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ORIGINAL ARTICLE

WILEY Ecology of FRESHWATER FISH

Patterns of fish movement at a desert river confluence

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Abstract

Quantifying fish movements in river networks helps identify critical habitat needs and how they change with environmental conditions. Some of the challenges in tracking fish movements can be overcome with the use of passive integrated transponder (PIT) tagging and antennas. We used PIT technology to test predictions of movement behaviour for four fish species at a mainstem–tributary confluence zone in an arid-land river system. Specifically, we focused on the McElmo Creek tributary confluence with the San Juan River in southwestern Utah, USA. We quantified variation in species occurrences at this confluence zone from May 2012 to December 2015 relative to temporal and environmental conditions. We considered occurrences among species relative to tagging origins (tributary versus mainstem), season and time of day. Generally, fishes tagged in the focal tributary were more likely to be detected compared to fish tagged in the mainstem river or other tributaries. Additionally, adults were most likely to be detected across multiple years compared to subadults. Based on a Random Forests model, the best performing environmental variables for predicting seasonal detections included mainstem discharge during run-off season (razorback sucker *Xyrauchen texanus*), tributary discharge during monsoon season (Colorado pikeminnow *Ptychocheilus lucius*) and mainstem water temperature (flannelmouth sucker *Catostomus latipinnis* and channel catfish *Ictalurus punctatus*). The variable responses by endemic and introduced fishes indicate tributary habitats provide several key functions within a fish community including spawning, rearing, foraging and refuge.

KEYWORDS
Catostomus latipinnis, confluence, edge effects, movement behaviour, PIT tag, *Xyrauchen texanus*

1 | INTRODUCTION

Quantifying movements of freshwater fish has been difficult due to logistical challenges of tagging and recapturing highly mobile individuals (Albanese, Angermeier, & Dorai-Raj, 2004; Gowan & Fausch, 1996; Rodriguez, 2002). Accordingly, conceptual frameworks such as the restricted movement paradigm (Gerking, 1959), long distance dispersal (Rodriguez, 2010) and confluence exchange hypothesis (Thornbrugh & Gido, 2010) that predict patterns of movement in riverine systems need testing with empirical studies. Despite the challenges studying riverine movement, advances in tagging methods now allow for freshwater fish populations within diverse communities to be studied at greater spatial and more continuous temporal scales (Cooke et al., 2013; Gowan, Young, Fausch, & Riley, 1994; Young, 2011).

Sampling continuously allows increased detectability of diverse movement behaviours within and among species compared to discrete sampling events (Fausch, Torgerson, Baxter, & Li, 2002; Schlosser & Angermeier, 1995; Wiens, 2002). Intensive temporal sampling can be optimised by selecting detection sites that maximise our ability to capture the diverse inter- and intraspecific movement behaviours across time. For example, previous movement behaviour studies have used locations where fish movements are concentrated (i.e. attractive fish passage structures at dams or diversions) or where exchange of fishes among linked heterogeneous habitats is enhanced, such as at confluences or among intermittent and perennial reaches (Albanese et al., 2004; Morgan & Beatty, 2006; Pelicice & Agostinho, 2008). Tributary confluences with mainstem rivers, in particular, have been identified as productive fish habitats because of their role as movement corridors and proximity to heterogeneous habitats types (Bottcher, Walsworth, Thiede, Budy, & Speas, 2013; Kiffney, Green, Hall, & Davies, 2006; Osborne & Wiley, 1992).

Tributary confluences are known to enhance aquatic diversity because of heterogeneity created by the joining of streams with potentially different size, flow, water quality and arrangement (Benda et al., 2004; Fernandes, Podos, & Lundberg, 2004; Rice, Greenwood, & Joyce, 2001). Edge effects between adjoining streams at nodes within river networks also can form contrasts in metacommunity function and species richness (Altermat, Seymour, & Martinez, 2013; Fernandes et al., 2004). Confluences represent a fork in the road where behavioural decisions of fishes are made according to species biology, environmental conditions and location of the confluence relative to other habitat features such as spawning or foraging habitats (Benda et al., 2004; Hitt & Angermeier, 2008; Thornbrugh & Gido, 2010). Despite the recognition of confluence zones as critical interfaces of geomorphological and ecological processes, empirical data on specific movement behaviours at these junctions are rare (Fisher, 1997; Grant, 2011; Nathan, 2001).

We used passive integrated transponder (PIT) tag and antenna technology to characterise movement behaviour in a desert fish community at a perennial tributary confluence with a mainstem river in the southwestern United States. Our primary objective was to continuously monitor species occurrences at this confluence and quantify behavioural patterns in relation to spatial factors (e.g. tagging location), environmental conditions (e.g. flow, temperature) and a hierarchy of temporal scales (diel, seasonal and annual). We generally predicted interspecific differences of movement in response to spatial or temporal variation in tagging locations (i.e. proximity to confluence area) and environmental factors respectively. Due to the antenna location at the confluence, detections of fishes tagged within the tributary represent movement to the mainstem, whereas detections of mainstem-tagged fishes represent movement into the tributary. We hypothesised that detections of fishes tagged in the tributary are more likely than those of fishes tagged in the mainstem because of better detectability through habitat-limited decisions (i.e. one way out of the tributary) and tagging methods that select for fishes with prior, or even innate, knowledge of the tributary (sensu Hasler, 1966). Fishes exhibit nocturnal patterns in response to predator avoidance or foraging behaviours; thus, we hypothesised detections would be highest at night unless seasonal flows and corresponding turbidity were elevated (Helfman, 1993; Bizzotto, Godinho, Vono, Kynard, & Godinho, 2009). Different seasonal and annual (i.e. repeated detections of individuals across multiple years) detection patterns were predicted because of ontogenetic or species-specific habitat preferences such as temperatures that induce annual tributary-spawning migrations in spring by catostomid species or high flows that cause opportunistic refuge-seeking behaviours during flooding (Makrakis et al., 2012; Thornbrugh & Gido, 2010; Young, 2011). Additionally, we predicted detections would be more likely for larger body sizes that have lower mortality and greater mobility (Skalski & Gilliam, 2000; Albanese et al., 2004). Finally, we modelled detections with environmental conditions from tributary and mainstem habitats (i.e. flow, temp) to rank explanatory variables that could predict species occurrences. Because species movements can be constrained or enhanced depending on flow directionality or magnitude within a river network (Altermat, Schreiber, & Holyoak, 2011; Datry et al., 2016), we hypothesised species occurrences would be enhanced by asynchronous flows between the tributary and mainstem whereby lower magnitude and duration of tributary flows would offer seasonal refuge or spawning habitat (Ross & Baker, 1983; Schlosser, 1991).

2 | METHODS

2.1 | Study area

The San Juan River drains 99,200 km^2 in Colorado, New Mexico, Arizona and Utah before it joins Lake Powell 365 km downstream

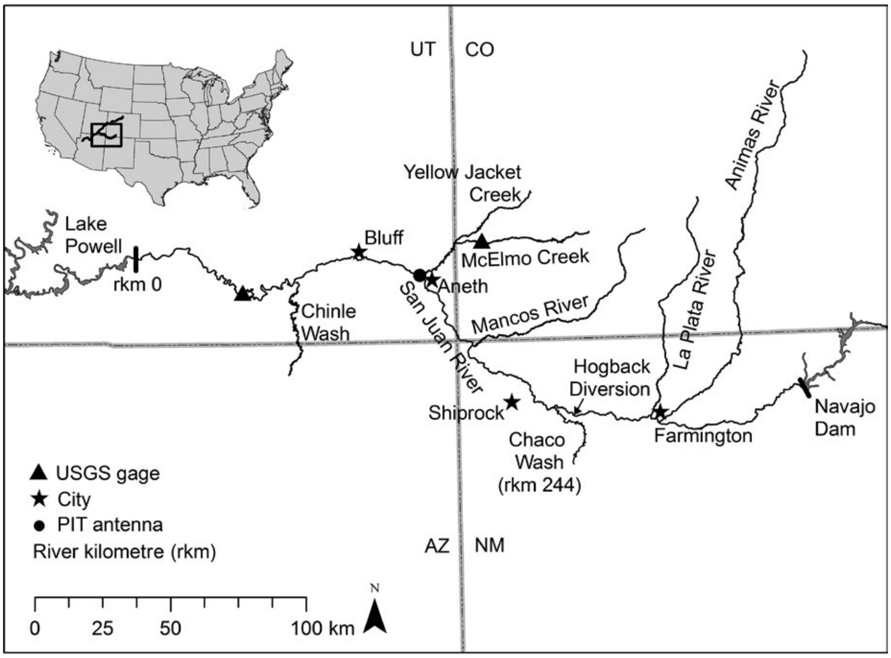

FIGURE 1 San Juan River basin study area with tributaries involved in the study and habitats containing passive integrated transponder (PIT) tagged fishes relative to the focal tributary (McElmo Creek) and the PIT antenna array stationed at the mouth as well as notable landmarks, cities and reference points. State abbreviations are as follows: UT (Utah), CO (Colorado), NM (New Mexico) and AZ (Arizona)

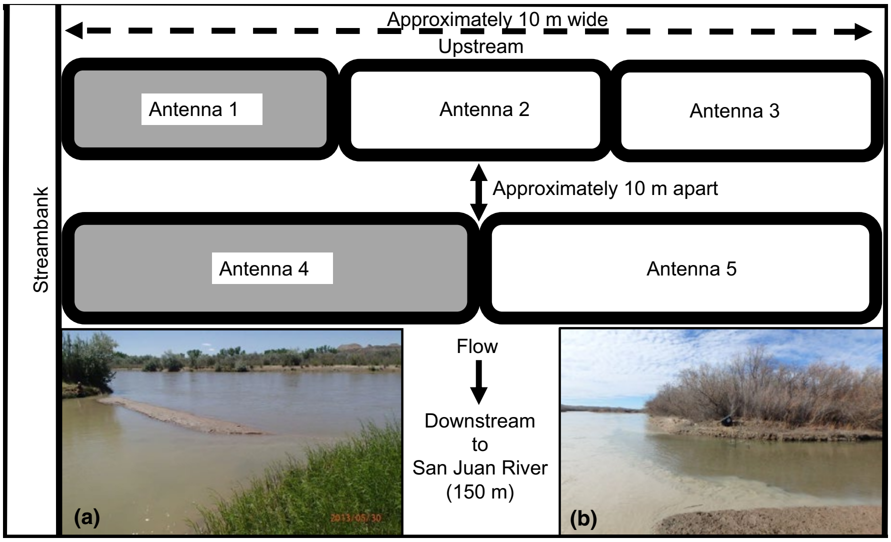

FIGURE 2 Design of the passive integrated transponder antenna array installed in McElmo Creek upstream of its confluence with the San Juan River and operated from 2 May 2012 through 31 December 2015. Shaded antennas (1 and 4) were destroyed and were not part of the entire period of data collection. Pictures show the view from the mouth of McElmo Creek looking towards the San Juan River (a; note the sand berm across the mouth and Russian olive-dominated riparian zone) and the mouth of McElmo Creek looking downstream in the San Juan River (b; note the turbidity difference between the mixing waters)

of Navajo Dam (Figure 1; Carlson & Carlson, 1982). Navajo Dam impounded the San Juan River in 1962 and modified downstream flow and temperature regimes in the river upstream of Lake Powell, an impoundment of the Colorado River (Ryden & Ahlm, 1996). The Animas River drains 2,823 km^2 and is the largest tributary, joining the San Juan River approximately 291 km upstream of Lake Powell. Critical habitat for federally listed endangered species in the San Juan River occurs between the mouth of the Animas River (near the city of Farmington, NM) and Lake Powell (river km 0), although endangered fish have been found—and stocked—upstream of the critical habitat boundary as well as in tributary systems like the Animas River (Cathcart, Gido, & McKinstry, 2015; Fresques, Ramey, & Dekleva, 2013). Besides the Animas River (mean annual flow >20 m^3/s), there are five smaller tributaries to the San Juan River downstream of Navajo Dam (mean annual flows <1.42 m^3/s; mean wetted widths <10 m) that are mostly intermittent (Figure 1).

The focus of this study was McElmo Creek, a small perennial tributary that enters the San Juan River and provides habitat for native and non-native fishes (Figure 1). McElmo Creek drains an area of 1,818 km^2 in Colorado and Utah and joins the San Juan River 163 km upstream of Lake Powell near the town of Aneth, UT (Navajo Nation Environmental Protection Agency, 2012). McElmo Creek confluences with its only perennial tributary, Yellow Jacket Creek, near the CO-UT border, approximately 32 km upstream of the San Juan River. In addition to tagging fish in McElmo Creek and the mainstem San Juan River, some fish were tagged in three other small, intermittent tributaries including Chaco Wash (drainage area: 11,396 km^2, confluence location: 244 km upstream of Lake Powell near the city of Shiprock, NM), Mancos River (drainage area: 2,075 km^2; confluence location: 197 km upstream from Lake Powell) and Chinle Wash (drainage area: exceeds 9,450 km^2; confluence location: 111 km upstream from Lake Powell near the town of Bluff, UT). Generally, riparian vegetation is dominated by Russian olive (*Elaeagnus angustifolia)* but also includes saltcedar (*Tamarisk* spp.), willow (*Salix* spp.) and eastern cottonwood (*Populus deltoides*). Land uses include agriculture, natural resource extraction and livestock grazing.

2.2 | Focal species

We focused on three native species of conservation concern and one non-native fish that is thought to negatively interact with native fishes. All four species were large-bodied (can >500 mm adult length) and relatively common. Two focal species are federally endangered (Colorado pikeminnow [*Ptychocheilus lucius*] and razorback sucker [*Xyrauchen texanus*]) and are augmented with annual stocking. Razorback sucker spawn during run-off season (typically May–June) in mainstem river habitats on large gravel bars and use backwater habitats as juveniles before migrating among mainstem river habitats as adults (Tyus & Karp, 1990). Colorado pikeminnow can have extensive postrunoff spawning migrations among mainstem rivers and tributaries (which historically included the Mancos River) to spawn in July or August, but have also used small tributaries as subadults (Fresques et al., 2013; Ryden & Ahlm, 1996; Tyus & McAda, 1984). The numbers and location of stocked endangered species could affect movement; thus, we limited their analyses to behavioural aspects of tributary confluence occurrence. The most common endemic fish in this study was the flannelmouth sucker (*Catostomus latipinnis*), which currently occupies ~ 45% of its historic range and has notable spawning migrations from mainstem rivers into small tributaries during prerunoff conditions in late winter to early spring (Bezzerides & Bestgen, 2002; Cathcart et al., 2015; Weiss, Otis, & Maughan, 1998). Channel catfish (*Ictalurus punctatus*) are the primary non-native fish targeted for removal in the San Juan River because of implied contributions to native fish population declines (Franssen, Davis, Ryden, & Gido, 2014). Channel catfish movements in river networks have some documentation, but data are lacking in their invasive range and as such, were included in our study to determine their movement patterns relative to native fishes (Cathcart et al., 2015; Dames, Coon, & Robinson, 1989). Channel catfish spawn in temperatures greater than 24°C which is during postrunoff conditions (July) in the San Juan River basin (Becker, 1983).

2.3 | Tagging and detection of fishes

Several tagging efforts were used to identify movement of fishes to the McElmo Creek tributary mouth. Tagging efforts involving McElmo and Yellow Jacket creeks included seasonal sampling from September 2011 through August 2015 by Colorado Parks and Wildlife personnel and Cathcart et al. (2015). Chaco Wash was seasonally sampled from June 2012 through March 2014. Chinle Wash was sampled once in June 2013. The Mancos River was sampled twice monthly from February to April 2015. Opportunistic tagging of fishes in the San Juan River with a raft-mounted electrofisher occurred in June and December 2012, June 2013 and December 2014 primarily near other tributary mouths including McElmo Creek, Chaco Wash and Chinle Wash. Additionally, stocked Colorado pikeminnow (>50,000 individuals since 2002; 21,016 since 2009; and 8,195 since 2011) and razorback sucker (>140,000 individuals since mid-1990s; 103, 849 since 2009; and 59,243 tags since 2011) in the mainstem were tagged by Utah Division of Wildlife Resources, New Mexico Department of Game and Fish, and the United States Fish and Wildlife Service. Generally, large-bodied (adult total length >300 mm) fishes greater than 115 mm total length were implanted anterior to the pelvic girdle with a 12 mm (134.2 kHz; BioMark, Boise, Idaho) full-duplex PIT tag using a spring-loaded tagging needle. Some channel catfish ~100 mm were tagged because other studies successfully used 12 mm tags in fishes >65 mm (Burdick, 2012). Most tagged fishes from tributaries were captured with backpack electrofishing, seining or a combination of backpack electrofishing and a bag seine. Although many tagged fishes were recaptured throughout subsequent tagging events, we focused on antenna detection data to show species responses to specific confluence zone factors rather than a mark–recapture study that is confounded by spatial variation in recapture locations.

To detect PIT tagged fish at the mouth of McElmo Creek, we installed a PIT antenna array (BioMark, Boise, Idaho) spanning the stream width (~ 10 m) of McElmo Creek on 2 May 2012 approximately 150 m upstream from the San Juan River. Data were compiled through 31 December 2015. This five-antenna array was anchored to the sandy streambed and required fish to pass over it to be detected (Figure 2). The antenna array consisted of three 3.05 m long by 1 m wide antennas laid end-to-end across the stream that were about 10 m upstream from two 4.6 m antennas arranged in a similar end-to-end fashion. Detection range measured over the course of the study was 10–51 cm above the antenna. To avoid excessive detections of one fish resting near the antenna, we limited detections to one unique tag per minute. Some antennas were disabled by ice flows in January 2013. Those antennas were replaced in March 2013, but then an October monsoon flood destroyed antennas (1 and 4) adjacent to the west side of the creek (Figure 2). As such, it was likely some fish could pass through the system without detection. While the disabled antennas from October 2013 were not replaced, we installed a weir made of wire fencing to funnel fish over the antenna from July 2014 to February 2015. During periods of low flow <0.65 m^3/s in McElmo Creek (50% of the time since October 2013), the channel restricted stream flow over the functional antennas.

2.4 | Data analyses

2.4.1 | Intra and interspecific patterns of detection

Tagging records were compiled to evaluate temporal patterns of detection among species and size classes. To separate reproductive behaviour, adult (≥350 mm) and subadult (<350 mm) flannelmouth sucker were divided into size groups (Cathcart et al., 2015). Similarly, channel catfish were split into subadult (<300 mm) and adult (≥300 mm) groups based on expected size at maturity in the San Juan River (Franssen et al., 2014). As only adult razorback sucker (>350 mm) were tagged and detected, our study is only relevant to adult fish. Conversely, adult Colorado pikeminnow (>400 mm) were rarely tagged and never detected so we only considered subadult fish.

To explore effects of tagging location (mainstem versus tributary) on detection, we calculated the proportions of nonendangered species detected at the confluence antenna originating from either McElmo Creek (tributary) or the San Juan River (mainstem). Fishes tagged before May 2012 were excluded from these analyses because of unequal days at large after tagging. Endangered fishes were excluded from tag location analysis due to low numbers tagged in McElmo Creek relative to the large number of tagged individuals tagged or stocked throughout the mainstem.

2.4.2 | Temporal patterns of detection

Time of day and season

Differences in diel behaviour patterns across seasons were tested for species with over 100 individuals detected. We partitioned the year into four seasons based on flow regime: winter base flow, run-off, summer base flow and monsoon season. Winter base flows were from November through April, run-off was May and June, and summer base flows were generally brief in late June through early July before monsoon season in mid-July through October. This classification was based on San Juan River daily discharge between May 2012 and December 2015 from the USGS gauge station near Bluff, UT (9379500).

All detections were summarised into hourly bins as well as day and night periods. Night and day periods were determined by sunset and sunrise rounded to the nearest hour in peak months (per hydrologic season) including December (winter base flow), June (run-off), July (summer base flow) and October (monsoon). To explore flow effects on movement behaviour, we compared the frequency of detections during high (>44 m^3/s) and low (<44 m^3/s) flows. This threshold represented flows that inundated the mouth of McElmo Creek upstream past the antennas by approximately 50 m and exhibits low flow velocity.

Annual returns

Frequently detected species (>100 unique PIT tags detected) were analysed to determine how many individuals returned to the mouth of McElmo Creek in multiple years. Individual tags were linked to yearly detection data and only individuals with the ability to have multiple years of detection (tagged in 2014 or prior) were used in this analysis. Species were then separated into proportions of tags detected multiple years with a maximum of 4 years possible (i.e. 2012, 2013, 2014 and 2015).

TABLE 1 Numbers of passive integrated transponder tags deployed and detected (in parentheses) in the San Juan River according to species and locations where they were deployed in stocked or wild fishes in the San Juan River. Tag numbers for endangered fishes include records from the mid-1990s through 2014. Tag numbers for nonendangered and non-native fishes are from tagging events between September 2011 and August 2015. Detection numbers were gathered by a PIT antenna array at the mouth of McElmo Creek between 2 May 2012 and 31 December 2015. Asterisk indicates non-native species. Numbers in parentheses below locations indicate river kilometre of the San Juan River and confluences of tributaries sampled in this study.

Species	Location (river kilometre of San Juan River or confluence upstream of Lake Powell)								Total
	Lower San Juan River (0–163)	ChinleWash (111)	McElmo Creek (163)	Yellow Jacket Creek	Mancos River (197)	Chaco Wash (243.5)	Upper San Juan River (163–315)	Animas River (291)	
Catostomus latipinnis adult	(103) 241		(1,845) 2,849		122		(28) 112		(1,976) 3,324
C. latipinnis subadult	(12) 143		(209) 991	(6) 97	(1) 27	74	31		(228) 1,363
Ictalurus punctatus adult*	(34) 214		(239) 335			11	(1) 67		(274) 627
I. punctatus subadult*	(26) 386		(82) 130	(1) 1		38	29		(109) 584
Ptychocheilus lucius[a]	(54) 4,483	1	(5) 18	(1) 6	3	(1) 38	(86) 29,438	3,724	(147) 37,771
Xyrauchen texanus[b]	(7) 2,874						(189) 120,440	(50) 18,125	(246) 143,439
Total									(2,981) 153,138

[a]Upper San Juan River tagging number includes 24 fish tagged by this study, Lower San Juan River includes three fish from this study out of a total of 93 tagged in this study. The total number of tagged fish shown is lower than actual due to some location records being unknown. [b]Lower San Juan River tagging number includes two fish tagged by this study, and Upper San Juan River tagging number includes 12 fish tagged or relocated to that location during this study.

2.5 | Abiotic predictors of detection

The Random Forests (RF) decision tree was used to identify principal environmental and tagging variables associated with species-specific detections of four frequently detected fishes (i.e. >100 unique detections): razorback sucker, Colorado pikeminnow, flannelmouth sucker (subadult and adult) and channel catfish (subadult and adult). We summarised detections and environmental variables by each week during the study period. This temporal scale achieved a balance between fine (i.e. daily detections that are difficult to predict because of small numbers of occurrence and high variability) and coarse (i.e. monthly detection summaries that mask environmental responses at finer temporal scales) temporal scales that can affect habitat availability and use by a population (Fahrig, 1992). Weekly summarised environmental variables included San Juan River discharge (m^3/s, USGS gauge at Bluff, UT), McElmo Creek discharge (m^3/s, USGS gauge in McElmo Creek at CO-UT border, 9372000), San Juan River water temperature (°C, USGS gauge at Bluff, UT), hydrologic season (i.e. winter base flows, run-off, summer base flows and monsoon) and cumulative PIT tags (tagged nonendangered species added to the system). The number of individuals of each species detected in a week was calculated, and for species with high numbers of weekly detections (>40 in a given week), the number of detections was log-transformed ($\log_{10}$+1) to achieve more normalised distributions and avoid undue influence of extreme values. Log-transformations of weekly detections were used for adult flannelmouth sucker, razorback sucker and both size classes of channel catfish.

RF analyses were performed in R with the "*randomForest*" package (Liaw & Wiener, 2002; R development core team, 2011). RF is a nonlinear machine learning tool for prediction and interpretation of variable importance. RF is useful because cross-validation can account for interactions and multicollinearity of continuous and categorical variables (Breiman, 2001a; Cutler et al., 2007). RF uses readily available data for prediction through first "bagging", or fitting regression trees to bootstrapped versions of the training data or essentially fitting observed detections sampled *with* replacement from the raw or original dataset (Breiman, 2001a). New trees (n = 2,000 in this study) are then grown on the training set using random covariate selection (including combinations of covariates that reduce variation by decreasing correlation among trees) and model averaged to attain a predictor with low variance and bias (also described as trees voting for the strongest predictor).

Variable importance was gauged by comparing node purity (an indicator of predictive value from nodes used in classification trees of the RF) and increases in mean-squared prediction error among each covariate averaged from all trees (a measure of how much predictive value would be lost if the covariate was omitted). In other words, variables in RF were not subject to a p-value or a universally recognised metric of statistical power, but mean-squared prediction error measures the relative importance of a variable by the harm a tree incurs in predictive power if random permutations during tree

TABLE 2 Characteristics of passive integrated transponder (PIT) tagged and detected fishes in the San Juan River basin from May 2012 through December 2015. Detections were collected at a PIT antenna array in McElmo Creek about 150 m upstream from the San Juan River, and all distances are given relative to that point. Asterisks indicate non-native fish. Endangered fishes are split to compare individuals tagged within augmentation programs and those within this study (bold font). However, detected metrics include data from all detected individuals per species. Numbers of tagged endangered fishes differ from values in Table 1 due to discrepancies in available data on size, location or date

			Detected fishes total length (mm)		Distance from antenna (km)				Days since being tagged	
					Tagged fishes		Detected fishes			
Species	Tags	Detects	μ ± *SD*	Range	μ	Range	μ	Range	μ	Range
C. latipinnis adult	3,324	1,976	454 ± 37	352–586	22.18	0.02–81.8	20.11	0.02–53.6	180	0–1,196
C. latipinnis subadult	1,363	228	202 ± 70	115–350	26.88	0.02–83	13.82	0.02–53.6	194	0–1,114
I. punctatus adult*	627	274	403 ± 76	300–620	17.11	0.02–80.7	9.1	0.02–32.6	276	0–1,231
I. punctatus subadult*	584	109	243 ± 50	126–299	19.48	0.02–81.9	5.84	0.02–53.4	170	0–1,112
P. lucius	93	7	217 ± 52	143–465	60.13	0.2–83	53.99	0.2–161.4	259	0–1,638
P. lucius	50,952	140	-	-	95.78	0.5–163.2	-	-	-	-
X. texanus	14	0	-	-	79.78	52.11–163.2	-	-	-	-
X. texanus	143,296	246	362 ± 71	110–556	101.2	0.4–163.2	97.4	2.9–152.5	806	7–6,092

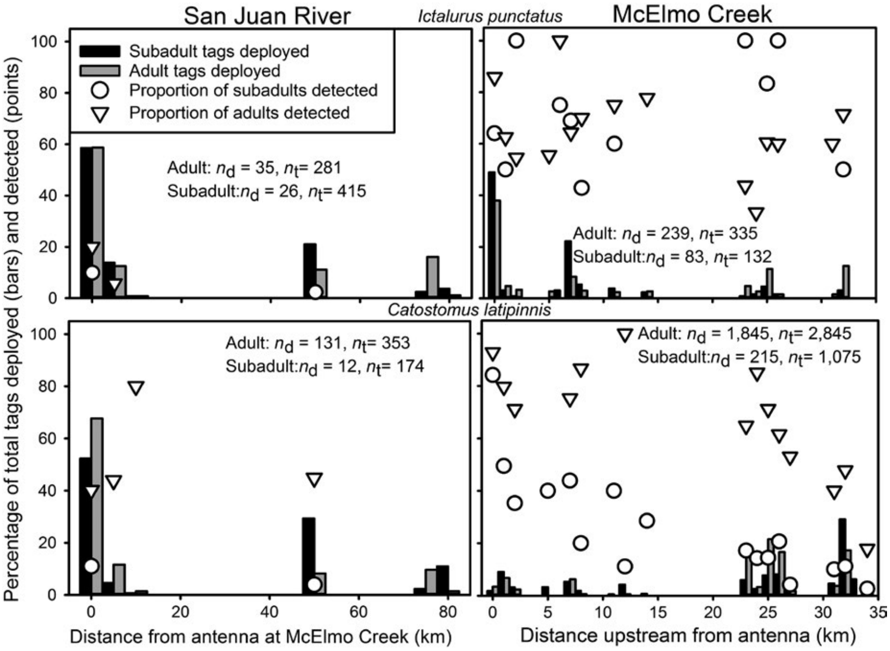

FIGURE 3 Percentages of tagged fish (n_t, bars) and of tagged fish that were detected (n_d, points) as a function of distance in the McElmo Creek (right panels) or San Juan River (left panels) systems from the passive integrated transponder antenna stationed at the mouth of McElmo Creek from 2 May 2012 through 31 December 2015

growing are absent of that variable (Breiman, 2001b). For the purposes of this study, we illustrate both metrics, but use mean-squared prediction error to rank explanatory variables because mean-squared prediction error is representative of all trees in the forest not just the nodes of a tree. Predictions were outside the scope of this paper due to model shortcomings whereby RF regression approaches average values across all trees that causes predictions to generally overestimate low values and underestimate high values (Kühnlein, Appelhans, Thies, & Nauss, 2014). As such, our RF analysis was performed for variable identification via rankings to determine main forces that influence species detections and guide future application towards prediction.

3 | RESULTS

3.1 | Characteristics of tagged and detected populations

From September 2011 through August 2015, we tagged 6,615 individuals throughout the San Juan River basin in addition to >30,000 Colorado pikeminnow and >140,000 razorback sucker tagged by other agencies (Table 1). We identified detections to 2,980 unique PIT tags implanted in our focal species, listed in order of abundance: Flannelmouth sucker, channel catfish, razorback sucker and Colorado pikeminnow (Table 2).

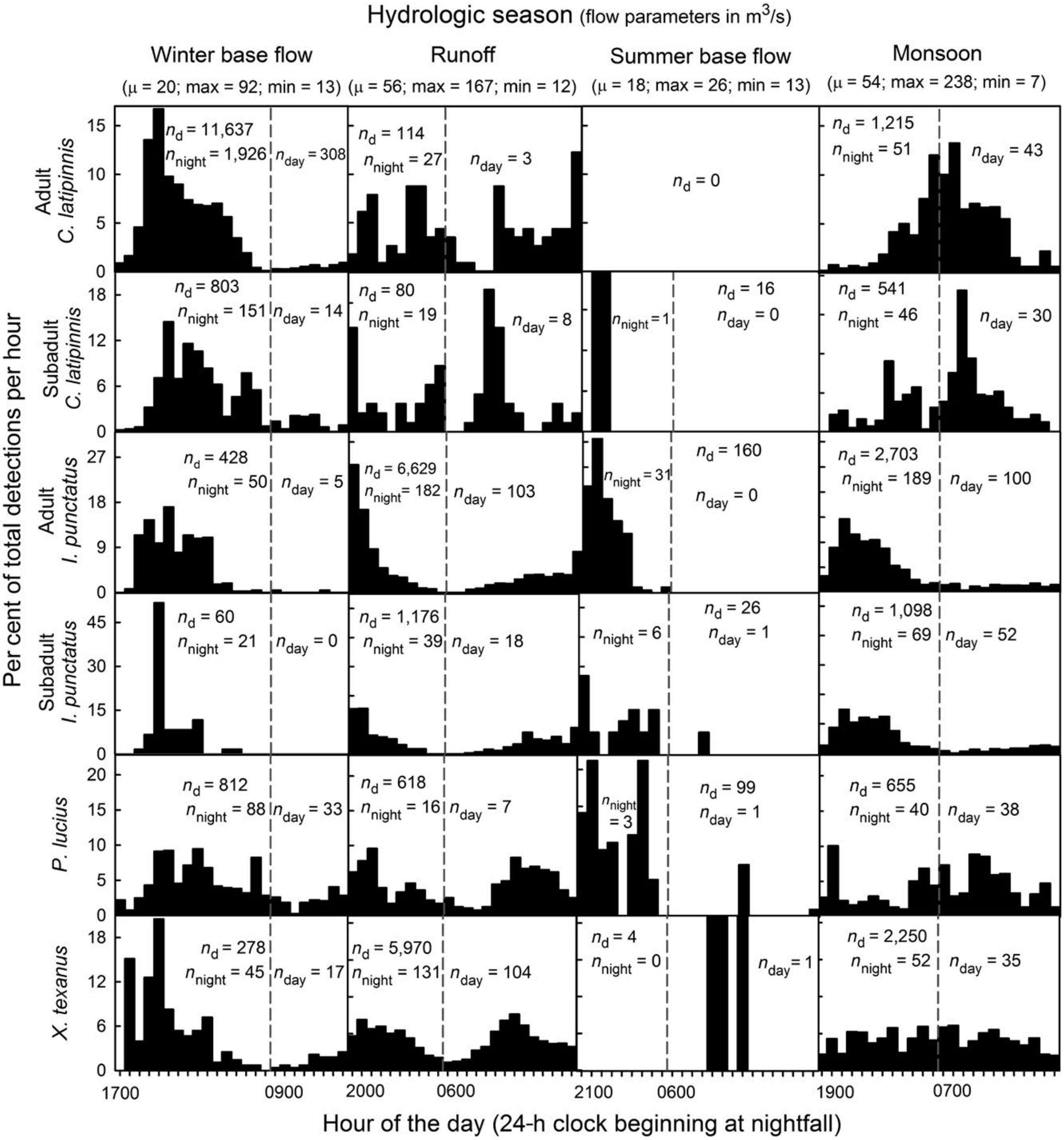

FIGURE 4 Per cent of total detections per hour of the day of passive integrated transponder (PIT) tagged fishes encountered during seasonal hydrologic regimes by a stationary PIT antenna array operated from May 2012 through December 2015 approximately 150 m upstream from the San Juan River in McElmo Creek. Hydrologic seasons are indicated along the top *x*-axis and contain mean, maximum and minimum flow values (m^3/s) for context. Vertical dashed line indicates sunrise. Subadult flannelmouth sucker were less than 350 mm total length (TL), whereas adult flannelmouth sucker exceeded 350 mm TL. Subadult channel catfish includes individuals tagged when they were less than 300 mm TL, while adult channel catfish exceeded 300 mm TL. All Colorado pikeminnow were subadults less than 400 mm TL and all razorback sucker were adults greater than 350 mm TL. Total raw detections (n_d) and unique tags per night and day (n_{night}; n_{day}) periods for each species are indicated per season. Summer base flow had relatively few detections and accordingly, and some species such as *X. texanus* and subadult *C. latipinnis* have percentage of hourly use that exceed the given scale

3.2 | Intra and interspecific patterns of detection

Detections at the confluence antenna indicated variable degrees of movement between the tributary and the mainstem, depending on distance away from the antenna. Fishes tagged upstream of the antenna in McElmo Creek were commonly detected moving downstream to the confluence more so than fishes tagged in the San Juan River moving upstream into the confluence (Figure 3). Adult

TABLE 3 Unique tag detections by a passive integrated transponder antenna array at the mouth of McElmo Creek according to hydrologic seasons in the San Juan River basin from 2 May 2012 through 31 December 2015

	Total unique tag detections per hydrologic season			
Species	Winter base flow	Run-off	Summer baseflow	Monsoon
C. latipinnis adult	1,952	27	0	79
C. latipinnis subadult	159	24	1	68
I. punctatus adult*	54	191	31	219
I. punctatus subadult*	21	42	7	92
X. texanus	48	165	1	62
P. lucius	99	16	3	55

*Indicates species is nonnative.

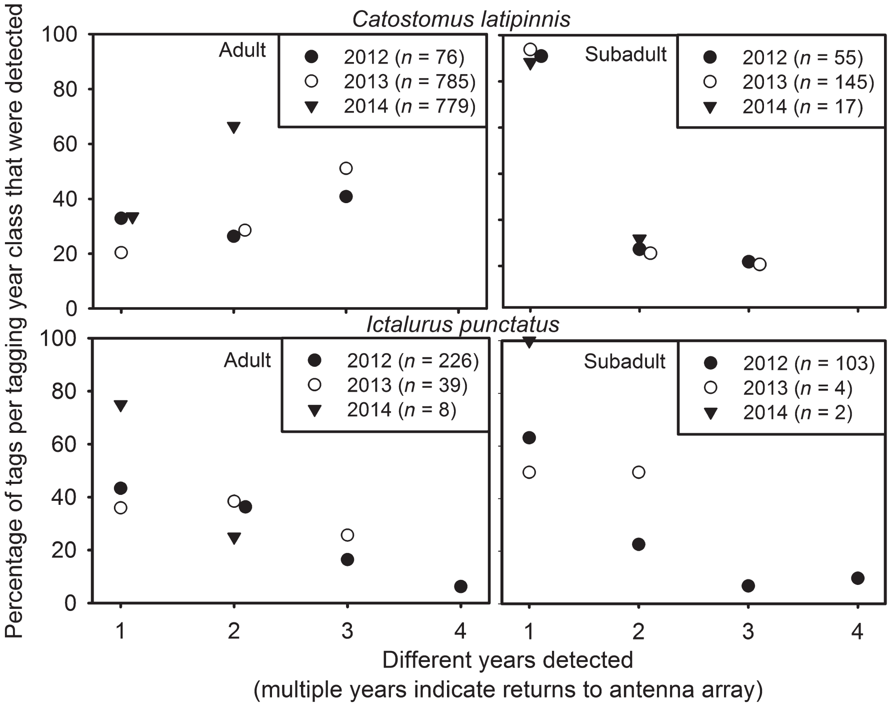

FIGURE 5 Percentages of tagged fishes that were detected one or more years based on tagging year class and size class. Fishes must have been tagged in 2014 or before to be included. Flannelmouth sucker is in the top panels and non-native channel catfish is in the bottom panels. Numbers in each legend indicate the total number of individuals from each year class that were eligible to be detected at the McElmo Creek passive integrated transponder antenna array for multiple years

flannelmouth sucker tagged in the San Juan River were detected at a much higher proportion (37%) than any other species or size class tagged in the mainstem. All species and size classes tagged in the San Juan River had individuals detected despite tagging locations >50 km away. Proportions of detected subadult flannelmouth sucker tagged in McElmo Creek (20%) were higher than subadult flannelmouth sucker tagged in the San Juan River (7%). However, the proportion of McElmo Creek-tagged subadult flannelmouth sucker detected was much lower than adult flannelmouth sucker (65%) and channel catfish (71% for adults, 63% for subadults) that received tags in the tributary.

3.3 | Temporal patterns of detection

3.3.1 | Time of day and season

Night-time detections were more common than daytime detections (Figure 4), but that depended on species, size class and hydrologic season (Table 3). Run-off and monsoon seasons contained substantial periods of confluence inundation relative to low flow conditions in winter and summer. Generally, fishes had a distinct peak in detections between 1900 hr and 2300 hr and night-time use was most pronounced across all species during winter and summer base flow. Both size classes of channel catfish (75% and 78% of all detections occurred at night for subadults and adults respectively) were most often detected in run-off and monsoon seasons. Adult flannelmouth sucker detections occurred primarily during the night (87%) during winter base flow compared to lower proportions of night-time detections (64%) for subadult flannelmouth sucker that occurred in winter base flow and monsoon seasons. Razorback sucker and Colorado pikeminnow detections were more equally balanced among night and day but the former was most likely detected in run-off season (70% of all detections), while the latter occurred primarily in winter base flow (37% of all detections but 67% of all detected individuals). Colorado pikeminnow were detected mostly in late 2012 (59% of all detected individuals), with the peak in November 2012 (28%). After December 2012 when 12 individuals were detected, detections were less than 10 fish per month and under 30 per year throughout the rest of this study.

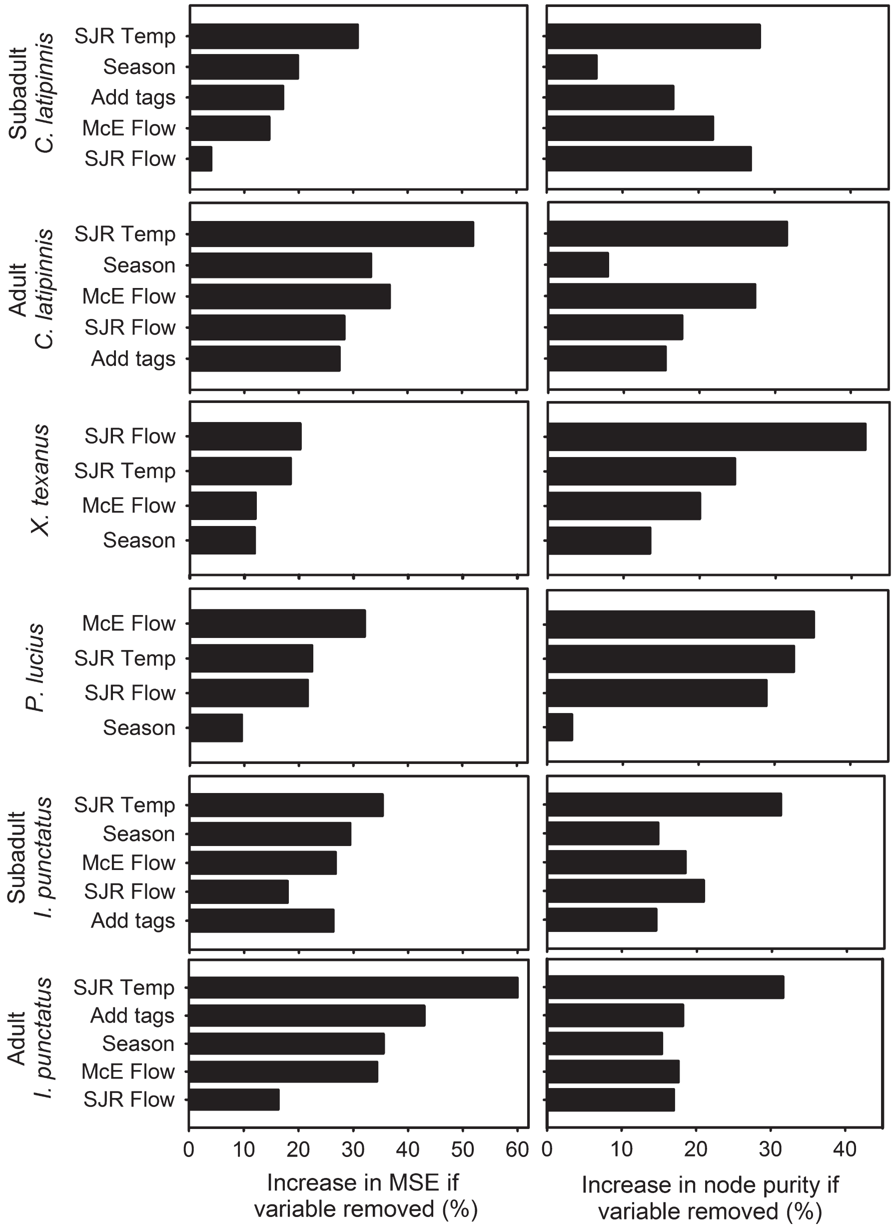

FIGURE 6 Variable-importance plots based on mean-square prediction error (MSE) and node purity of regression trees calculated using Random Forests models of detections for common species at a passive integrated transponder (PIT) antenna operated at the mouth of McElmo Creek, UT from May 2012 through December 2015. Weekly habitat variables are as follows: “SJR Temp” is the mean water temperature (°C) from the San Juan River; “SJR flow” is the mean discharge (m^3/s) for the San Juan River; “McE flow” is the mean discharge (m^3/s) for McElmo Creek; “Season” is a categorical variable indicating the hydrologic season (winter base flow, run-off, summer base flow and monsoon seasons) based on the San Juan River hydrograph; and “Add tags” is the cumulative number of species-specific tags throughout the duration of the study (i.e. only PIT tags deployed in subadult *I. punctatus* were used in analysis of subadult *I. punctatus*)

3.3.2 | Annual returns

Using only tagged fish with potential to have multiple years of detections (i.e. tagged in 2014 or before), flannelmouth sucker and channel catfish had the highest annual repeat occurrence rates across all years of this study. Adult flannelmouth sucker consistently returned to the confluence in multiple years, whereas the proportion of returning subadult flannelmouth suckers and both age classes of channel catfish diminished over time (Figure 5). Seventeen per cent of razorback sucker were detected multiple years (2 years: 10%; 3 years: 4%; 4 years: 3%). Eleven Colorado pikeminnow were detected 2 years and none in 3 years or more.

3.4 | Abiotic predictors of detection

Variation in weekly detections explained by the RF model was highest for adult channel catfish (54%) followed by razorback sucker (46%), adult flannelmouth sucker (46%), subadult channel catfish (30%), subadult flannelmouth sucker (19%) and Colorado pikeminnow (18%). Environmental variables such as season, San Juan River discharge (razorback sucker), McElmo Creek discharge (Colorado pikeminnow) and San Juan River water temperature (both flannelmouth sucker size classes, both channel catfish size classes) provided the most informative ecological covariates to predict detections (Figure 6). To simplify interpretation at a broader temporal scale besides a weekly unit, and to illustrate the dynamics of the environment, we combined the best performing covariate identified by RF for each species (besides adult channel catfish where we show the second-best performing covariate to add diversity in interpretation) with their monthly PIT tag detections over the course of the study (Figure 7). Flannelmouth sucker (both size classes) detections peaked during winter base flows as water temperatures rose. Razorback sucker detections were largely associated with run-off flows in spring. Colorado pikeminnow

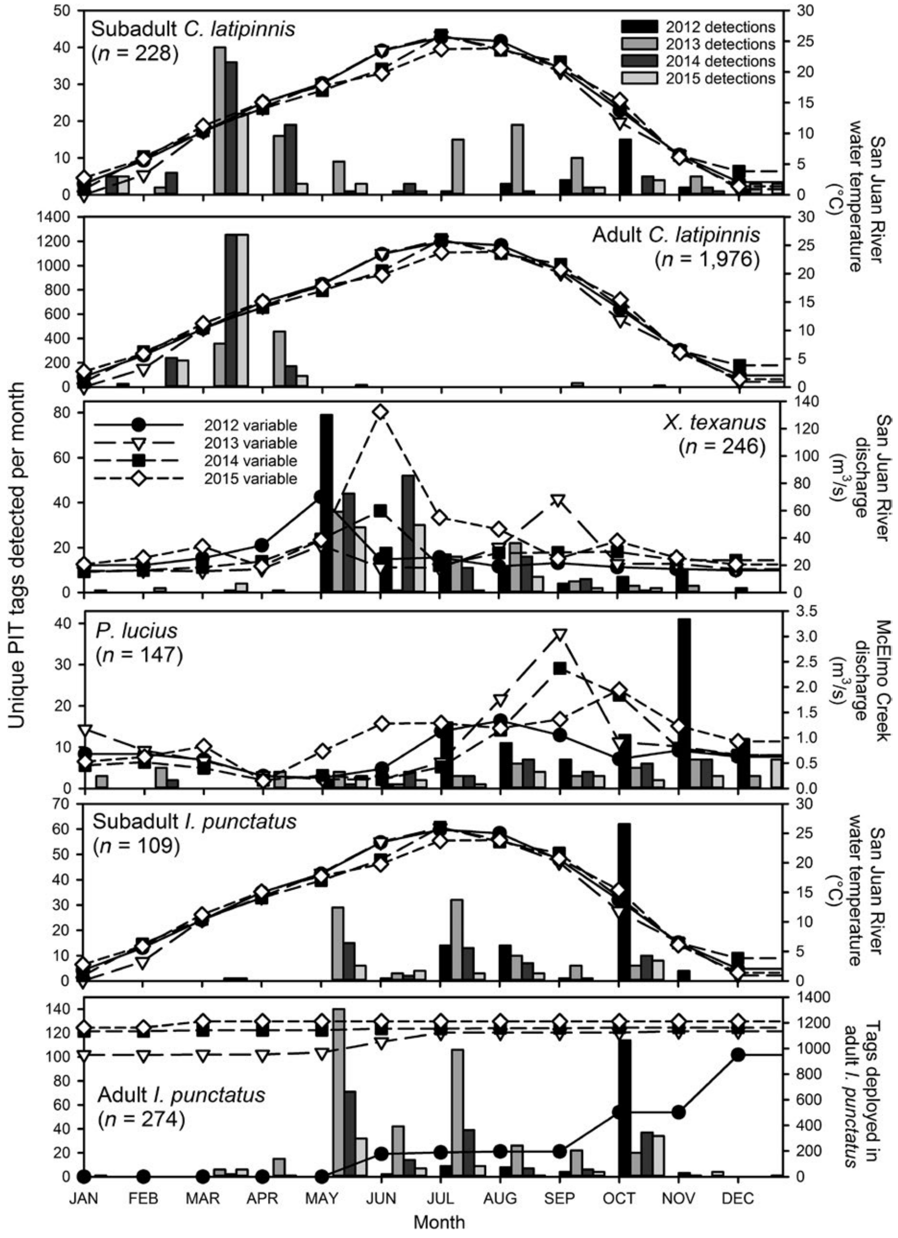

FIGURE 7 Monthly unique detections of fishes across years (May 2012–December 2015) at a passive integrated transponder array stationed in McElmo Creek 150 m upstream from the San Juan River near Aneth, UT. Lines correspond to environmental or tagging variables identified as best predictors by the Random Forests model shown on second *y*-axis (exception is adult *I. punctatus* which shows cumulative tags deployed because it was the next best performing variable). Number in parentheses indicates the total number of individuals detected throughout the study

detections increased in frequency during and following the monsoon season according to tributary flow. Channel catfish (both size classes) detections were explained by San Juan River temperature associated with May through October of each year; however, adult channel catfish were the only species that had the tagging variable ranked in the top two variables. Of 192 weeks of detection data, 28 contained zero detections with 68% of those weeks occurring in winter base flow season between November and February.

4 | DISCUSSION

4.1 | Intra and interspecific patterns of detection

Monitoring fishes at a perennial tributary confluence adjacent to a mainstem river captured inter and intraspecific differences in movement behaviours depending on species biology and environment. Remarkable patterns detected included annual spawning migrations of flannelmouth sucker and flood-related occurrence by razorback sucker. The seasonally flooded McElmo Creek mouth provided opportunities for razorback sucker and other fishes to access tributary habitats that may have beneficial temperatures, allochthonous resources or refugia from high mainstem flows. Seasonally, flooded habitats adjacent to mainstem systems are known to enable lateral movements for foraging, growth and spawning by fish communities worldwide including in floodplains of the Amazon River and Mississippi River basins (Junk, Bayley, & Sparks, 1989; Osorio et al., 2011; Winemiller & Jepsen, 1998). Maintaining or enhancing lateral connectivity between perennial tributaries and mainstem streams might support native fish processes but also potentially create more interactions with non-native species implicated in native species declines. Specifically, maintaining tributary–mainstem connections could be especially fruitful for suckers (among other iteroparous fishes) because of their migrations, long lifespans and relatively large body size that enable predictably continuous nutrient linkages between freshwater systems (Childress, Allan, & McIntyre, 2014; Childress & McIntyre, 2015; Flecker et al., 2010).

Occurrence of fishes at this tributary mouth illustrates the dynamics between habitats and different species and size classes within or among mainstem and tributary systems (Pracheil, Pegg, & Mestl, 2009; Thornbrugh & Gido, 2010). For example, Cathcart et al. (2015) linked PIT tag detections—or lack thereof—of mainstem (i.e. razorback sucker) and headwater (i.e. bluehead sucker *Catostomus discobolus* and roundtail chub *Gila robusta*) fishes to catch data from sites sampled in McElmo Creek. They concluded that mainstem species have greater detections at the tributary confluence despite infrequent use of tributary habitat upstream of the confluence. In contrast, headwater species that permanently reside upstream within McElmo Creek have shorter movements and are infrequently detected because they rarely leave the tributary. Flannelmouth sucker are one exception and annually travel between the mainstem and McElmo Creek during spawning migrations. In this study, adult flannelmouth sucker detections primarily represented fish (91%) originally tagged during March spawning events in McElmo Creek, whereas subadult flannelmouth sucker were mainly tagged outside of the spawning season (92% tagged in months besides March). Although often studied in a single-species context (Colorado pikeminnow in Osmundson et al., 1998; Colorado River, cutthroat trout *Oncorhynchus clarkii pleuriticus* in Young, 2011), we showed how the interaction of stream network spatial factors with ontogenetic differences extends to fish community movement patterns.

4.2 | Temporal patterns of detection

4.2.1 | Time of day and season

We saw a pattern consistent with terrestrial predator avoidance behaviour with peaks of movement during the night except during seasons characterised by elevated discharge. For example, adult flannelmouth sucker might swim in the tributary at low light levels to avoid predators during their spawning migration during winter base flows. Alternatively, razorback sucker diel detections were similar between night and day during run-off season when the mouth of McElmo Creek was often flooded and more turbid. Diel findings for catostomids corroborate Booth, Hairston, and Flecker (2013) who found Sonora sucker (*C. insignis*) and desert sucker (*C. clarkii*) moved more often during low light periods unless the flows were higher and had more turbid water. Diurnal and high-flow related patterns of localised movements occur in other riverine sucker species that exhibit predictable, short-term foraging movements (Jeffres, Klimley, Merz, & Cech, 2006; Matheney & Rabeni, 1995). Subadult fishes detected more frequently in daytime like flannelmouth sucker, and Colorado pikeminnow potentially have more free-ranging movements owing to smaller body size and less likelihood of capture by avian predators (Steinmetz, Kohler, & Soluk, 2003). We do not suggest small body size is correlated with more frequent movements necessarily, but frequent daytime use of a fish passage by predominantly smaller fishes also occurs in Australian galaxiids (Morgan & Beatty, 2006). True to documented nocturnal behaviour (Bailey & Harrison, 1948; Becker, 1983), channel catfish were detected most often at night. Frequent seasonal detections of channel catfish during high discharge are similar to the timing of movements found in their native range where individuals moved among tributary and mainstem habitats most frequently during elevated flows in spring and autumn (Dames et al., 1989). Flow mediates temporal variation in confluence movement behaviours whereby low stream flows coincident with clear water enhance nocturnal movements and high flows (i.e. backwater formation) associated with higher turbidity can enable diel occupancy (or refuge).

Detections were lowest during winter baseflow. This could be due partly to partial destruction of the antenna array from disturbances in January and October 2013, yet the three remaining winters suggest low detections were not anomalous. With the exception of Colorado pikeminnow, limited winter detections were attributed to overall reduced movement during periods of cold water temperature (Brown, Hubert, & Daly, 2011).

4.2.2 | Annual returns

Besides Colorado pikeminnow, every species or size class with greater than 100 tags detected had individuals detected in three or more years. Repeated detections could be due to site fidelity in migratory fishes as well as some form of residency where a home range is inclusive of both mainstem and tributary habitats. Adult flannelmouth sucker exhibited the highest repeat occurrence in McElmo Creek across years due to their annual spring migration which suggests some level of fidelity. The potential for catostomids to home towards—and return to—their natal ranges (i.e. imprinting) has been posited for stream-migrating populations of white sucker (*C. commersonii*) based on the larval development of olfactory anatomy (Werner & Lannoo, 1994). In their native range, channel catfish vary in their homing ability to tributaries, but larger fish can exhibit high site fidelity in mainstem waters, which our data partially corroborated (Becker, 1983; Hubley, 1963; Pellett, van Dyck, & Adams, 1998). Elsewhere in the Colorado River Basin, razorback sucker and Colorado pikeminnow exhibit homing to spawning locations (Bottcher et al., 2013; Tyus, 1990; Tyus & Karp, 1990; Tyus & McAda, 1984). However, our data suggest McElmo Creek may not be, or be near, spawning habitat for Colorado pikeminnow. The varying returns of species to this tributary illustrate how the presence of repeated use may indicate robust populations of some native fish (i.e. flannelmouth sucker), while the absence may be symptomatic of a population bottleneck or habitat avoidance for others (i.e. subadult Colorado pikeminnow).

4.3 | Abiotic predictors of detection

As found in other freshwater fishes (Albanese, Angermeier, & Gowan, 2003; Lucas, Baras, Thom, Duncan, & Slavik, 2001), temperature, flow regimes and tagging history explained tagged fish detections (i.e. behaviour) in this study. Periods of warming and cooling water temperatures correspond to movements of fishes including salmonids, catostomids and cyprinids that seek refuge, spawning or foraging habitats (Albanese et al., 2004; Gowan

& Fausch, 1996; Weiss et al., 1998). San Juan River water temperature explained flannelmouth sucker and subadult channel catfish weekly detections but probably for different reasons. Adult flannelmouth sucker spawning cues are initiated at temperatures between 2–10°C (Weiss et al., 1998), whereas subadult channel catfish may be seeking a higher optimum temperature for performance (28–32°C, range of 18–34°C; Wismer & Christie, 1987). Deacon, Schumann, and Stuenkel (1987) quantified thermal preference of subadult flannelmouth sucker (mean TL 155 ± 20 mm) as 25.9°C which explains the abundant detections during periods of warm water exceeding 20°C in July, August and September (Figure 7). Alternatively, given this study duration encompassed the maturation time of flannelmouth sucker (3–4 years), some individuals tagged as subadults likely recruited to adulthood, which would partly explain higher detections of subadult fish in March and April (McAda & Wydoski, 1977; Mueller & Wydoski, 2004). Razorback sucker occurrences coincident with spawning activity are linked to the ascending limb of a run-off hydrograph throughout the Colorado River Basin (Modde & Irving, 1998; Tyus & Karp, 1990), as appears to be the case here. We attribute abundant subadult Colorado pikeminnow to the tributary flow regime during and after monsoon season which is characterised by flashy, elevated discharge followed by winter base flows (Fresques et al., 2013; Marsh, Douglas, Minckley, & Timmons, 1991; Wick, Hawkins, & Nesler, 1991). Besides mainstem temperature, adult channel catfish detections were explained by cumulative tags implanted during the study probably because of an October 2012 tagging event within 30 m of the antenna array that resulted in almost immediate detection of >100 individuals and thus masked other associated environmental conditions. The environmental triggers of these movement behaviours suggest movement patterns may be sensitive to changes in thermal regimes and regional climate that support seasonal flow regimes via precipitation.

5 | CONCLUSION

Managers of Colorado River Basin native fish must consider how to adequately study an imperiled fish community characterised by long lifespans in a harsh, remote ecosystem that has undergone intense hydrologic alteration (Minckley & Deacon, 1968). Increased and continuous use of remote monitoring via PIT antennas in large river networks spanning multiple jurisdictions (i.e. Columbia and Colorado river basins) provides unique opportunities for exploring dynamic long-term network-wide movement patterns of imperiled fishes with special consideration to the interfaces among mainstem, floodplain and tributary habitats (Booth, Flecker, & Jr, 2014; Galat & Zweimüller, 2001; PTAGIS, 2011). Diverse movement patterns within fish communities at mainstem–tributary confluences can continuously link different streams via life histories that divide a shared space across time (Benda et al., 2004; Braaten & Guy, 1999; Kiffney et al., 2006). Predictors of fish movement behaviours showed mainstem and tributary conditions likely affect the utility of confluences as off-channel refuge, migratory corridors and foraging routes used by fishes.

Although we lacked spatial replication in this tributary-limited riverscape, our fine-scale confluence study integrated multiple ecological frameworks such as the confluence exchange hypothesis (Thornbrugh & Gido, 2010), edge effects (Murcia, 1995) and the natural flow regime as they apply to fish (Poff et al., 1997). Specifically, we generated empirical evidence of how the frequency, timing, duration, and magnitude of individual (sensu biomass) and species exchanges across permeable habitat edges are mediated by temporal variation in fish behaviours. Remotely monitoring nodes in river networks is widely applicable to objectives that range from management of cryptic, migratory and sensitive species (i.e. fish passage, population estimates) to testing ecological frameworks (i.e. metacommunity theory, individual-based movement models) that need further empirical support. Confluence zones provide and connect variable habitat and streams respectively, which are valuable to fishes during different times of the year depending on life stage. River network complexity may be critical for species that require certain conditions at certain periods (i.e. spawning) that are not available perennially in a single stream.

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