North American Journal of Fisheries Management

ISSN: 0275-5947 print / 1548-8675 online
DOI: 10.1002/nafm.10371

MANAGEMENT BRIEF

We Ain't Afraid of No Ghosts: Tracking Habitat Interactions and Movement Dynamics of Ghost Tags under Differing Flow Conditions in a Sand-Bed River

J. Benjamin Stout*
Department of Watershed Science, Utah State University, 5200 Old Main Hill, Logan, Utah 84322, USA; and The Ecology Center, Utah State University, 5210 Old Main Hill, Logan, Utah 84322, USA

Mary M. Conner
The Ecology Center, Utah State University, 5210 Old Main Hill, Logan, Utah 84322, USA; and Department of Wildland Science, Utah State University, 5200 Old Main Hill, Logan, Utah 84322, USA

Phaedra Budy
U.S. Geological Survey, Utah Cooperative Fish and Wildlife Research Unit, Utah State University, 5205 Old Main Hill, Logan, Utah 84322, USA; Department of Watershed Science, Utah State University, 5200 Old Main Hill, Logan, Utah 84322, USA; and The Ecology Center, Utah State University, 5210 Old Main Hill, Logan, Utah 84322, USA

Peter D. Mackinnon
Department of Watershed Science, Utah State University, 5200 Old Main Hill, Logan, Utah 84322, USA

Mark C. McKinstry
U.S. Bureau of Reclamation, 125 State Street, Office of Adaptive Management, Salt Lake City, Utah 84138, USA

Abstract

The use of PIT tags has rapidly proliferated since their introduction, and new mobile detection methods have been developed. However, the presence of ghost tags (i.e., PIT tags left in the system after a fish dies) creates uncertainty about the status (live or dead) of tags detected. Herein, we describe our raft-based mobile PIT tag antenna system, which was used to evaluate the movements of "seeded tags" (i.e., PIT tags that we placed in the river as ghost tag analogs) and their interactions with habitat features. We deployed 5,000 seeded tags in the San Juan River, a large sand-bed river in the southwestern USA. Total distances moved by PIT tags ranged from 0.8 to 4,124 m, but 75% of movements were less than 100 m. Flow conditions causing the smallest to largest movements were (1) base flows, (2) spring runoff flows, (3) flash flood flows, and (4) a combination of spring runoff and flash flood flows. Based on Ivlev's electivity index, tags were more likely to be detected in riffles than in runs. These findings will help to classify mobile PIT tag detections as ghost tags or live fish, a critical data gap limiting the accurate estimation of demographic rates, population status metrics, and descriptions of the habitat use of fishes.

The ability to track individual animals through time and space has allowed researchers and biologists to answer some of the more interesting and challenging questions in fisheries ecology and management. The introduction of technology to the marking of individuals in fisheries began in 1956 with the use of sonic tags to observe salmon movement in relation to dams in the Pacific Northwest (Trefethen 1956). In 1984, PIT tags were first used in fisheries as a part of a study involving salmon in the Pacific

*Corresponding author: stout_ben@hotmail.com
Received April 22, 2019; accepted September 19, 2019

Northwest (Prentice and Park 1984). The use of PIT tags has increased dramatically since their introduction, in part because of the relatively low cost of the tags. Passive integrated transponder tags have been used widely to explore fish behavior (Fetherman et al. 2015), describe habitat use (Bottcher et al. 2013; Conner et al. 2016; Richer et al. 2017), quantify movement patterns (Zydlewski et al. 2001; Homel and Budy 2008; Cathcart et al. 2018), assess fish passage (Lokteff et al. 2013; Pennock et al. 2018; Baker et al. 2019), estimate survival (Osmundson and Burnham 1998; Budy and Schaller 2007; Conner et al. 2015), and estimate abundance (Fetherman et al. 2015; Richer et al. 2017). Collaborations across spatial scales and the creation of databases to share data allow for the tracking of fish beyond individual study goals. The PIT tag database for the Columbia River basin, the PIT Tag Information System (PTAGIS), contains records of over 42 million tags (PSMFC 2018). The Species Tagging, Research, and Monitoring System (STReaMS) database, which is used for endangered fish in the Colorado River basin, has over 1 million tag records (CNHP 2018). Despite the large numbers of PIT tags deployed, the marking of fish provides little information in itself; subsequent detections or recaptures are needed to estimate demographic vital rates, estimate population status metrics, or describe habitat use and movement. This need has led to a corresponding increase in the number and diversity of interrogation techniques.

Even though stationary antennas have the potential to provide a large amount of data, there are still limitations. Despite the increases in tag numbers and the use of stationary antennas, the probability of recapture or detection is often low, especially for desert fishes (Hewitt et al. 2010; Dudgeon et al. 2015; Osmundson and White 2017). Fish behavior can make it difficult to improve the probability of detection or recapture, as fish may move in ways that might not take them past antennas (Brodersen et al. 2014; Holmes et al. 2014) or they may use reaches or tributaries without antennas (Bottcher et al. 2013; Cathcart et al. 2018). Furthermore, many individuals appear sedentary and do not move more than a few kilometers for years at a time. Mobile PIT tag detection tools and techniques have been developed to complement data collected with traditional capture methods and stationary antennas. Mobile methods allow for the sampling of large spatial extents and areas that would otherwise be unsampled, including reaches of streams between stationary antenna arrays (Holmes et al. 2014; Hodge et al. 2015). Many different mobile detection methods have been developed. In marine environments, researchers have developed towed sledges with attached antennas used like a trawl to survey for the Turbot *Scophthalmus maximus*, a large benthic flatfish (Sparrevohn et al. 2014). Boat-mounted antennas have been used to survey mussels in non-wadeable habitats (Fischer et al. 2012), and backpack antennas have been used to sample fish in wadeable streams (Hill et al. 2006; O'Donnell et al. 2010; Hodge et al. 2015). Some systems combining a PIT tag interrogation system with a raft and GPS unit have been developed (Fetherman et al. 2014; Richer et al. 2017), with the ability to cover long reaches (>5 km). Our system, the PIT Portable Antenna System (PITPASS), is capable of floating much greater distances (>32 km in 1 d depending on flows). Because these mobile methods can sample larger areas, they potentially allow us to increase detection probability and fill in knowledge gaps in life histories and demographics, habitat use, and movement. However, mobile sampling detection data cannot be used as easily as data from either stationary antennas or traditional capture methods because the status (e.g., live or dead) of detected PIT tags is uncertain.

The status of PIT tags detected with mobile detection tools is uncertain due to the presence of ghost tags in aquatic systems. Ghost tags are PIT tags that have been left in the environment after being expelled from live fish or after the fish dies (O'Donnell et al. 2010). Passive integrated transponder tags theoretically have an infinite life because the tags do not require a battery; thus, PIT tags can continue to be detected long after they have been expelled. The combination of mobile sampling and the presence of ghost tags prevents the classification of live fish and ghost tags without additional information. In smaller streams, pinpointing a PIT tag's location with backpack scanners potentially allows the tag's status to be confirmed (Fetherman et al. 2014; Bond et al. 2018), but this technique is impractical on larger rivers with large floating antenna arrays. In some cases, the movement of PIT tags has been used to assume that a detection belongs to a live fish (Zydlewski et al. 2001), but PIT tags can still move after a fish dies. Fish carcasses can be transported great distances (Havn et al. 2017), but carcasses can shed PIT tags relatively quickly after death. For example, the average amount of time for White Sucker *Catostomus commersonii* carcasses to shed an abdominally located tag into the environment was only 73.3 h (Muhametsafina et al. 2014); however, this shedding rate has rarely been quantified and remains largely unknown in natural systems. Even after tags are expelled, they can still move (Bond et al. 2018). There are currently few data available about ghost tag dynamics because of the relative novelty of these mobile antenna systems.

Our goal was to determine the effect of high flows and habitat features on the movement and detection of ghost PIT tags in lotic waters, with a broader goal of informing PIT-tag-based analyses of demographic rates and population indices. First, we described and quantified how "seeded tags" (bare PIT tags that we placed in the river; i.e., ghost tag analogs) moved during base flows, flash

flood flows, spring runoff flows, and the combination of flash flood and spring runoff flows. Secondly, we described the interactions of seeded tags with habitat features (e.g., riffles, runs, etc.). To accomplish these goals, we used the PITPASS, a new configuration for a mobile PIT tag antenna system.

METHODS

Study site.— The San Juan River basin is part of the upper Colorado River basin and covers about 99,200 km^2 in Colorado, New Mexico, Utah, and Arizona. The river is about 616 km long, with headwaters located in the San Juan Mountains of Colorado. Navajo Dam was completed in 1962 and is the only major impoundment on the river. The Animas River, the largest and largely unregulated tributary, joins the San Juan River 70 km downstream of Navajo Dam, resulting in a more natural hydrograph below the confluence. Since 1993, the dam has been operated to match flows with the Animas River to mimic natural flow regimes for the benefit of native fish (Gido and Propst 2012). The San Juan River contains approximately 280 km of designated critical habitat for multiple federal endangered species (USFWS 1990, 1998).

Native fish in the San Juan River, including the Razorback Sucker *Xyrauchen texanus*, Colorado Pikeminnow *Ptychocheilus lucius*, and Flannelmouth Sucker *Catostomus latipinnis*, are routinely PIT-tagged as part of a large recovery program (San Juan River Basin Recovery Implementation Program; https://www.fws.gov/southwest/sjrip/). Fish are tagged before stocking and when encountered in the river through sampling efforts. Overall, we completed 13 sampling passes of various sections of the San Juan River and sampled about 2,233 km during differing flow conditions (Table S.1 available in the Supplement in the online version of this article) by using the PITPASS. Our study area began at the Public Service Company of New Mexico Diversion at river kilometer (RKM) 268.2 (measuring from the inflow of Lake Powell) and ended at the Clay Hills takeout at RKM 4.6, just upstream of the Lake Powell inflow area (Figure 1). We sampled from July to October in 2016 and 2017. The optimum flow rate for sampling (deep enough to prevent boats from becoming grounded but shallow enough to still allow for detection of PIT tags) in the San Juan River is about 28.3 m^3/s, but some sampling occurred when precipitation events unexpectedly raised flows above this level while we already were on the river (after a pass began, there was no opportunity to take out until the end).

Antenna system.— We used a mobile floating PIT tag antenna system, the PITPASS, developed by the U.S. Bureau of Reclamation and Utah State University (USU) researchers beginning in 2008. Since 2008, there have been many improvements to the system. The current PITPASS (Figure 2) was comprised of five components: (1) two 3.1-$\times$ 0.9-m Biomark (Boise, Idaho), high-density polyethylene rigid antennas (for a total antenna length of 6.1 m); (2) a multiplexing transceiver system consisting of one Biomark IS1001 Master Controller and two Biomark IS1001 autotuning tag readers; (3) a 24-V, 50-ampere-hour battery bank; (4) a 30-W solar panel; and (5) a solar controller. The Biomark Master Controller, tag readers, battery bank, and solar controller were housed in a waterproof plastic enclosure, with the solar panel mounted on top. The solar panel eliminated the need for a generator to recharge the batteries of the system on multiple-day trips. We used two 3.1-m antennas to maximize detection distance and total scanning area and to allow greater portability. We used a 4.2-m, frameless cataraft (AIRE, Boise, Idaho) in order to avoid possible noise issues associated with metal frames (Fetherman et al. 2014), with the two antennas attached parallel with the main tubes underneath the boat.

We used an Xplore Bobcat (Xplore Technologies, Austin, Texas) rugged tablet to collect data. The Xplore tablet was chosen for its extended battery life, its ability to handle heat (field conditions could exceed 38°C in direct sunlight), and its waterproof rating. A Bluetooth dongle allowed the Biomark Master Controller to send detection data to the tablet, while at the same time the software (Biomark Data Logger Suite) on the tablet collected the GPS data. The GPS data were collected from a Qstarz BT-Q818XT Bluetooth GPS receiver (Qstarz International, Taipei, Taiwan) with a 10-Hz refresh rate (updates GPS satellite data every 0.1 s). We collected and organized the data with Biomark software, which also allowed for the immediate input of habitat data with each detection while floating.

We measured and recorded detection distance, antenna noise, and antenna power every 2 h to ensure that the system was functioning correctly while on the river. We checked detection distance for each antenna while floating down the river to determine detection distance under normal operating conditions. We measured detection distance vertically from the edge of the antenna. The PIT tag that was used to test detection distance was held in a horizontal orientation and perpendicular to the antenna. Detection distance fluctuated but generally ranged from 51 to 99 cm.

We used three PITPASS boats to maximize our coverage of the river. We sampled a different section of the river with each boat: river left, river right, and the center. Boat operators oriented the boats perpendicular to the flow of the river and shoreline unless river conditions dictated a different orientation for maneuvering around obstacles. Tag orientation is known to be a factor affecting the detection distance of PIT tag antennas (Zydlewski et al. 2001). When choosing how to orient the boats on

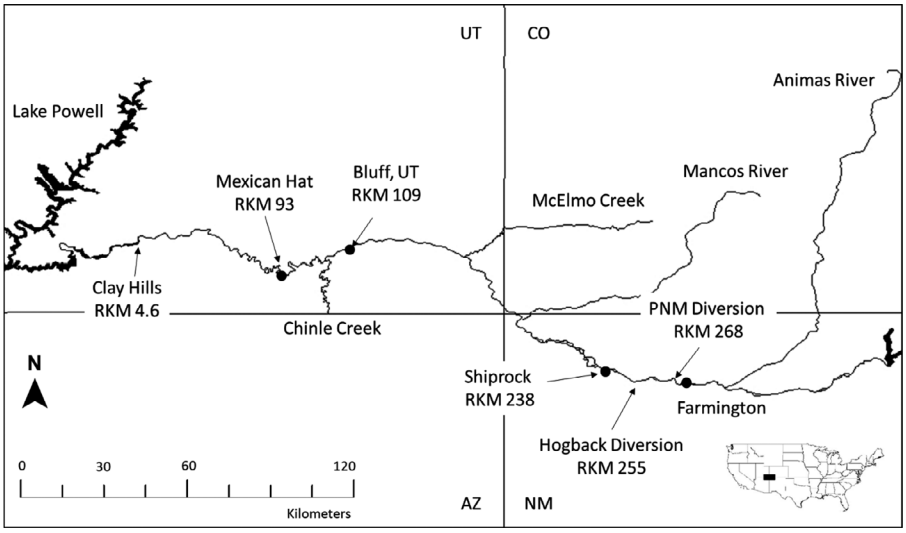

FIGURE 1. Map of the San Juan River study area. The vertical and horizontal lines are the state lines dividing Colorado, Arizona, New Mexico, and Utah. River kilometers (RKM) are provided for select landmarks (PNM = Public Service Company of New Mexico).

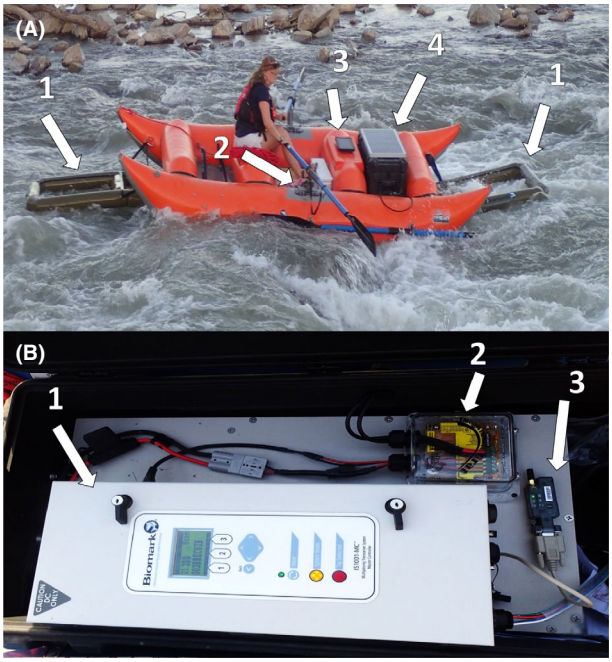

FIGURE 2. **(A)** Sampling with the PIT Portable Antenna System (PITPASS) on the San Juan River occurred during 2016 and 2017 (labeled parts: 1 = two antennas [3.05 × 0.9 m each]; 2 = location of the GPS receiver; 3 = tablet collecting data through Bluetooth; 4 = waterproof plastic box with a solar panel mounted on top, housing the electronics [i.e., Biomark Master Controller, tag readers, and battery bank]); and **(B)** the interior of the electronics box is shown (labeled parts: 1 = Biomark Master Controller; 2 = solar converter; 3 = Bluetooth dongle).

the river, tag orientation was considered, but it is impossible to know the angle at which a tag (i.e., in a live fish, in a dead fish, or expelled) will meet the antenna. Therefore, boat orientation was chosen to maximize area covered, and we moved slowly with the current.

Seeded tags.— We seeded 5,000 bare PIT tags into the San Juan River to mimic tags that had been shed from either live or dead fish. Half of the tags were seeded at the beginning of each field season (i.e., 2,500 in 2016; 2,500 in 2017). We used Biomark HPT12 tags (frequency = 134.2 kHz; dimensions = 12.5 mm long × 2.12 mm in diameter; weight = 115 mg; density = 2.61 g/cm^3), the same tags used for all PIT-tagged fish in the San Juan River. We seeded the tags randomly across all available habitat features from moving rafts at a rate of 1 tag/min. The spacing of seeded tags minimized the possibility of tag collisions. We distributed one-third of the tags from each boat. After tags were scanned, they were dropped into the river from the upstream side of the raft.

We distributed the seeded tags in about 16 km each of two distinct morphological units: canyon and braided. The canyon reach was bound on both sides by canyon walls and was characterized by a deeper, narrower, single-thread channel. The braided reach was not constrained on both sides at the same location and was characterized by a wide, shallow, multi-thread channel (Bliesner and Lamarra 2000). Generally speaking, the braided reach was wider, shallower, and slower moving than the canyon reach. The braided reach began at the Hogback Diversion near Farmington, New Mexico, at RKM 255 and ended at the bridge in Shiprock, New Mexico, at RKM 238. The canyon reach began when both walls of the canyon converged about 14.4 km below Bluff, Utah, at RKM 109 and ended about 8 km above Mexican Hat, Utah, at RKM 93 (Figure 1). We seeded each reach with approximately 1,250 tags/year. We distributed tags during the first

sampling trip of 2016 (July 11–22) and during the first sampling trip of 2017 (July 8–17).

Tag movement.— We recorded the PIT tag number, time and date of detection, latitude and longitude (World Geodetic System [WGS84]), GPS error as determined by the GPS receiver, habitat features, and habitat unit for each detection. We calculated the total distance a tag moved, the average distance moved per day, the distance of individual movements, and the distance moved during different flow events. We calculated the total distance as the sum of all movements of a tag and the average distance moved per day by dividing the total distance moved per tag by the number of days in between the first and last detections (initial release was considered the first detection). We performed a linear regression with distance moved as a function of time to test whether time spent in the river was related to the distance a tag moved.

We calculated linear distance (ignoring the sinuosity of the river) between observed locations in program R (package "geosphere," function "distGeo"; Hijmans 2017). Another possible method for determining linear distance calculates the difference between points on a river network; this method was not used in the present study. A river network is represented by a series of lines in a GIS; as a result, many PIT tag detections do not fall directly on the lines. To calculate distance, the GPS points are "snapped" to the nearest point on the network. This method accounts for the sinuosity of the river in its calculations but is most useful in application to smaller streams and rivers because error is introduced to the measurement when moving GPS points to the river network (line). We did not use this method because the San Juan River is up to 150 m wide in some places, meaning that the resulting error could be up to 75 m for each detection. Most of the distances we calculated were small and would be described by a straight line in the channel; therefore, our calculations would be appropriate even when considering the sinuosity of the river. River sinuosity may have caused some of the larger distances to be underreported. We would urge others calculating distances to use the linear or actual distance (accounting for sinuosity) moved as appropriate for the system of interest depending on the sinuosity and scale of the study area. We classified (while moving; according to depth, velocity, and flow direction) habitat features as riffle, run, pool, shoal, or low velocity as the PITPASS floated over the detected tag. We classified habitat units as belonging to two different classifications: canyon bound or braided reaches; and single-thread or multi-thread reaches.

We used the Shields entrainment criterion τ (Wilcock et al. 2009) to calculate the flow depths necessary for PIT tag movement, and we used the Rouse number (Rouse 1937) to predict how PIT tags would be transported (bedload, suspended load, or wash load). Based on the tag specifications reported above, we performed the calculations by using a 2-mm grain size (PIT tags were held by a 2-mm sieve and therefore were classified as a gravel) and we used critical τ (τ_{cr}) values of both 0.02 and 0.06. Based on a calculated slope of 0.002 for the San Juan River (Bliesner and Lamarra 2000), when the river's depth exceeds 0.19 m we expect to see movement of ghost PIT tags in the system. Flows experienced 100% of the time in the San Juan River (USGS 2018) are capable of moving PIT tags. Nevertheless, stream velocities are typically low near banks and backwaters; thus, we might expect PIT tag deposition in these areas. Physical analysis predicts the potential for ghost tags to be widely distributed in the system. Our Rouse number calculations predicted that the tags will move in the bedload, and we should expect deposition in the same locations as gravels.

High-flow events.— We expected environmental variables, such as flow regime, to have the greatest influence on tag movement. High-flow events (spring runoff or flash floods) can move the majority of sediment loads in rivers, including sediment particles with the same size and density as PIT tags (Malmon et al. 2004); therefore, high-flow events would likely cause different tag movement than base flows. During the study, two natural high-flow events occurred, allowing us to examine their influence on the movement of seeded tags. A large flash flood occurring between August 5 and August 9, 2016, was the first high-flow event. This flash flood occurred because of monsoonal rains in the basin, and its duration was much shorter than a spring runoff event driven by snowmelt. The river rose from 56.3 m^3/s to over 566 m^3/s in less than 12 h but then returned to 56.3 m^3/s 3 d later. The second high-flow event was the spring runoff of 2017. During this snowmelt flood, the high flows were above 141 m^3/s for about 2 months and peaked at around 254 m^3/s (USGS 2018).

We considered tag movements to be a result of base flows when both detections occurred between high-flow events. In other words, either both detections occurred in 2016 before the flash flood, both detections occurred in 2016 after the flash flood, or both detections occurred in 2017 after the spring runoff. Tag movements during the flash flood were defined as tags that were initially detected in 2016 before the flash flood and then detected again in 2016 after the flash flood. Tag movements during spring runoff were detected first in 2016 after the flash flood and then again in 2017 after the spring runoff. Movements affected by both spring runoff and flood flows involved tags that were first detected in 2016 before the flash flood and then detected again in 2017 after the spring runoff. We conducted an ANOVA to evaluate the effect of flow conditions on movement, and if significant effects were detected ($P < 0.05$) we used Tukey's honestly significant difference test to quantify differences.

Electivity index.— One of our goals was to determine how the seeded tags were distributed among different

habitat types and how the distribution changed over the course of two field seasons. We used an electivity index (defined below) to describe the distribution among habitat types. Electivity indices are often used to determine how diet items are consumed relative to their abundance in the environment (Figueroa et al. 2010; Friedenberg et al. 2012) or to determine the distribution of organisms relative to the availability of habitat features (Acolas et al. 2017). We used the electivity index to describe how the river sorted PIT tags into different habitat features relative to the abundance of the habitat features in the river.

Available habitat began at the Hogback Diversion (Figure 1), where we began the distribution of PIT tags, and continued downstream to the location of the downstream-most detected PIT tag. We only considered habitat features contained within wetted width at base flows as available. We used ArcGIS to calculate the availability of habitat features by drawing polygons around habitat features on aerial imagery to calculate their surface area. We only included the tags seeded in 2016 for use in the electivity indices to better describe how the tags interacted with habitat features over time and with the influence of various flows. The first location was the random location from the initial distribution at the beginning of the 2016 field season. The second set of locations comprised subsequent detections in 2016, and the third set of locations encompassed detections in 2017.

All electivity indices exhibit some bias regarding rare items; any item composing less than 10% of the available options should be omitted from the analysis because of this bias (Lechowicz 1982). With this caveat, we omitted three habitat types (pool, shoal, and low velocity) from our initial analysis because combined, these habitat types constituted less than 3% of available habitat. We used Ivlev's original electivity index (Ivlev 1961),

$$E_i = (r_i - p_i)/(r_i + p_i),$$

where i is the habitat type; E_i is the index value; r_i is the proportion of tags in the habitat type; and p_i is the proportion of the habitat type available in the environment. The index scales from −1 to 1; a value of zero indicates a random association, positive values indicate positive correlation (e.g., more PIT tags were found in a habitat type than would be expected by random association given the proportion of that habitat available in the study reach), and negative values indicate negative correlation. We report how those index values changed over time.

RESULTS

We were able to describe 1,401 movements of seeded tags based on the resight data we collected. In the 2016 field season, we detected 305 of the 2,500 tags seeded, resulting in a raw resight rate of 12.2%. The 305 unique tags moved a total of 430 times. When all of the resights from both years were combined after the 2017 field season, the overall raw resight rate improved to 18%, with 899 unique tags detected. The 899 resighted tags moved a total of 1,401 times. We were able to describe more movements than tags because some tags were detected more than two times (up to eight times, translating into seven movements). Despite our efforts to determine differences in movement in the canyon and braided reaches of the river, we resighted only 12 of the tags distributed in the canyon reach. The raw resight rate for the braided reach was 35.5%, and the raw resight rate for the canyon reach was 0.5%. All data are combined in our results.

Tag movement was extremely variable, but the distances moved were generally small. Total distances moved ranged from 0.8 to 4,124 m ($\bar{x} = 1{,}098.7$ m; Table 1), with 90% of all movements being less than 250 m. Movement rates (m/d) were also generally low, but we did observe some extremely high values. The tags generally moved in a downstream direction, but 15.9% of movements were directed upstream. The movements upstream ranged from 0.3 to 99.7 m ($\bar{x} = 8.3$ m), with 97% of all upstream movements being less than 30 m. These distances help to demonstrate the potential error band of tag detection using our GPS equipment because PIT tags most likely are not moving upstream.

We were only able to explain a small amount of the variability in distances moved based on our linear model, which we used to describe the relationship of time between detections and distance moved. The time between the first and last detections was extremely variable (0–469 d; 0 d between detections occurred when more than one boat detected the same tag on the same day), as were the movements associated with them. Although the model was statistically significant ($F_{1,\ 1{,}399} = 261.4$, $P < 0.0001$), we only described a small amount of the variability (Figure 3; $R^2 = 0.16$) with our linear regression.

Passive integrated transponder tags moved greater distances during times of higher discharge (Figure 4). The median distances (±SD) moved during different flow conditions (from smallest to largest) were (1) 7.9 ± 177.6 m at base flows, (2) 18.3 ± 501.4 m at runoff flows, (3) 37.2 ± 387.1 m at flash flood flows, and (4) 192.6 ± 699.4 m for the combination of both flash flood and spring runoff flows. Base flows and the combination of flash flood and spring runoff flows were both significantly different than

TABLE 1. Cumulative distances (m) moved by individual seeded PIT tags detected with the PIT Portable Antenna System (PITPASS) in the San Juan River study area during 2016 and 2017. The total number of unique PIT tags detected more than once was 899.

Variable	Median	Mean	SD	Maximum
Total distance (m)	22.8	168.4	413.1	4,124.0
Movement rate (m/d)	1.6	15.9	174.3	4,086.0

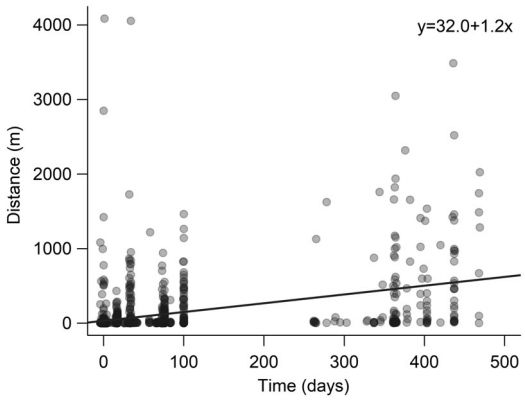

FIGURE 3. Relationship between the number of days between detections and the distance moved (m) between detections of seeded PIT tags in the San Juan River study area during 2016 and 2017. Each circle represents one movement of a seeded tag (darker areas are a result of many circles on top of each other). The line represents the linear regression fit to the data ($R^2 = 0.16$, $F_{1,\ 1,399} = 261.4$, $P < 0.001$).

all other flow conditions ($P < 0.001$), but flash flood and spring runoff flows were not significantly different from each other ($P = 0.87$). The mean distances moved were 3–14 times larger than the median distances for all categories. Minimal tag movement occurred during base flows (93% moved <100 m).

Based on Ivlev's E, we predicted that PIT tags would be more likely to settle in riffles than in runs (Figure 5). The E-value for riffle habitat trended in a positive direction through time, and the E for run habitat trended in a negative direction over the course of the study. These trends demonstrate that tags moved out of run habitats and into riffle habitats over time.

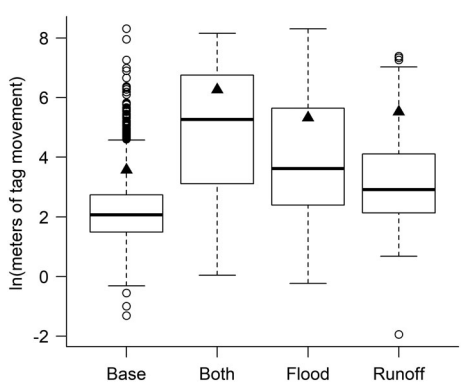

FIGURE 4. Distribution of distances moved ($\log_e$ [ln] transformed) by seeded PIT tags, grouped by flow conditions during the time of the movement, in the San Juan River study area during 2016 and 2017 (base = base flows; both = both flash flood and spring runoff flows; flood = flash flood flows; runoff = spring runoff flows). Triangles represent the mean distance moved ($\log_e$ transformed) for each flow condition. The line inside the box represents the median. The ends of the box are the 25% and 75% quartiles. The whiskers are either 1.5 times the interquartile range from the 25% or 75% quartile or the most extreme value, which ever is closest to the median. The open circles are any values that fall outside the whiskers.

DISCUSSION

Herein, we quantified the movement of ghost tags and their interactions with habitat features and flows in a riverine system and described the PITPASS, a new portable, floating PIT antenna system. Tag movements were generally small (e.g., 90% were <250 m), but large movements were much greater than expected (e.g., 4 km). The magnitude of movements increased with higher flows whether from spring runoff or monsoonal flash floods. As was expected based on physical analysis, ghost tags were more likely to be found in riffles than in runs. Our results suggest that ghost tag dynamics are driven by their interactions with flow and habitat features.

Unsurprisingly, the distances moved by ghost tags were influenced by discharge. Base flows produced the smallest movements, and as one might expect the combination of the two high-flow events (spring runoff and flood flows) produced the largest movements. In addition to the cumulative effect of the greater discharge, the additional time at base flows between the two events allowed for even more movement. In contrast and unexpectedly, there was no statistical difference between tag movements due to monsoonal flash flood flows and movements due to spring runoff flows despite important hydrologic differences in the two flow events. The magnitude of runoff flows was one-fourth that of flash flood flows, even though flash flood flows only lasted one-twentieth the duration of the runoff flows. Furthermore, flash floods can move more sediment than spring runoff flows under certain conditions (Malmon et al. 2004; Vanmaercke et al. 2010). Burial and

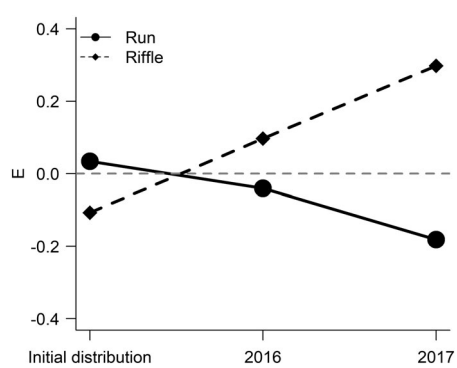

FIGURE 5. Ivlev's electivity index (E) values for the association of seeded PIT tags with riffle and run habitat types in the San Juan River study area during 2016 and 2017. Lines are drawn only to help illustrate the trend in PIT tag association of each habitat type and do not have any statistical meaning. The dashed line at zero indicates where a random distribution across the available habitat features would lie.

exhumation of sediments (Hassan 1990; Hassan and Church 1994) and PIT tags (Bond et al. 2018) through vertical mixing can occur during high flows. Burial and exhumation could explain, in part, smaller movements during base flows (i.e., they were buried) compared to those during high-flow events (i.e., they were exhumed and moved). Additionally, even though burial generally does not affect the detection of PIT tags, vertical mixing can move PIT tags to depths exceeding the detection distance of mobile systems.

Ivlev's *E* indicated that seeded tags tended to settle differentially in riffles relative to runs in this river system. Such a result is unsurprising because our Rouse number calculations indicated that the tags should move in the bedload at all flows (Rouse 1937) and, as a result, should settle in similar locations as gravels. The San Juan River is a sand-dominated river, and the substrate characteristics of habitat features could have contributed to the deposition of tags into riffles. Larger interstitial spaces occur in riffles because the coarsest bed materials are likely to be deposited in riffles (Hirsch and Abrahams 1981), and there is a lack of fine-sediment deposition (Keller 1971). Additionally, if tags accumulated in the troughs of larger bedforms (i.e., dunes) at a depth exceeding our detection distance, then our ability to detect tags in runs may have been limited. In either case, based on seeded tag dynamics, we predict that ghost tags will be differentially detected in riffles in sand-bed rivers.

Some ghost tags moved much greater distances than we expected, despite movements being generally small (90% of movements were <250 m; 97% were <1 km). This is an important observation to inform future movement studies, as the lack of movement has been used to signify the death of the fish (e.g., Carr and Whoriskey 2008). In some cases, this may be appropriate, but both dead fish (Havn et al. 2017) and ghost tags can move large distances, as demonstrated here and elsewhere (Bond et al. 2018). As such, we recommend that investigators determine some measure of ghost tag movement in their systems of interest. This can be done by seeding some tags, as was done here; alternatively, if there are known dead tags in the system of interest, the movement of those tags could be used (the age span of the fish can also provide information regarding ghost tags).

Although we describe patterns of movement and habitat association for seeded tags, there are some issues to consider, including GPS error and habitat-based detection bias. There is a higher level of uncertainty about tag movements when all of the potential sources of GPS error are considered cumulatively. Our GPS antenna was located in the center of the PITPASS, and a tag detected at either end of the system could be up to 6 m away. Depending on which end of the PITPASS subsequent detections of the tag occurred, this could easily account for 12 m of error, not counting error from the GPS itself. Therefore, GPS error could explain most of the upstream movements of tags, which makes sense intuitively. Despite potential errors, the difficulty of the GPS reciever in acquiring satellites in the canyon reach was not to blame for upstream movements, as none of the upstream movements occurred in the canyon reach. Furthermore, small upstream movements could result from circular currents in eddies, but only 8% of upstream movements occurred in habitat that could have been classified as an eddy; therefore, eddies could not account for all upstream movements. When we consider habitat-based detection bias, several factors could have influenced our resight rate. First, the width of the river limited the area sampled. The San Juan River measures up to 150 m in width; at most, all of our boats combined could only sample 18 m at a time. Second, the detection distance of the antennas or the depth of the river could also account for undetected tags (Connolly et al. 2008; O'Donnell et al. 2010; Fischer et al. 2012). This effect was evident in the canyon reach, where we only resighted 12 PIT tags, most likely due to the depth of the river. In the braided reach, the San Juan River is generally shallow, but in places the depth did exceed the detection distance of the PITPASS, although this was rare.

River depth or detection distance can limit the number of tags detected by mobile systems. The inability to effectively detect tags in deeper habitats might have created a bias in our electivity index. However, in the braided reach of the San Juan River, deeper habitats (pools) are extremely rare (~0.1% of available habitat). Therefore, the area that we might have ineffectively sampled in the braided reach was small. We suggest that this is unimportant. Ghost tags only become an issue for users of mobile detection systems when they are detected. If ghost tags are not detected because of depth (i.e., in the canyon reach), then there is no issue, regardless of the research or management question.

In many studies using PIT tags, the antenna efficiency or tag detection probability can be an important variable to quantify (Aymes and Rives 2009; O'Donnell et al. 2010; Richer et al. 2017). For example, when evaluating the effectiveness of a fish passage structure (Castro-Santos et al. 1996), the quantification of antenna efficiency can allow correction of bias caused by undetected fish. We were investigating the movement of PIT tags and habitat characteristics of tag locations, and antenna efficiency was not important to accomplish the goals of our study. Therefore, no effort was made to measure or quantify the efficiency or tag detection probability.

Our work contributes to the growing body of literature on mobile PIT tag detection systems and the fate of tags after death of the fish. Mobile PIT tag detection systems range from backpack systems (Hill et al. 2006; O'Donnell et al. 2010; Hodge et al. 2015) to raft-based (Fetherman et al. 2014; Richer et al. 2017) and boat-based (Fischer et

al. 2012; Sparrevohn et al. 2014) systems. Although limited to larger rivers and streams, our system improved on previous raft-based systems (Fetherman et al. 2014; Richer et al. 2017) by (1) providing the ability to float long distances (>32 km in a day), (2) increasing maneuverability to navigate technical water (e.g., we successfully navigated class 3 rapids), (3) allowing flexibility in the size of the antenna array (i.e., by adding or subtracting antennas), (4) being operable by an individual, and (5) eliminating the need to postprocess the habitat type for detections. All of these features combined will allow us to study broad-scale fish distribution and habitat type by association as well as many other aspects of fish ecology in river systems—and with the added benefit of minimal capture and handling and associated stress to often-imperiled fishes. We demonstrated the potential for large movements of ghost tags, which could bias data collected with floating antenna systems, and we documented the effects of habitat features on their fate. We recommend an evaluation of the movement of ghost tags before using the lack of movement as an indicator of mortality and subsequently using raw detections to estimate survival, for example, or to infer fish movement patterns. To fully develop the emerging picture of ghost tag dynamics, we recommend that researchers evaluate tag dynamics in other aquatic systems with different geomorphic characteristics. The next step is to develop a statistical classification approach for determining whether a detected PIT-tagged fish is alive or dead; we suggest that a random forest classification approach would work well to correctly sort detected tags based on the distance and direction moved and the response to high-flow events (authors' unpublished data).

Ignoring the possibility of ghost tag detection is not an option, as the presence of ghost tags can lead to incorrect conclusions regarding habitat use and fish movement and can even lead to strong bias in estimates of survival and abundance. As more mobile systems are developed and PIT tag use continues, the number of ghost tags in rivers will only increase. An improved understanding of ghost tag dynamics will become increasingly important. As such, there are several important insights gained from our study. First, because ghost tags are capable of large movements, a lack of tag movement should no longer be used to characterize fish death. Second, high-flow events cause the largest movements of ghost tags in river systems. This knowledge could help managers and researchers when designing studies using mobile sampling methods. The timing of sampling could be chosen to minimize the movement of ghost tags (i.e., sampling during low flows). Third, there are river conditions under which the presence of ghost tags may not matter when using mobile systems. In deeper habitats, detection distance will limit the ability to detect ghost tags, perhaps making their presence irrelevant. These insights into the dynamics of ghost tags in lotic systems will assist us in achieving a broader goal of classifying mobile antenna PIT tag detections as live fish or ghost tags, which is essential for using mobile antenna data without bias.

ACKNOWLEDGMENTS

Primary funding for this project was provided by the U.S. Bureau of Reclamation. Additional support and funding were provided by the Ecology Center of USU and the U.S. Geological Survey's Utah Cooperative Fish and Wildlife Research Unit (in-kind) at USU. Jack Schmidt and Peter Wilcock provided essential help with the sediment transport aspects of this work. Tal Avgar and Brian Healy provided insightful manuscript advice. We thank Gary P. Thiede for assisting with project logistics, and we are grateful to P. Hladick, J. Dunnigan, C. Brucker, B. Eachus, C. Carpenter, C. Pullano, T. Laub, B. Laub, C. Stout, N. Malmborg, J. Davies, D. Sullivan, H. Lucas, and H. Moore for assisting with fieldwork. We appreciate Kim Yazzie and Jerrod Bowman (Navajo Nation) for providing logistical support. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government or the State of Utah. This study was performed under the auspices of Protocol 2479 approved by the USU Institutional Animal Care and Use Committee; U.S. Fish and Wildlife Service Permit TE067729-5; and Navajo Nation Permit 1127. There is no conflict of interest declared in this article.

ORCID

J. Benjamin Stout https://orcid.org/0000-0001-9794-7345

REFERENCES

Acolas, M. L., C. Le Pichon, and E. Rochard. 2017. Spring habitat use by stocked one-year-old European Sturgeon *Acipenser sturio* in the freshwater–oligohaline area of the Gironde estuary. Estuarine, Coastal and Shelf Science 196:58–69.

Aymes, J. C., and J. Rives. 2009. Detection efficiency of multiplexed passive integrated transponder antennas is influenced by environmental conditions and fish swimming behavior. Ecology of Freshwater Fish 18:507–513.

Baker, N., A. Haro, B. Watten, J. Noreika, and J. D. Bolland. 2019. Comparison of attraction, entrance, and passage of downstream migrant American Eels (*Anguilla rostrate*) through airlift and siphon deep entrance bypass systems. Ecological Engineering 126:74–82.

Bliesner, R., and V. Lamarra. 2000. Hydrology, geomorphology, and habitat studies. San Juan River Basin Recovery and Implementation Program, Final Report, Logan, Utah.

Bond, R. M., C. L. Nicol, J. D. Kiernan, and B. C. Spence. 2018. Occurrence, fate, and confounding influence of ghost PIT tags in an intensively monitored watershed. Canadian Journal of Fisheries and Aquatic Science 76:286–298.

Bottcher, J. L., T. E. Walsworth, G. P. Thiede, P. Budy, and D. W. Speas. 2013. Frequent usage of tributaries by the endangered fishes of the upper Colorado River basin: observations from the San Rafael River, Utah. North American Journal of Fisheries Management 33:585–594.

Brodersen, J., B. B. Chapman, P. A. Nilsson, C. Skov, L. Hansson, and C. Bronmark. 2014. Fixed and flexible: coexistence of obligate and facultative migratory strategies in a freshwater fish. PLoS ONE [online serial] 9:e90294.

Budy, P., and H. Schaller. 2007. Evaluating tributary restoration potential for Pacific salmon recovery. Ecological Applications 17:1068–1086.

Carr, J. W., and F. G. Whoriskey. 2008. Migration of silver American Eels past a hydroelectric dam and through a coastal zone. Fisheries Management and Ecology 15:393–400.

Castro-Santos, T., A. Haro, and S. Walk. 1996. A passive integrated transponder (PIT) tag system for monitoring fishways. Fisheries Research 28:253–261.

Cathcart, C. N., K. B. Gido, M. C. McKinstry, and P. D. MacKinnon. 2018. Patterns of fish movement at a desert river confluence. Ecology of Freshwater Fish 27:492–505.

CNHP (Colorado National Heritage Program). 2018. Species tagging, research and monitoring system (STReaMS) [online database]. CNHP, Fort Collins. Available: https://streamsystem.org. (November 2019).

Conner, M. M., S. N. Bennett, W. C. Saunders, and N. Bouwes. 2015. Comparison of tributary survival estimates of steelhead using Cormack–Jolly–Seber and Barker models: implications for sampling efforts and designs. Transactions of the American Fisheries Society 144:34–47.

Conner, M. M., W. C. Saunders, N. Bouwes, and C. Jordan. 2016. Evaluating impacts using a BACI design, ratios, and a Bayesian approach with a focus on restoration. Environmental Monitoring and Assessment 188:555–568.

Connolly, P. J., I. G. Jezorek, K. D. Martens, and E. F. Prentice. 2008. Measuring the performance of two stationary interrogation systems for detecting downstream and upstream movement of PIT-tagged salmonids. North American Journal of Fisheries Management 28:402–417.

Dudgeon, C. L., K. H. Pollock, J. M. Braccini, J. M. Semmens, and A. Barnett. 2015. Integrating acoustic telemetry into mark–recapture models to improve the precision of apparent survival and abundance estimates. Oecologia 178:761–772.

Fetherman, E. R., B. W. Avila, and D. L. Winkelman. 2014. Raft and floating radio frequency identification (RFID) antenna systems for detecting and estimating abundance of PIT-tagged fish in rivers. North American Journal of Fisheries Management 34:1065–1077.

Fetherman, E. R., D. L. Winkelman, L. L. Bailey, G. J. Schisler, and K. Davies. 2015. Brown Trout removal effects on short-term survival and movement of *Myxobolus cerebralis*-resistant Rainbow Trout. Transactions of the American Fisheries Society 144:610–626.

Figueroa, R., V. H. Ruiz, P. Berrios, A. Palma, P. Villegas, and A. Andreu-Soler. 2010. Trophic ecology of native and introduced fish species from the Chillan River, south-central Chile. Journal of Applied Ichthyology 26:78–83.

Fischer, J. R., T. E. Neebling, and M. C. Quist. 2012. Development and evaluation of a boat-mounted RFID antenna for monitoring freshwater mussels. Freshwater Science 31:148–153.

Friedenberg, L. E., S. M. Bollens, and G. Rollwagen-Bollens. 2012. Feeding dynamics of larval Pacific Herring (*Clupea pallasi*) on natural prey assemblages: the importance of protists. Fisheries Oceanography 21:95–108.

Gido, K. B., and D. L. Propst. 2012. Long-term dynamics of native and nonnative fishes in the San Juan River, New Mexico and Utah, under a partially managed flow regime. Transactions of the American Fisheries Society 141:645–659.

Hassan, M. A. 1990. Scour, fill, and burial depth of coarse material in gravel bed streams. Earth Surface Processes and Landforms 15:341–356.

Hassan, M. A., and M. Church. 1994. Vertical mixing of coarse particles in gravel bed rivers: a kinematic model. Water Resources Research 30:1173–1185.

Havn, T. B., F. Okland, M. A. K. Teichert, L. Heermann, J. Borcherding, S. A. Saether, M. Tambets, O. H. Diserud, and E. B. Thorstad. 2017. Movements of dead fish in rivers. Animal Biotelemetry [online serial] 5:7.

Hewitt, D. A., E. C. Janney, B. S. Hayes, and R. S. Shively. 2010. Improving inferences from fisheries capture–recapture studies through remote detection of PIT tags. Fisheries 35:217–231.

Hijmans, R. J. 2017. Geosphere: spherical trigonometry. R package version 1.5-7. Available: https://CRAN.R-project.org/package=geosphere. (November 2019).

Hill, M. S., G. B. Zydlewski, J. D. Zydlewski, and J. M. Gasvoda. 2006. Development and evaluation of portable PIT tag detection units: PIT-packs. Fisheries Research 77:102–109.

Hirsch, P. J., and A. D. Abrahams. 1981. The properties of bed sediments in pools and riffles. Journal of Sedimentary Petrology 51:757–760.

Hodge, B. W., R. Henderson, K. B. Rogers, and K. D. Battige. 2015. Efficacy of portable PIT detectors for tracking long-term movement of Colorado River Cutthroat Trout in a small montane stream. North American Journal of Fisheries Management 35:605–610.

Holmes, R., J. W. Hayes, W. Jiang, A. Quarterman, and L. N. Davey. 2014. Emigration and mortality of juvenile Brown Trout in a New Zealand headwater tributary. Ecology of Freshwater Fish 23:631–643.

Homel, K., and P. Budy. 2008. Temporal and spatial variability in the migration patterns of juvenile and subadult Bull Trout in northeastern Oregon. Transactions of the American Fisheries Society 137:869–880.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut.

Keller, E. A. 1971. Areal sorting of bed material: the hypothesis of velocity reversal. Geological Society of America Bulletin 82:753–756.

Lechowicz, M. J. 1982. The sampling characteristics of electivity indices. Oecologia 52:22–30.

Lokteff, R. L., B. B. Roper, and J. M. Wheaton. 2013. Do beaver dams impede the movement of trout? Transactions of the American Fisheries Society 142:1114–1125.

Malmon, D. V., S. L. Reneau, and T. Dunne. 2004. Sediment sorting and transport by flash floods. Journal of Geophysical Research: Earth Surface 109(F2):F02005.

Muhametsafina, A., J. D. Midwood, S. M. Bliss, K. M. Stamplecoskie, and S. J. Cooke. 2014. The fate of dead fish tagged with biotelemetry transmitters in an urban stream. Aquatic Ecology 48:23–33.

O'Donnell, M. J., G. E. Horton, and B. H. Letcher. 2010. Use of portable antennas to estimate abundance of PIT-tagged fish in small streams: factors affecting detection probability. North American Journal of Fisheries Management 30:323–336.

Osmundson, D. B., and K. P. Burnham. 1998. Status and trends of the endangered Colorado Squawfish in the upper Colorado River. Transactions of the American Fisheries Society 127:957–970.

Osmundson, D. B., and G. C. White. 2017. Long-term mark–recapture monitoring of a Colorado Pikeminnow *Ptychocheilus lucius* population: assessing recovery progress using demographic trends. Endangered Species Research 34:131–147.

Pennock, C. A., D. Bender, J. Hofmeier, J. A. Mounts, R. Waters, V. D. Weaver, and K. B. Gido. 2018. Can fishways mitigate fragmentation

effects on Great Plains fish communities? Canadian Journal of Fisheries and Aquatic Sciences 75:121–130.

Prentice, E. F., and D. L. Park. 1984. A study to determine the biological feasibility of a new fish tagging system. National Oceanic and Atmospheric Administration, Seattle.

PSMFC (Pacific States Marine Fisheries Commission). 2018. Columbia Basin PIT Tag Information System (PTAGIS) [online database]. PSMFC, Portland, Oregon. Available: https://www.ptagis.org. (November 2019).

Richer, E. E., E. R. Fetherman, M. C. Kondratieff, and T. A. Barnes. 2017. Incorporating GPS and mobile radio frequency identification to detect PIT-tagged fish and evaluate habitat utilization in streams. North American Journal of Fisheries Management 37:1249–1264.

Rouse, H. 1937. Modern conceptions of the mechanics of fluid turbulence. Transactions of the American Society of Civil Engineers 102:463–543.

Sparrevohn, C. R., K. Aarestrup, C. Stenberg, and D. Righton. 2014. Scanning for PIT-tagged flatfish in a coastal area using a sledge equipped with an RFID antenna. Journal of Fish Biology 85:523–529.

Trefethen, P. S. 1956. Sonic equipment for tracking individual fish. U.S. Fish and Wildlife Service Special Scientific Report Fisheries 179.

USFWS (U.S. Fish and Wildlife Service). 1990. Colorado Squawfish recovery plan. USFWS, Denver.

USFWS (U.S. Fish and Wildlife Service). 1998. Razorback Sucker (*Xyrauchen texanus*) recovery plan. USFWS, Denver.

USGS (U.S. Geological Survey). 2018. National Water Information System: USGS 09379500 San Juan River near Bluff, UT. USGS, Reston, Virginia. Available: https://nwis.waterdata.usgs.gov/usa/nwis/uv/?cb_00060=on&format=gif_default&site_no=09379500&period=&begin_date=2017-04-01&end_date=2017-07-15. (November 2019).

Vanmaercke, M., A. Zenebe, J. Poesen, J. Nyssen, G. Verstraeten, and J. Deckers. 2010. Sediment dynamics and the roll of flash floods in sediment export from medium-sized catchments: a case study from the semi-arid tropical highlands in northern Ethiopia. Journal of Soils and Sediments 10:611–627.

Wilcock, P., J. Pitlick, and Y. Cui. 2009. Sediment transport primer estimating bed-material transport in gravel-bed rivers. U.S. Forest Service General Technical Report RMRS-GTR-226.

Zydlewski, G. B., A. Haro, K. G. Whalen, and S. D. McCormick. 2001. Performance of stationary and portable passive transponder detection systems for monitoring of fish movements. Journal of Fish Biology 58:1471–1475.

SUPPORTING INFORMATION

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