 Water temperatures from McElmo and Yellow Jacket creeks relative to McElmo Creek discharge measured by USGS gage 09372000 from 2 June through 2 August 2013. McElmo Creek water temperatures were not measured after 23 July 2013 due to monsoonal floods dislodging the temperature logger.

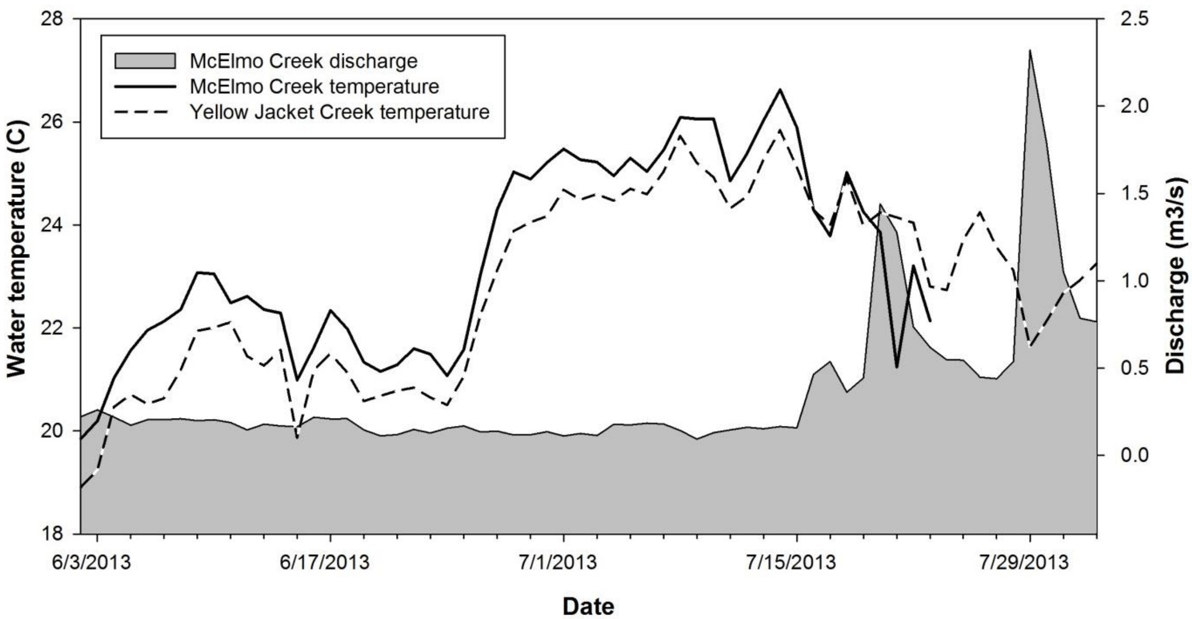


Figure 2.6 Boxplots comparing a) species richness b) log-transformed fish abundance with Tukey's HSD c) maximum pool depths with Tukey's HSD contrasts and d) mean wetted widths with Tukey's HSD among reaches around the confluence of McElmo and Yellow Jacket creeks near the border of Colorado and Utah, U.S.A. Reaches were sampled 10 times for fish and nine times for habitat between June 2012 and June 2014. Boxplot letters correspond to Tukey's HSD contrasts and different letters correspond to significant differences existing between reaches tested at α = 0.05.

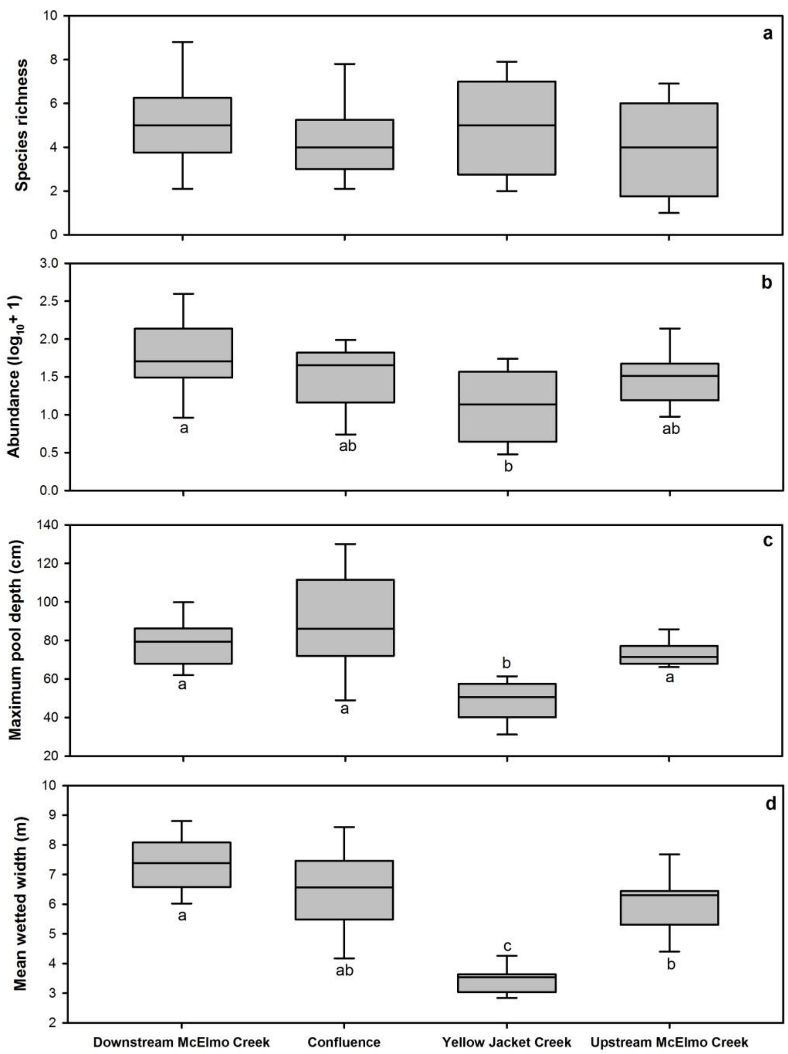


Figure 2.7 Detections of passive integrated transponder (PIT) tagged fishes by PIT antennas stationed in three habitats around the confluence of McElmo and Yellow Jacket creeks at the border of Colorado and Utah from May 29 to August 2, 2013.

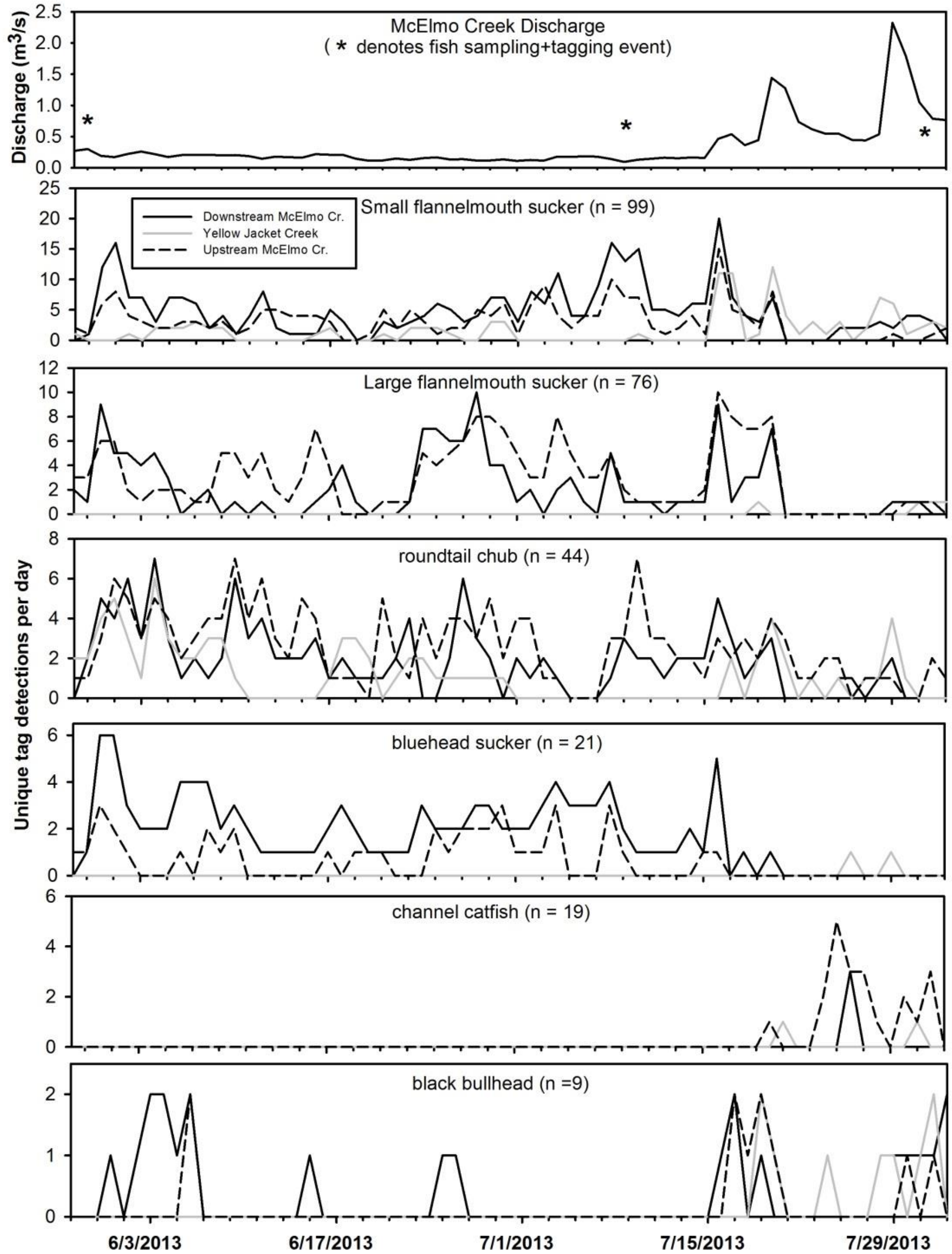


Figure 2.8 Venn diagrams illustrating seven potential movement behaviors of passive integrated transponder (PIT) tagged fishes around the confluence of McElmo and Yellow Jacket creeks based on PIT antennas stationed from May 29 – August 2, 2013. Venn diagrams either depict behavior limited to one reach (white boxes), a combination of movement among two reaches (gray boxes), or a combination of movement among all three reaches (dark gray box in the center).

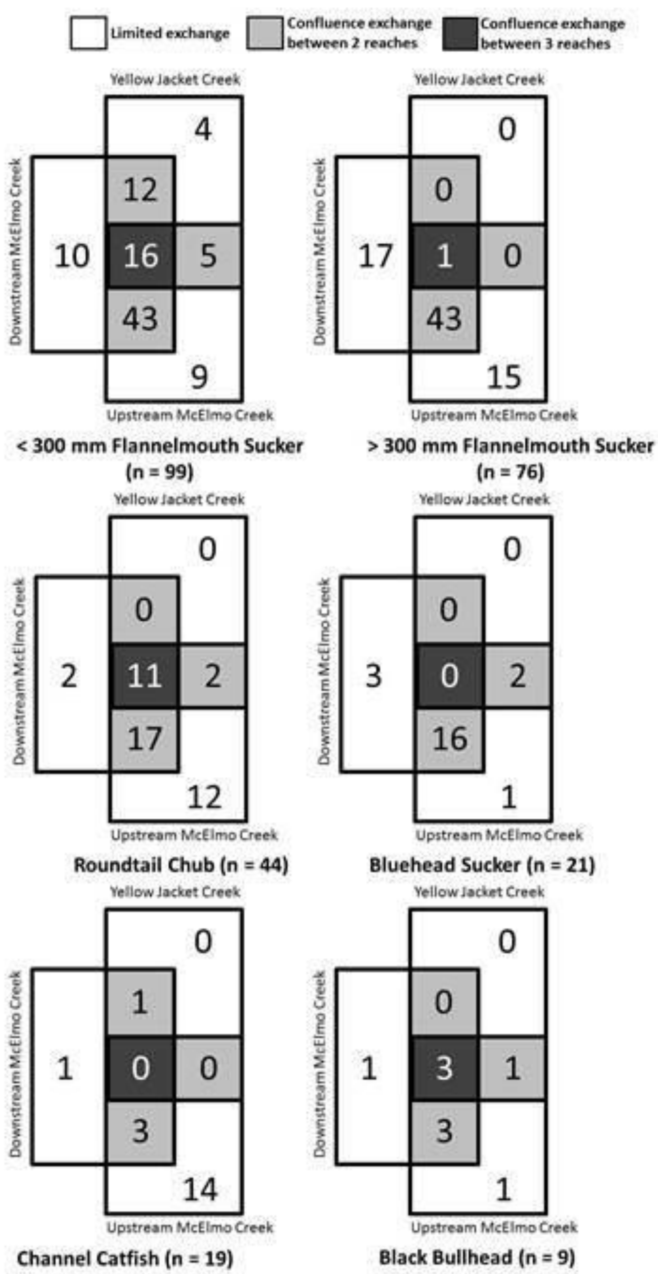


Figure 2.9 Cluster analysis classification of 5 species detected by three passive integrated transponder antennas deployed around the confluence of McElmo and Yellow Jacket creeks between 29 May and 2 August 2013. Movement characteristics are summarized in Figure 7.

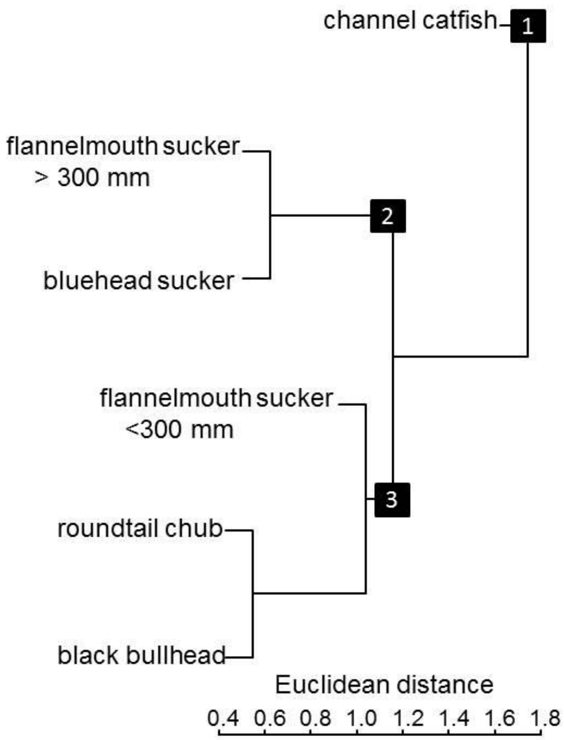


Table 2.1 Fish species and abundances sampled 10 times at 17 habitats around the confluence of McElmo and Yellow Jacket creeks between June 2012 and June 2014.

	Site																	
	Downstream McElmo Cr.					**CONFLUENCE**	*Upstream McElmo Cr.*						*Yellow Jacket Cr.*					
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**Total**
< 100 mm Flannelmouth sucker	167	59	11	7	6	124	0	1	9	11	1	7	38	0	13	4	9	467
100-300 mm Flannelmouth sucker	15	72	37	25	0	47	7	1	5	2	0	32	5	2	0	8	4	262
300-400 mm Flannelmouth sucker	8	41	18	36	0	50	11	0	10	1	1	20	0	0	0	0	1	197
> 400 mm Flannelmouth sucker	20	38	18	32	0	70	4	1	6	2	0	28	0	0	0	0	0	219
Bluehead sucker	7	34	24	7	5	13	5	1	2	4	4	13	1	2	1	1	5	129
Roundtail chub	4	46	4	18	0	48	6	1	9	4	1	16	8	2	1	6	3	177
Colorado pikeminnow	1	0	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	7
Speckled dace	53	56	19	8	17	17	12	0	6	13	2	40	3	4	7	7	4	268
Channel catfish	2	4	2	6	1	15	0	0	5	3	1	5	0	0	1	0	0	45
Black bullhead	0	7	0	1	0	1	0	0	0	0	1	0	2	0	1	6	0	19
Red shiner	1	8	1	0	5	13	2	0	3	8	1	20	5	4	3	5	1	80
Fathead minnow	2	2	0	0	0	0	0	0	0	0	0	1	6	0	6	1	6	24
Largemouth bass	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0	1	2	6
Green sunfish	0	1	0	0	0	4	0	0	0	0	0	0	1	0	0	2	0	8
White sucker	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2
Hybrid sucker	0	0	1	1	0	2	1	0	0	0	0	0	0	0	0	0	0	5
Total	280	368	135	141	34	411	48	5	58	48	12	182	70	14	33	41	35	1915

Table 2.2 Fish community metrics of 17 habitats sampled 10 times around the confluence of McElmo (sites 1 – 12) and Yellow Jacket (13 – 17) creeks near the border of Utah and Colorado between June 2012 and June 2014.

	Site																	
	Downstream McElmo Cr.					**CONFLUENCE**	*Upstream McElmo Cr.*						*Yellow Jacket Cr.*					
Species/Sample	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**Total**
Fishless Samples	0	0	1	0	4	0	1	5	1	1	4	0	3	3	2	2	3	30
Native	275	346	131	133	28	372	55	10	22	26	26	45	5	50	37	9	156	1726
Nonnative	5	22	4	8	6	39	15	4	11	15	9	3	0	8	11	3	26	189
Species Richness	8	9	7	7	5	12	9	5	8	9	7	6	3	7	6	7	7	12

Table 2.3 Movement metrics from 2013 summer detection data collected by three passive integrated transponder antennas stationed around the confluence of McElmo and Yellow Jacket creeks near the border of Colorado and Utah, U.S.A. from May 29 – August 2, 2013. Tagged fishes only include those tagged prior to August 2013.

Species	Total tagged in McElmo Creek network*	Total tagged within study area	Total detected	Detected fish mean TL (mm)	Mean distance moved (m)	Maximum distance moved (m)	Mean days at large	Range days at large
flannelmouth sucker (<300 mm)	699	175	99	156	1,359	32,340	42	0-607
flannelmouth sucker (>300 mm)	1336	222	76	374	571	23,580	168	0-458
roundtail chub	151	90	44	193	689	7,130	159	0-820
bluehead sucker	184	56	21	185	470	5,940	84	0-310
channel catfish	423	30	19	409	10,628	35,570	224	43-392
black bullhead	49	14	9	208	720	4,910	60	0-231
Colorado pikeminnow	12	4	1	273	-	132	1	-
green sunfish	14	1	1	96	-	358	1	-
largemouth bass	5	2	0	-	-	-	-	-
Total	*2873*	*594*	*270*	-	-	-	92	

*Includes native fishes tagged by Colorado Parks and Wildlife researchers (39 flannelmouth sucker < 300 mm, 74 flannelmouth sucker > 300 mm, 33 bluehead sucker, and 3 Colorado pikeminnow).

Table 2.4 Mean daily individual fish detections per species, per antenna from passive integrated transponder antennas stationed around the confluence of McElmo and Yellow Jacket creeks from May 29 – August 2, 2013. Superscript letters correspond to Tukey's Honest Significant Differences contrasting antenna use for each species tested at α = 0.05.

	Mean daily fish detections		
Species	Downstream McElmo	Yellow Jacket	Upstream McElmo
flannelmouth sucker <300 mm	4.85[a]	1.56[b]	3.11[c]
flannelmouth sucker >300 mm	2.09[a]	0.06[b]	2.98[a]
roundtail chub	1.86[ab]	1.15[a]	2.58[b]
bluehead sucker	1.74[a]	0.03[b]	0.64[ab]
channel catfish	0.06[a]	0.03[b]	0.318[c]
black bullhead	0.35[a]	0.136[a]	0.152[a]
Total	1.83[a]	0.49[b]	1.63[a]

Table 2.5 Proportions of passive integrated transponder (PIT) tagged individuals exhibiting different movement behaviors, as determined by the number and location of detections at three antennas stationed around the confluence of McElmo and Yellow Jacket creeks near the border of Utah and Colorado between May 29 and August 2, 2013. Movement behaviors fall into seven categories depending on the combination of antennas used according to each stream reach.

Species	Number detected	Downstream McElmo Cr.	Yellow Jacket Cr.	Upstream McElmo Cr.	Upstream and Downstream McElmo Cr.	Downstream McElmo Cr. and Yellow Jacket Cr.	Upstream McElmo Cr. And Yellow Jacket Cr.	All three reaches
Small flannelmouth sucker	99	0.101	0.04	0.091	0.434	0.121	0.051	0.162
Large flannelmouth sucker	76	0.224	0	0.197	0.566	0	0	0.013
Roundtail chub	44	0.045	0	0.274	0.386	0	0.045	0.25
Bluehead sucker	21	0.143	0	0.048	0.762	0	0.095	0
Channel catfish	19	0.053	0	0.737	0.158	0.053	0	0
Black bullhead	9	0.111	0	0.111	0.333	0	0.111	0.333

Appendix A - Chapter 1 Supplementary Information

Figure A.1 Mean daily discharge for the San Juan River at Bluff, UT (1st Y axis; United States Geological Survey (USGS) gage 09379500) and McElmo Creek, CO (2nd Y axis; USGS gage 09372000) from 2 May 2012 through 31 January 2014 for the Passive Integrated Transponder antenna array at the mouth of McElmo Creek. McElmo Creek gage was ice affected from 4 December 2013 through 31 January 2014.

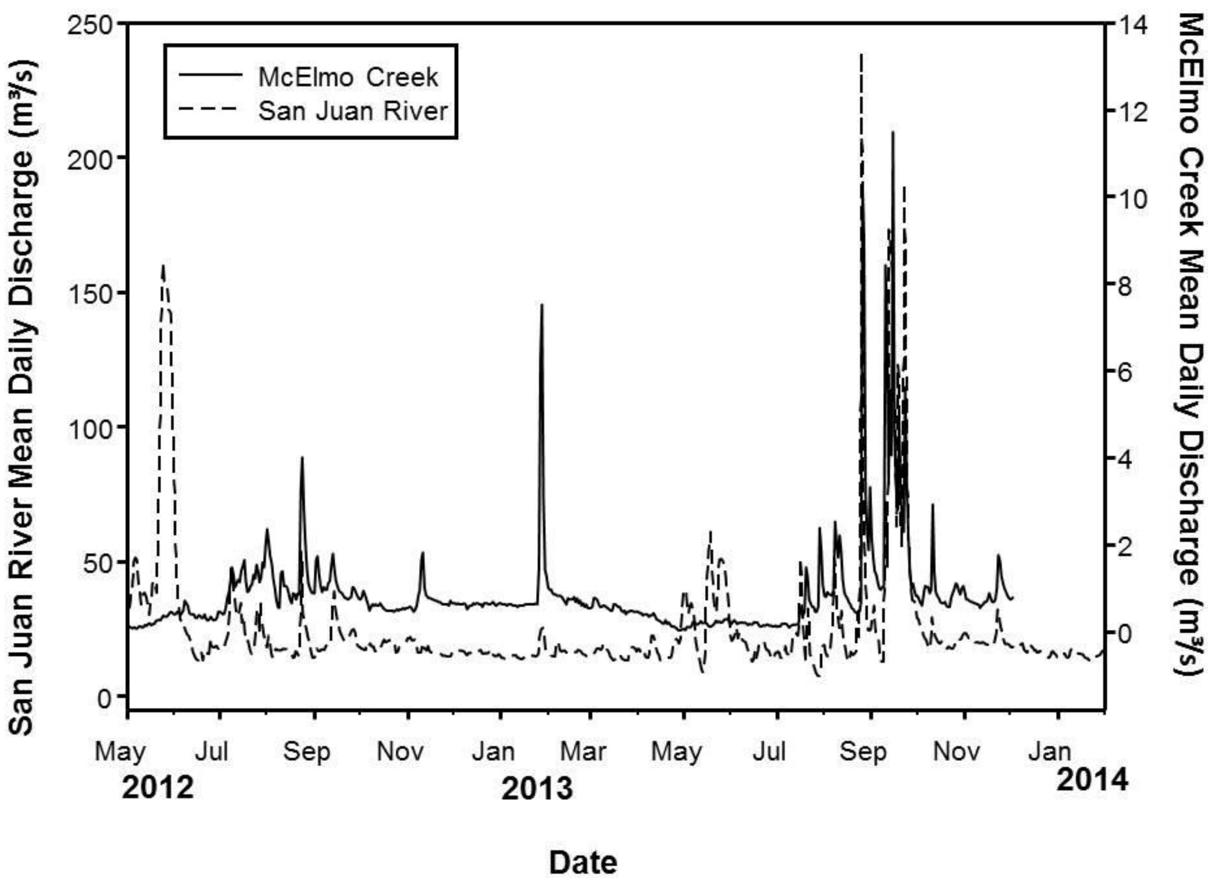
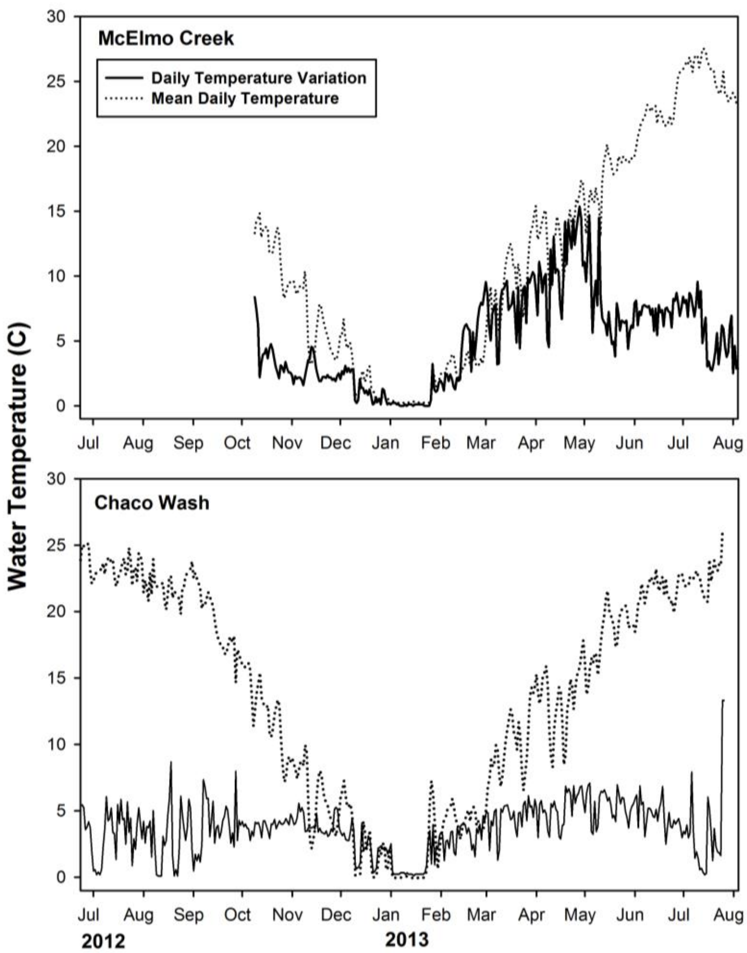


Figure A.2 Daily variation (range) and mean daily water temperatures of McElmo Creek, UT and Chaco Wash, NM. McElmo Creek data were collected approximately 150 m upstream from the San Juan River from 9 October 2012 to 4 August 2013. Chaco Wash, NM data were collected approximately 600 m upstream from the San Juan River between 23 June 2012 and 19 July 2013. Temperature was collected at 30 min intervals.



Appendix B - Chapter 2 Supplementary Information

Figure B.1 Seasonal tagging dates of 270 fishes detected by the three passive integrated transponder antennas deployed around the confluence of McElmo and Yellow Jacket creeks from May 29- August 2, 2013.

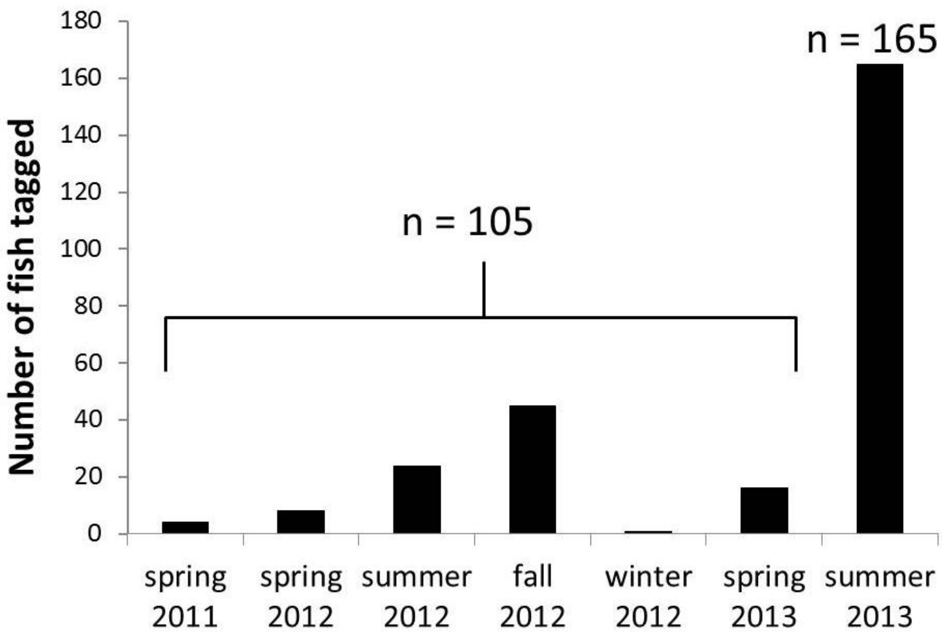


Figure B.2 Daily unique detections at PIT antennas stationed around the confluence of McElmo and Yellow Jacket creeks, Utah from May 29 – August 2, 2013.

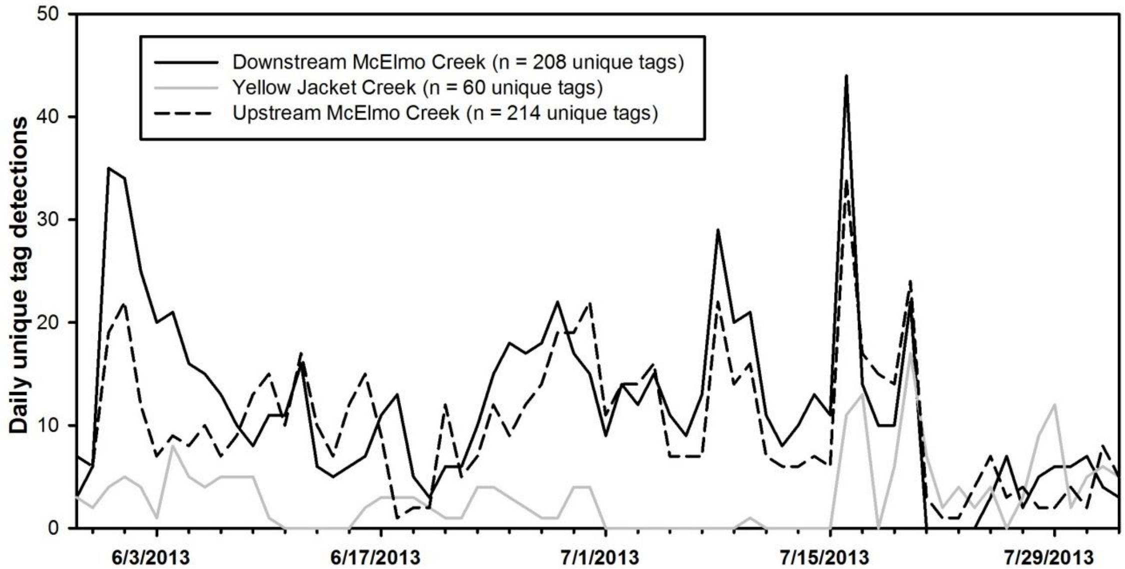


Figure B.3 Bubble Plots of selected metrics of the fish community based on 17 habitats sampled 10 times between June 2012 and June 2014 at the confluence of McElmo and Yellow Jacket creeks near the border of Colorado and Utah. a) Native fish composition b) Nonnative fish composition, c) Fishless samples, d) Species richness.

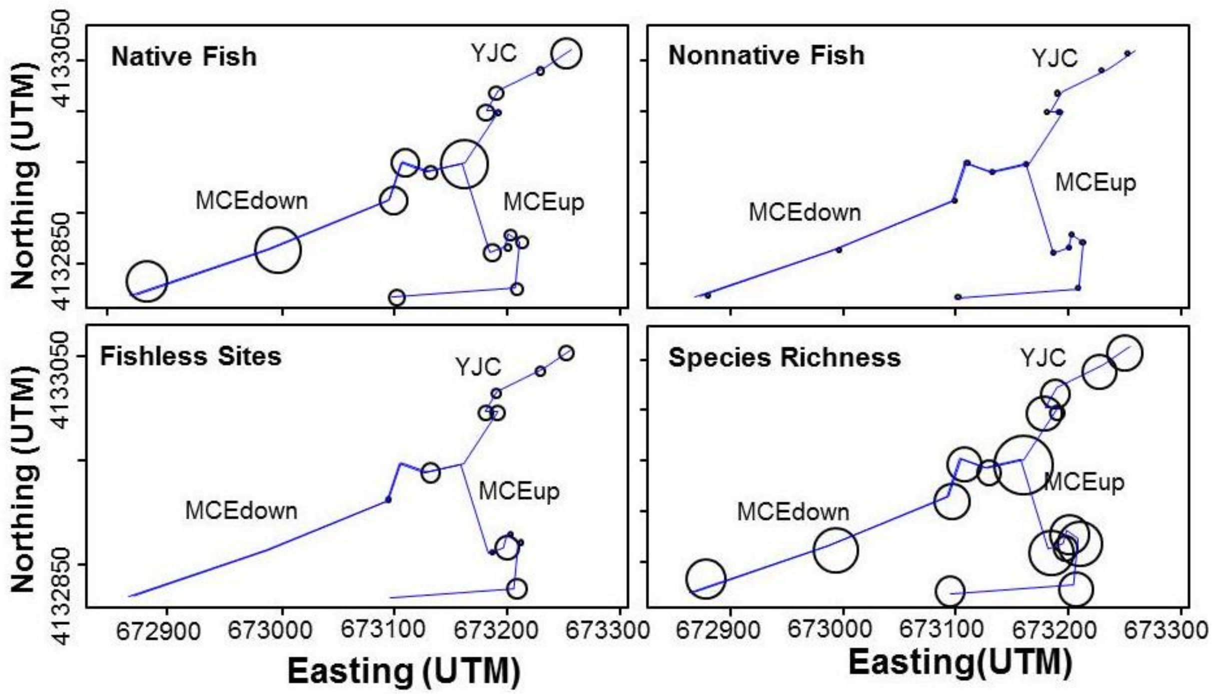


Figure B.4 Bubble plots of square-root transformed abundances of four size classes of Flannelmouth Sucker sampled at 17 habitats 10 times between June 2012 and June 2014 around the confluence of McElmo and Yellow Jacket creeks near the border of Colorado and Utah.

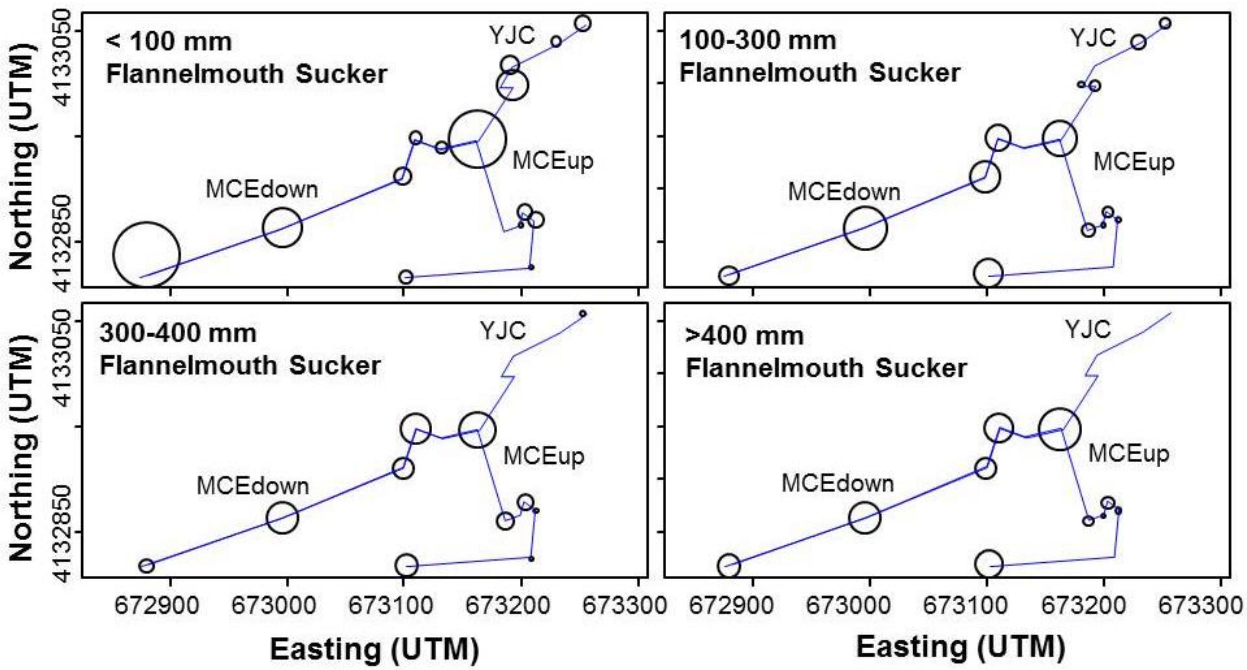


Figure B.5. Bubble plots of square-root transformed abundance data of native fishes sampled at 17 habitats 10 times between June 2012 and June 2014 around the confluence of McElmo and Yellow Jacket creeks near the border of Colorado and Utah.

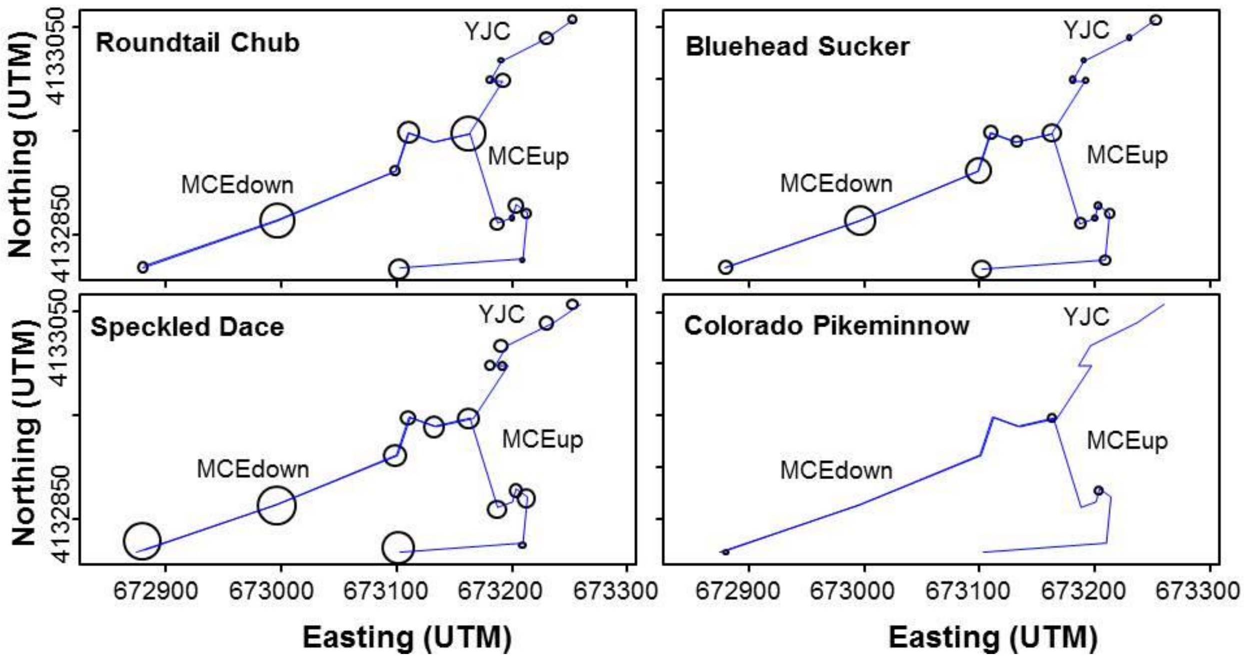


Figure B.6 Bubble plots of square-root transformed abundance data of frequently encountered nonnative fishes sampled at 17 habitats 10 times between June 2012 and June 2014 around the confluence of McElmo and Yellow Jacket creeks near the border of