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ARTICLE

Incorporating GPS and Mobile Radio Frequency Identification to Detect PIT-Tagged Fish and Evaluate Habitat Utilization in Streams

Eric E. Richer,* Eric R. Fetherman, Matt C. Kondratieff, and Taylor A. Barnes
Colorado Parks and Wildlife, 317 West Prospect Road, Fort Collins, Colorado 80526, USA

Abstract
The use of mobile radio frequency identification (RFID) systems to detect PIT tags has increased in support of research on fish movement, population dynamics, and habitat use. We describe the development and application of a mobile RFID system that incorporates GPS to detect PIT-tagged fish and evaluate habitat utilization in streams. The study was conducted in two distinct phases. First, development and testing of the RFID–GPS system were conducted using georeferenced, PIT-tagged rocks to evaluate detection probability and GPS accuracy. Second, the system was field deployed to estimate the abundance of PIT-tagged fish and evaluate habitat utilization. Detection probability was negatively influenced by stream width, distance from the stream center, and water depth, whereas detection probability increased with the number of passes. The GPS error between detected and surveyed positions averaged 4.5 m, with greater error observed in longitude than in latitude. Because of high capture and recapture probabilities, abundance estimation of PIT-tagged fish was not only possible but also relatively precise. All detections during field deployment were assigned habitat types using the "intersect," "closest," and "buffer" methods in ArcGIS. Analysis of habitat utilization was limited to two bedform classes, riffles and pools, because the average area of runs and glides was smaller than the average GPS error. More Brown Trout *Salmo trutta* were detected in pools (76–80%) than in riffles, and all Rainbow Trout *Oncorhynchus mykiss* and cutbow trout (Cutthroat Trout *O. clarkii* × Rainbow Trout) were detected in pools. The detection field covered more cross-sectional area in pools than in riffles, which could have influenced the analysis of habitat utilization. The influence of GPS error on habitat evaluations will depend on stream size, as erroneous habitat associations should diminish as stream size increases. The flexibility of the RFID–GPS system makes it useful for a variety of studies related to habitat utilization, fish migration, and population trends.

The use of PIT tags to estimate fish growth, movement, and mortality has become an important tool for biologists due to their relatively low cost, longevity, ability to identify unique individuals, ease of application, and minimal effects on fish survival, growth, feeding behavior, and swimming performance (Zydlewski et al. 2006; Newby et al. 2007; Ficke et al. 2012). Radio frequency identification (RFID) systems have been used in small, wadeable rivers to detect PIT-tagged fish via both stationary (Horton et al. 2007; Connolly et al. 2008; Fetherman et al. 2015; Ficke 2015; Fox et al. 2016) and mobile designs (Roussel et al. 2000; Cucherousset et al. 2005; Hill et al. 2006; Lokteff et al. 2013; Fetherman et al. 2014; Holmes et al. 2014; Hodge et al. 2015). Stationary antennae have been used to analyze fish survival and movement patterns in rivers (Compton et al. 2008; Connolly et al. 2008; Fetherman et al. 2015) and to examine habitat use on inundated floodplains (Conrad et al. 2016). Mobile RFID systems have been used to analyze fish survival, movement, and habitat utilization. Fetherman et al. (2014) deployed river-spanning mobile antennas to estimate abundance and determine the fate of PIT-tagged fish within relatively short river reaches (<2 km) and used raft antennas to determine the location and fate of PIT-tagged fish in longer river reaches (>10 km). Holmes et al. (2014) synchronized a mobile RFID system with GPS to

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*Corresponding author: eric.richer@state.co.us

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evaluate fish emigration and mortality in a New Zealand headwater tributary, and RFID–GPS systems are being applied to evaluate vital rates for endangered fishes in the San Juan River, Utah (M. McKinstry, Bureau of Reclamation; P. MacKinnon, Utah State University; and B. Stout, Utah State University, unpublished data).

Application of RFID studies in streams can be limited by a number of factors, including damage to arrays during floods (Holmes et al. 2014), antenna distortion (Ficke 2015), tag loss, predation, and site access. The detection efficiency (detection probability) for stationary and mobile arrays can be affected by stream discharge, tag size, tag orientation, power source, proximity to other antennae (Zydlewski et al. 2006; Fetherman et al. 2014), tag collision (Axel et al. 2005; O'Donnell et al. 2010), and electromagnetic interference (Greenberg and Giller 2000; Bond et al. 2007; Horton et al. 2007). Hodge et al. (2015) utilized a backpack PIT tag detector with internal GPS (manufactured by Biomark) and suggested that the utility of that system in mountain streams might be limited to low-flow, ice-free seasons and relatively small study reaches due to limited detection distance and time constraints. Mobile RFID arrays are also more likely to detect ghost tags (O'Donnell et al. 2010) because they are an active gear type. Ghost tags are PIT tags that are no longer inside the fish due to tag expulsion or fish mortality. Retention rates of PIT tags are highly variable and can be influenced by tagging location; tagger experience; and the age, size, sex, and species of the tagged fish (Bateman et al. 2009; Dieterman and Hoxmeier 2009; Meyer et al. 2011; Ficke et al. 2012). Failure to account for ghost tags can lead to incorrect interpretations regarding fish location and fate (Fetherman et al. 2014). Regardless of these limitations, RFID technology provides a variety of useful applications for both fisheries research and management.

Incorporation of mobility and GPS technology into RFID systems permits a range of applications, including linking the spatial distribution of fish to individual characteristics, such as species, length, sex, and age (Morhardt et al. 2000; O'Donnell et al. 2010; Holmes et al. 2014; Hodge et al. 2015). Combining individual characteristics with spatial data leads to a number of research possibilities, including investigating fish migration patterns, the effects of instream barriers and fish passage structures on population dynamics, habitat utilization, mark–recapture population estimation, the response of aquatic organisms to climate change, and the impact of land use on aquatic species. This goal of this study was to develop a mobile RFID–GPS system and test its utility for detecting PIT-tagged fish in streams. The study was conducted in two distinct phases. First, development and testing of the RFID–GPS system were conducted by using georeferenced, PIT-tagged rocks, with the objectives of evaluating detection probability, operator bias, and GPS accuracy. Second, the system was field deployed, with the objectives of estimating PIT-tagged fish abundance, evaluating various spatial association methods, and linking detected locations with individual habitat units to evaluate habitat utilization by species and length. Analyses of detection probability, GPS accuracy, population estimates, and habitat utilization were used to identify strengths and limitations of the RFID–GPS system. These analyses were intended to develop application methods for future studies.

METHODS

Development and Testing of the RFID–GPS System

Design and construction.—We designed a rectangular, floating antenna, with the objective of maximizing the depth at which a PIT-tagged fish could be detected. The antenna consisted of two continuous loops of 12-gauge, thermoplastic, high-heat-resistant, nylon-coated (THHN) wire. The wire was run through 19-mm-diameter, polyvinyl chloride (PVC) pipe with rectangular dimensions of 0.9 × 3.0 m (Figure 1). As deformation of the antenna could affect detection distance, two PVC cross-braces were placed inside the antenna frame to improve rigidity. Foam pipe insulation was placed around the PVC to improve antenna buoyancy. The antenna was deployed from a 2.7-m pontoon raft that supported the weight of all system components. The antenna was attached to the raft by using a flexible connection made of rope run through 19-mm PVC that allowed the antenna to rotate around obstacles and float closer to the raft in areas of slower water velocity. The maximum distance between the GPS sensor and the downstream edge of the antenna was 3.6 m.

The antenna was connected to an Oregon RFID half-duplex (HDX) single antenna reader. The HDX reader was interfaced with a Campbell Scientific CR1000 datalogger, which supported incorporation of GPS and temperature sensors. The Garmin GPS sensor was mounted above the center of the raft frame, and the temperature sensor was submerged underneath the raft frame. The system recorded the GPS position and water temperature every time a PIT tag was detected. Both the HDX reader and CR1000 datalogger were powered by a single 12-V, 30-ampere-hour, deep-cycle battery. The HDX reader, tuner box, data logger, and battery were placed in a plastic, top-locking, waterproof case, which was strapped to the rigid raft frame to prevent submersion and movement of system components during deployment.

Detection distance.—Detection distance was measured in the field with the antenna lying flat on the ground. Detailed measurements for detection distance were obtained once during system development and testing. For these detailed measurements, a 32-mm PIT tag was passed over the antenna in two different orientations (perpendicular and parallel) and in four planes of detection (horizontal, vertical, a 45° angle outward from the antenna, and a 45° angle inward toward the center of the antenna). The planes of detection represented different locations within the water column where a fish could be detected: the horizontal plane represented detection at or near the water surface, the

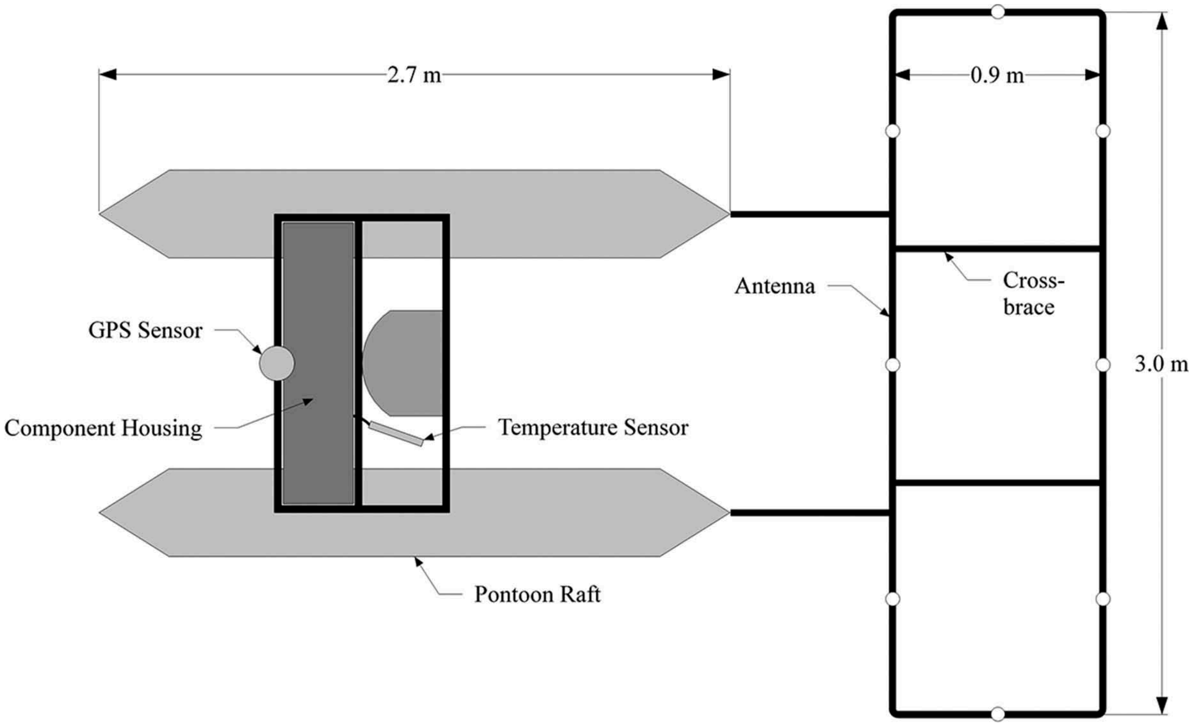

FIGURE 1. Schematic for the raft-mounted radio frequency identification–GPS system, showing approximate dimensions. The antenna consists of two continuous loops of 12-gauge, thermoplastic, high-heat-resistant, nylon-coated (THHN) wire inside 19-mm, polyvinyl chloride pipe. The Campbell Scientific CR1000 datalogger, Oregon RFID half-duplex reader, tuning box, and 12-V, 30-ampere-hour, deep-cycle battery are located inside the waterproof component housing. White circles on the antenna denote measurement locations for detection distance.

vertical plane represented detection directly under the antenna wire, the 45° outward plane represented detection of fish not directly under the surface area of the antenna (e.g., within an undercut bank), and the 45° inward plane represented detection under the surface area of the antenna but not directly under the antenna wire. Maximum continuous detection distance was defined as the point at which a continuous beep from the piezoelectric buzzer attached to the antenna was broken, indicating missed detections (Fetherman et al. 2014). Detection distance was measured at eight locations along the antenna: in the center of the left, middle, and right panels on the long (3-m) sides of the antenna; and in the center of the left and right shorter (0.9-m) sides of the antenna (Figure 1).

Factors affecting detection distances were analyzed by using a generalized linear model implemented with the GLM procedure in the Statistical Analysis System (SAS Institute 2014). The model set included an intercept-only model as well as models in which detection distance was affected by tag orientation only, plane of detection only, or the additive and interactive effects of tag orientation and plane of detection (Fetherman et al. 2014). Models were ranked by using Akaike's information criterion corrected for small sample sizes (AIC$_c$) and were compared by using AIC$_c$ differences (ΔAIC$_c$) and model weights (w_i). We report parameter estimates and associated SEs from the most supported model (Burnham and Anderson 2002).

Detection probability.—For initial evaluation of the RFID–GPS system, a controlled study was conducted at the stream inlet to Parvin Lake (Red Feather Lakes, Colorado) by using 98 georeferenced, PIT-tagged rocks. The PIT tags were attached to rocks with two-part epoxy, and all rocks were painted orange to facilitate placement and retrieval. Rocks were distributed within the stream channel by using randomly generated values for distance to the next downstream transect and distance from the left bank. The width of the stream channel averaged 8.4 m, with a range of 5.1–12.5 m. Water depth at each rock location averaged 0.34 m, with a range of 0.03–0.64 m. Rock placement resulted in a density of 1,246 PIT tags/km. Detection probability was estimated using 12 downstream passes made through the stream inlet to Parvin Lake. Four different operators each made one pass down three separate paths—along the center, left bank, and right bank of the stream channel. The order in which left, center, and right passes were conducted was randomized for each operator prior to deployment. For passes down the left and right banks, the outer edge of the antenna was run as close to each bank as possible.

Detection probability was estimated using the Huggins closed capture–recapture estimator in Program MARK

(White and Burnham 1999). The Huggins closed capture–recapture estimator differs from a traditional closed capture–recapture estimator in that only two parameters—capture probability or detection probability (p) and recapture probability (c)—are included in the likelihood; abundance (N) is conditioned out of the likelihood and estimated as a derived parameter by using estimates of p (Huggins 1989). This quality allows individual covariates affecting p to be included in the Huggins estimator (Huggins 1991). Primary assumptions include that the tags are not lost, the tags are correctly identified, and the system is closed. The PIT tags were epoxied to the rocks, and rocks were not moved during or between passes; therefore, the assumptions of no tags lost and a closed system were met. Furthermore, there was no evidence of incorrectly identified PIT tags during RFID–GPS system testing.

Encounter histories were constructed for each rock such that if it was detected on a pass, it was given a 1; if the rock was not detected, it was given a 0. Water depth, stream width, distance from the center of the stream channel (DFC), and distance from the nearest rock (DFNR) were included as individual covariates for each rock. The DFC was measured in the field as PIT-tagged rocks were deployed; the DFNR was calculated with ArcGIS using the surveyed GPS coordinates for each PIT-tagged rock. The model set included an intercept model as well as models in which p was influenced by depth, width, DFC, DFNR, operator (each operator made three passes), location of the pass within the stream (i.e., left, center, or right), and all additive combinations therein; p equaled c in all models, as c was not expected to be affected by previous detections (Fetherman et al. 2014). Models were ranked and compared using AIC_c, ΔAIC_c, and w_i (Burnham and Anderson 2002), and a model-averaged parameter estimate and unconditional SE were reported (Anderson 2008). Information from all models with w_i values greater than 0 was included in the model-averaged parameter estimate. In addition, cumulative AIC_c weights were used to assess the relative importance of each covariate.

A thirteenth pass was made through the inlet stream during which a single operator guided the raft antenna down the center of the inlet channel and then dragged the raft back up the center of the inlet channel. This pass was used to determine whether p would increase by changing the direction (from downstream to upstream) in which the tagged rocks were being detected. Detection probability was estimated for pass 13 by using the Cormack–Jolly–Seber (CJS) estimator in Program MARK. The encounter history included a release event and the recapture event populated from the detection histories obtained in both the downstream and upstream directions. The CJS estimator includes an estimate for apparent survival (φ) and detection probability (p; Burnham et al. 1987). Because the rocks were known to both "survive" and be retained within the inlet stream during pass 13, φ was set to 1.0 to obtain an accurate and unbiased estimate of p. Similarly, we estimated the increase in detection probability with additional passes by using the detection history data collected by operator 1. Three models similar to those described for pass 13 were constructed using the CJS estimator. The one-pass p was estimated using detection histories from the center pass only, whereas the two-pass p was estimated using the combined detection histories from the passes made on the left and right sides of the stream channel, and the three-pass p was estimated using the combined detection histories from all three passes. Detection probability and associated SE were reported for each model.

Accuracy of the GPS sensor.—Because most GPS sensors do not produce survey-grade coordinates, particularly in topographically complex terrain, it was important to quantify the accuracy of the GPS sensor prior to associating detected positions with individual habitat units during field deployment. Furthermore, the location of the GPS sensor on the raft was offset from the antenna (Figure 1), which could also lead to inaccurate coordinates for detected positions. For this study, a Garmin GPS sensor was used to determine the GPS coordinates of the raft every time the mobile antenna detected a PIT tag. Published specifications for the GPS sensor listed the following position accuracies at 95% typical: within 15 m for standard position service (SPS), 3–5 m for differential GPS (DGPS) with U.S. Coast Guard (USCG)/Radio Technical Commission for Maritime Services (RTCM) correction, and within 3 m for DGPS with Wide-Area Augmentation System (WAAS) correction. Absolute position error was used to evaluate GPS accuracy, which we define as the shortest distance between the detected and surveyed GPS coordinates. "Detected position" refers to the GPS coordinates that were recorded by the RFID–GPS system when a PIT tag was detected. "Surveyed position" was established for each PIT-tagged rock by using a Trimble Global Navigation Satellite System (GNSS) Real-Time Kinematic (RTK) surveying system with a horizontal accuracy of 8 mm. The absolute error between the detected and surveyed GPS coordinates was calculated from the difference in northing and easting coordinates and accounted for GPS error as well as the offset between the antenna and location of the GPS sensor on the raft.

Field Deployment

Study sites.—The RFID–GPS system was deployed at two field sites to evaluate performance of the system when detecting PIT-tagged fish. The primary site for field deployment was a 2.3-km study reach on the Middle Fork South Platte River within the Tomahawk State Wildlife Area, Colorado (hereafter, "the Tomahawk reach"; Figure 2). The Tomahawk reach is characterized by riffle–pool morphology with high sinuosity and is classified as a Rosgen C4 stream type and valley type VIII (Rosgen 1996). Habitat surveys for the Tomahawk reach were conducted concurrently with RFID–GPS system deployment and were used to

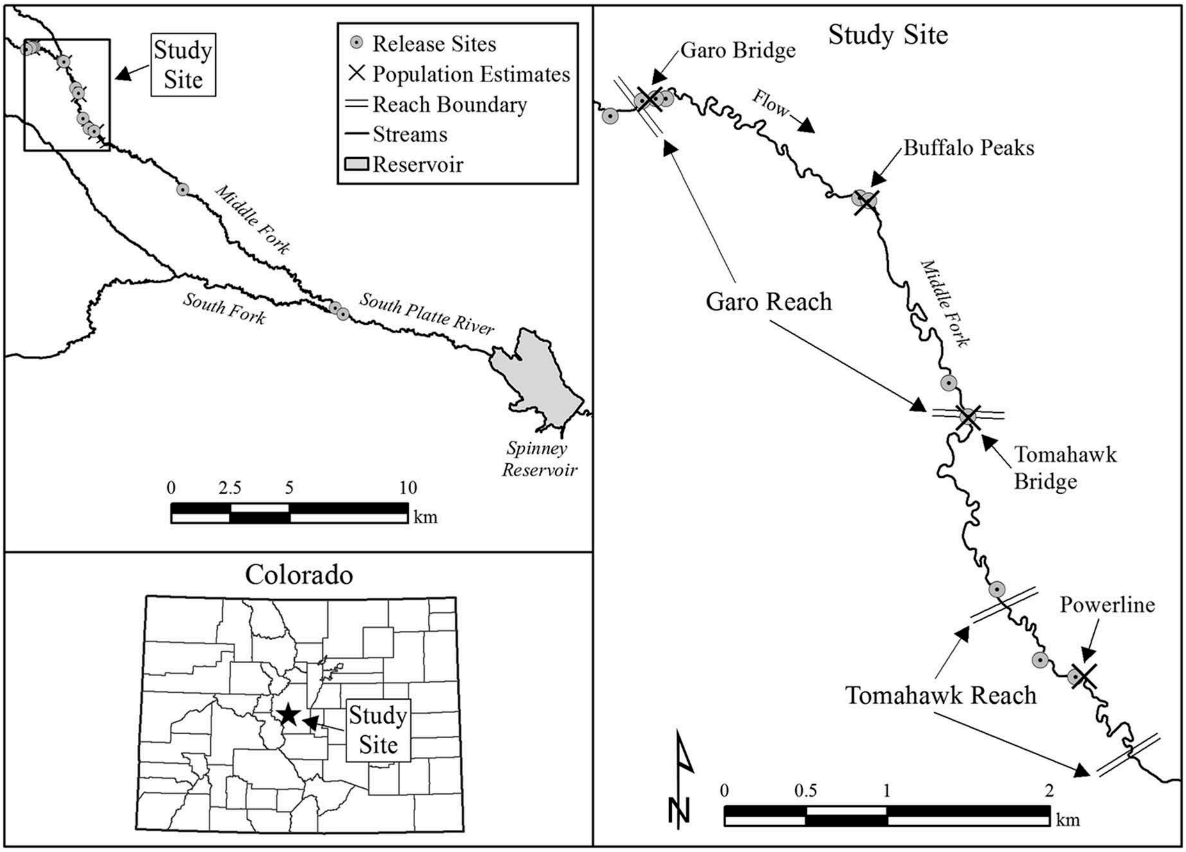

FIGURE 2. Locations of study sites used during field deployment of the radio frequency identification–GPS system in the Middle Fork South Platte River, Colorado, including release sites for PIT-tagged fish, electrofishing sites used for population estimates, and boundaries of the Garo and Tomahawk study reaches.

characterize channel morphology. The wetted width for the stream channel in the Tomahawk reach averaged 8.0 m (SD = 2.5), with a range of 3.0–15.5 m. Water depth averaged 0.55 m (SD = 0.24), with a maximum depth of 1.25 m. The RFID–GPS system was also deployed in a 5.0-km reach upstream of the Tomahawk reach near Garo, Colorado (hereafter, "the Garo reach"; Figure 2). Field deployment in the Garo reach occurred as part of a companion study on fish movement but was included in system development to evaluate detection probabilities during higher flows. Habitat surveys were not conducted for the Garo reach. Although the RFID–GPS system included a temperature sensor, the temperature data collected during field deployment were not analyzed for this study but may be useful for other research applications.

Fish tagging.—Prior to deployment of the RFID–GPS system, 1,272 trout were PIT-tagged and released as part of the companion study on fish movement. Fish were tagged and released during 14 separate events, including 6 tagging events between August and October 2013 and 8 tagging events between September and October 2014. Fish were released at 14 different sites within a 40-km stream reach above Spinney Reservoir (Figure 2). The majority of fish were released within the upper 9.2 km of the 40-km reach: 58% of tagged fish were released within the Garo reach, and 32% of tagged fish were released within the Tomahawk reach. The remaining 10% of tagged fish were released at sites 8–18 km downstream of the Tomahawk reach.

All fish were tagged with 32-mm HDX tags, which were inserted posterior to the pectoral fin through the midventral body wall into the peritoneal cavity by using a hypodermic needle (Prentice et al. 1990; Acolas et al. 2007). Only trout larger than 12 cm TL were considered eligible for tagging to ensure that the tag weight was less than 12% of individual body weight (Brown et al. 1999). During tagging events, we released 1,207 (95%) Brown Trout *Salmo trutta*, 57 (4.4%) cutbow trout (Cutthroat Trout *Oncorhynchus clarkii* × Rainbow Trout *O. mykiss*), and 8 (0.6%) Rainbow Trout. At the time of tagging, mean TLs were 31.5 cm (SD = 9.7) for Brown Trout, 26.2 cm (SD = 5.1) for cutbow trout, and 25.7 cm (SD = 7.4) for Rainbow Trout. The smallest (17.3 cm) and largest (61.4 cm) fish tagged were both Brown Trout.

Deployment of the RFID–GPS system.—Two consecutive passes were made through the Tomahawk reach during base flow (0.85–1.1 m^3/s) conditions on October 29, 2014; two passes were made through the Garo reach on consecutive days during higher flows (4.5–4.8 m^3/s) on July 13–14, 2015. The RFID–GPS system was floated down the thalweg of the stream during field deployment. In locations where the stream divided into multiple channels, the raft was navigated down the primary channel based on the amount of flow in each channel. The raft and antenna were maneuvered to cover as much of the channel area as possible. Ropes were tied to the frame to control the raft and to allow researchers to walk behind the raft along streambanks in an effort to minimize disturbing the fish from their locations in the channel. Approximately the same path through the stream reaches was followed on both passes.

Detection distance and channel morphology.—Detection distance was measured prior to field deployment to (1) confirm that antenna efficiency was similar to performance during system development and (2) evaluate consistency in detection distance between deployments. For pre-deployment measurements, detection distance was recorded for a single location in the center panel of the antenna on the downstream side. All pre-deployment measurements of detection distance utilized a perpendicular tag orientation and a vertical plane of detection. Pre-deployment detection distance measurements were used in conjunction with measurements from system development to compare the area of the detection field to the wetted area of the stream channel during field deployment in the Tomahawk reach. Test tags were used periodically during field deployment to ensure that the system was working, but all test tags were removed from detection records prior to analysis.

Detection probability and abundance estimation.—After system deployment in the Tomahawk and Garo reaches, the two-pass detection data were analyzed using the Huggins closed capture–recapture estimator in Program MARK to obtain estimates of capture probability (p), recapture probability (c), and abundance (N). Although fish were previously marked with PIT tags and released, deployment of the mobile RFID–GPS system was treated as a traditional mark–recapture study in which the first pass was the “mark” pass and the second pass was the “recapture” pass. The PIT tag retention rate was assumed to be 100% for the purposes of this study (i.e., no tag loss). Encounter histories were constructed for each fish such that fish encountered only on the first pass had a history of “10”; fish encountered only on the second pass had a history of “01”; and fish encountered on both passes had a history of “11.” Length was included as an individual covariate, and species were included as groups in the analysis. Fish length was thought to affect both p and c. Dominance hierarchy and selection of profitable stream positions (Fausch 1984, 2014) may have caused larger individuals in profitable feeding positions to be encountered first and caused smaller fish to move into areas where they were less likely to be detected. Additionally, larger fish may be more likely to return to these profitable positions after disturbance but prior to recapture. Models were run in which p did or did not (estimated separately) equal c, and the model set included intercept models (models in which no covariates affected p or c) as well as various structures of effects (covariates included) for p and c. The model set included a total of 18 models. Models were ranked using AIC_c, compared using ΔAIC_c, and ranked using w_i (Burnham and Anderson 2002), and we report model-averaged parameter estimates and associated unconditional SEs using models with w_i values greater than 0 (Anderson 2008). In addition, cumulative AIC_c weights were used to assess the relative importance of each covariate.

Fish population estimates.—Population estimates for trout were obtained from routine monitoring surveys and were used to compare the density of PIT-tagged trout to the total number of trout (tagged and untagged) within the study reaches. Trout populations were sampled using two-pass removal with a bank electrofishing unit to estimate trout density (number of fish/km; Seber and Le Cren 1967) at three sites within the Garo reach (Garo Bridge, Buffalo Peaks, and Tomahawk Bridge) and at one site within the Tomahawk reach (Powerline; Figure 2). Electrofishing surveys took place during spring and fall 2012, spring and fall 2013, and fall only in 2015. Population estimates were used to evaluate the number of fish present in each reach relative to the number of PIT-tagged fish detected within each reach by the RFID–GPS system. No electrofishing surveys were conducted during fall 2014 or summer 2015, when RFID–GPS surveys were conducted; therefore, population estimates from fall 2013 and fall 2015 were used to estimate the number of fish within each reach during RFID–GPS deployment. For the Garo reach, Brown Trout population estimates were averaged across all sites sampled during fall 2013 and fall 2015 and then were multiplied by the reach length. Population estimates for the Powerline site were used to estimate the total number of Brown Trout within the Tomahawk reach.

Habitat utilization.—Habitat units were surveyed within the Tomahawk reach using a Trimble GNSS RTK surveying system and were mapped in ArcGIS to evaluate habitat utilization for detected fish. The study reach was initially mapped into individual habitat units using four habitat types based on bedform morphology: riffle, run, pool, and glide (Rosgen 2014). These habitat types were subsequently simplified into two habitat types by combining runs and glides into the pool classification, while areas classified as riffles remained unchanged. Runs and glides were merged into the pool classification because the average area of those habitat types (24–50 m^2) was smaller than the average GPS error (62 m^2) established during system development and testing at the stream inlet to Parvin Lake. Habitat maps and detected locations were analyzed in ArcGIS to determine the proportion of PIT-tagged fish that were detected within each habitat type. The mean absolute GPS error obtained during system development and testing was used to create a buffer around the detected position and to account for uncertainty in GPS coordinates.

All detected PIT tags were assigned to a surveyed habitat unit with associated habitat type (riffle or pool) by using three different approaches in ArcGIS. First, detected positions were assigned a habitat type by using the "intersect" method, meaning that the detected position had to occur within the spatial extent of the nearest surveyed habitat unit. Second, habitat types were associated with each detected position by using the "closest" method, which simply placed each detected position in the closest habitat unit. Finally, with the "buffer" method, a 4.5-m buffer was created around each detected position to account for GPS error in the detected position. The 4.5-m buffer represents the average GPS error calculated during system development and testing at the stream inlet to Parvin Lake. Detected positions were assigned a habitat type by calculating the proportion of the buffered area that overlapped surveyed habitat units. For example, if 60% of the buffered area occurred within a pool, 30% overlapped a riffle, and 10% occurred outside the wetted channel area, then the detected position was assigned to the pool. For the initial buffer analysis, detected PIT tags were assigned to the habitat type with the highest proportion of buffered area, even if the tag was assigned to the nonwetted area (NWA) outside of the channel. As PIT-tagged fish should not be associated with areas outside of the wetted channel, a secondary buffer analysis was performed in which NWA was excluded and detected tags were assigned to the habitat type with the greatest proportion of buffered area. These approaches were compared to evaluate differences in habitat utilization by spatial association method, and a single method was selected to evaluate habitat utilization by species and size.

RESULTS

Development and Testing of the RFID–GPS System

Detection distance.—Model results suggested that detection distance was influenced by both tag orientation and plane of detection ($w_i = 1.00$; Table 1). Overall, detection distances were greater when the tag was oriented perpendicular (mean = 1.10 m; SE = 0.11) rather than parallel (mean = 0.52 m; SE = 0.10) to the antenna, and this pattern held true for all detection planes. With the perpendicular orientation (the optimal orientation for detection), detection distances were greatest in the 45° angle inward detection plane and lowest in the horizontal plane, although detection distances did not vary greatly among the horizontal, 45° angle outward, and vertical detection planes (Figure 3).

TABLE 1. Model selection results for factors influencing maximum detection distance of PIT tags with the radio frequency identification–GPS system. The maximized log-likelihood (log[L]), the number of model parameters (K), and Akaike's information criterion corrected for small sample sizes (AIC$_c$) are shown for each model. Models are ranked based on the AIC$_c$ difference (ΔAIC$_{c,i}$) relative to the best model in the set. Akaike weights (w_i) quantify the probability that a particular model is the best model in the set given the data and the model set.

Model	R^2	Log(L)	K	AIC$_c$	ΔAIC$_{c,i}$	w_i
Orientation + Plane	0.72	–7.86	6	29.19	0.00	1.00
Orientation × Plane	0.72	–9.10	10	42.35	13.16	0.00
Orientation	0.49	–24.85	2	53.90	24.71	0.00
Plane	0.22	–39.51	4	87.70	58.51	0.00
Intercept	0.00	–46.04	1	94.15	64.97	0.00

Detection probability.—Stream width, DFC, and rock depth all influenced the detection probability of PIT-tagged rocks. All of these factors appeared in various additive combinations in the top models of the set, and the cumulative AIC$_c$ weights for all three were at least 0.88 (Table 2). Water depth, stream width, and DFC all had negative influences on p, suggesting that (1) the deeper a rock was located beneath the water surface, (2) the wider the stream, or (3) the farther a rock was from the center of the stream, the less likely it was to be detected. Location of the pass within the stream (left, center, or right) and DFNR had lesser effects on p (Table 2), although p was slightly higher for passes made on the left and right sides of the stream than for passes made down the center of the stream (Figure 4). Operator did not appear to affect p (Table 2), as p was similar across operators for a given pass location (Figure 4).

Guiding the antenna downstream and walking it back upstream (pass 13) resulted in a nonsignificant increase in p (mean = 0.58; SE = 0.05) in relation to the other passes where the antenna was only guided downstream (mean = 0.45; SE = 0.02). Detection probability increased with the number of passes made with the RFID–GPS system. The p was lowest when only the center pass was used (mean = 0.47; SE = 0.05), increased significantly when left and right passes were combined (mean = 0.85; SE = 0.04), and increased only slightly when detections from all three passes were combined for operator 1 (mean = 0.93; SE = 0.02). The locations of tags

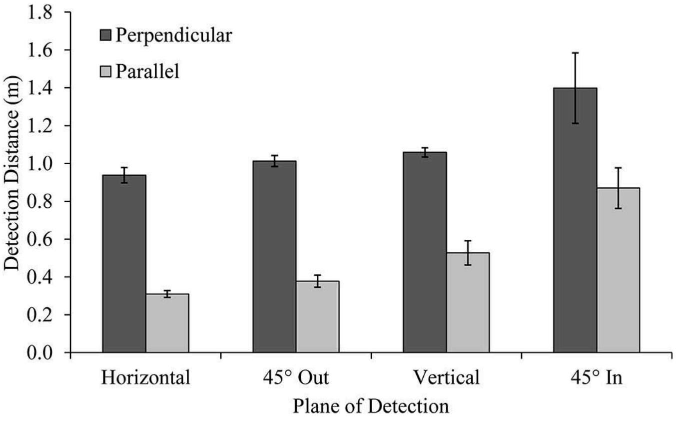

FIGURE 3. Average detection distances (±SE) for the radio frequency identification–GPS system with PIT tags oriented perpendicular and parallel to the antenna wire in the horizontal, 45° angle outward (45° out), vertical, and 45° angle inward (45° in) detection planes.

TABLE 2. Cumulative weights (Akaike's information criterion corrected for small sample sizes [AIC_c]), beta values (β_i; coefficients representing the direction and magnitude of the effect of a parameter on detection probability), and lower and upper 95% confidence limits (CLs) of β_i for the parameters included in the model selection analysis for detection probability of PIT-tagged rocks (DFC = rock distance from the center of the stream channel; LCR = left, center, or right [i.e., pass location]; DFNR = distance from the nearest rock). The β_i values and CLs are from the top model in which the given parameter appeared.

Parameter	Cumulative AIC_c weight	β_i	Lower 95% CL	Upper 95% CL
Stream width	1.00	–0.08	–0.11	–0.05
DFC	1.00	–0.15	–0.19	–0.12
Rock depth	0.88	–0.41	–0.73	–0.09
LCR	0.67	0.31	0.01	0.61
DFNR	0.45	0.04	–0.02	0.10
Operator	0.06	0.02	–0.32	0.37

detected by operator 1 on individual passes (left, center, and right) and all passes combined are illustrated in Figure 5.

Accuracy of the GPS sensor.—The GPS accuracy for the mobile antenna was evaluated during system development by using PIT-tagged rocks with surveyed positions. Although all PIT-tagged rocks were placed within the wetted channel at the Parvin Lake stream inlet, detected positions were observed outside of the wetted channel along distinct lines of longitude (easting) and latitude (northing; Figure 5). The distance between lines of longitude averaged 14.0 m, while the average distance between lines of latitude was 1.9 m. The absolute error between the detected and surveyed GPS coordinates was used to evaluate the accuracy of detected positions. The average error in easting coordinates was 3.7 m, which was almost double the average error in northing coordinates (2.0 m; Table 3). Absolute error, which represents the shortest distance between the detected and surveyed positions, averaged 4.5 m, with a range of 0.3–12.4 m (Table 3). The average absolute error of 4.5 m was used as a buffer around detected positions from field deployment in the Tomahawk reach to account for GPS error when evaluating habitat utilization.

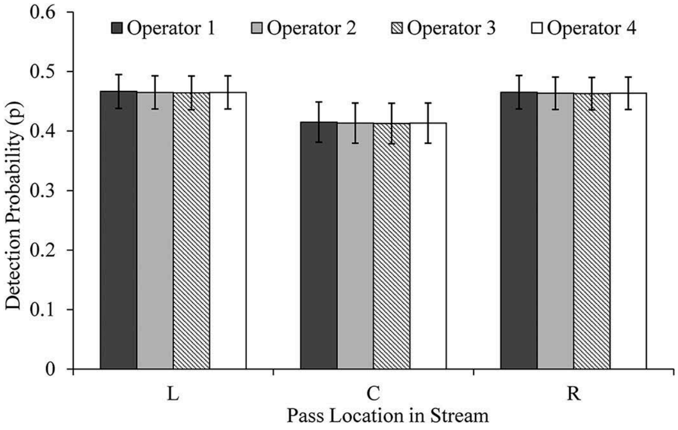

FIGURE 4. Model-averaged estimates of detection probability (±unconditional SE) for the effects of operator and pass location in the stream (L = left; C = center; R = right). Model-averaged estimates include effects of rock depth, stream width, rock distance from the center of the stream, and distance from the nearest rock, which, on average, affected both the estimate and SE bars.

Field Deployment

Detection distance and channel morphology.—The average pre-deployment detection distance was 1.15 m (SD = 0.18), which was slightly less than the maximum pool depth of 1.25 m observed during habitat surveys. Pre-deployment measurements of detection distance were similar to measurements for perpendicular tag orientations observed during system development and testing (Figure 3). The antenna produced a detection field with a maximum width of 4.6 m—assuming a perpendicular tag orientation and a vertical plane of detection—resulting in a maximum detection area of 5.3 m^2. Riffle cross-sections in the Tomahawk reach had an average wetted width of 8.8 m and depth of 0.30 m during field deployment, resulting in a cross-sectional area of 2.7 m^2. Pool cross-sections were narrower and deeper than riffles, with an average width of 7.3 m and depth of 0.58 m, resulting in a cross-sectional area of 4.2 m^2. Based on detection distance measurements, the detection field only covered 52% of the wetted area within an average riffle cross-section. However, coverage of wetted cross-sectional area improved to 63% for the average pool, indicating that the antenna was more efficient in narrower, deeper pool habitats than in wider, shallower riffles.

Detection probability and abundance estimation.—Seventy unique PIT tags were captured by the RFID–GPS system in the Tomahawk reach, 35 of which were captured on both passes. In the Garo reach, the system detected 67 individual tags, with 26 of those tags captured on both passes. Brown Trout were the predominant species detected, accounting for 86% of detected fish in the Tomahawk reach and 96% of detected fish in the Garo reach. More cutbow trout and Rainbow Trout were detected in the Tomahawk reach (10) than in the Garo reach (3). The influence of covariates on p was analyzed for the Tomahawk reach only, and all 18 models contained information regarding p and c (i.e., $w_i > 0$). Examining cumulative AIC_c weights of the covariates, length had the largest effect on p, whereas species had less of an effect (cumulative AIC_c weights = 0.43 and 0.33, respectively). Conversely, species had a larger effect on c than did length (cumulative AIC_c weights = 0.26 and 0.23, respectively). However, neither parameter had a significant effect on either p or c, as confidence intervals (CIs) for the beta values overlapped zero.

Abundance of PIT-tagged fish was estimated within the Tomahawk reach during base flow conditions and within the

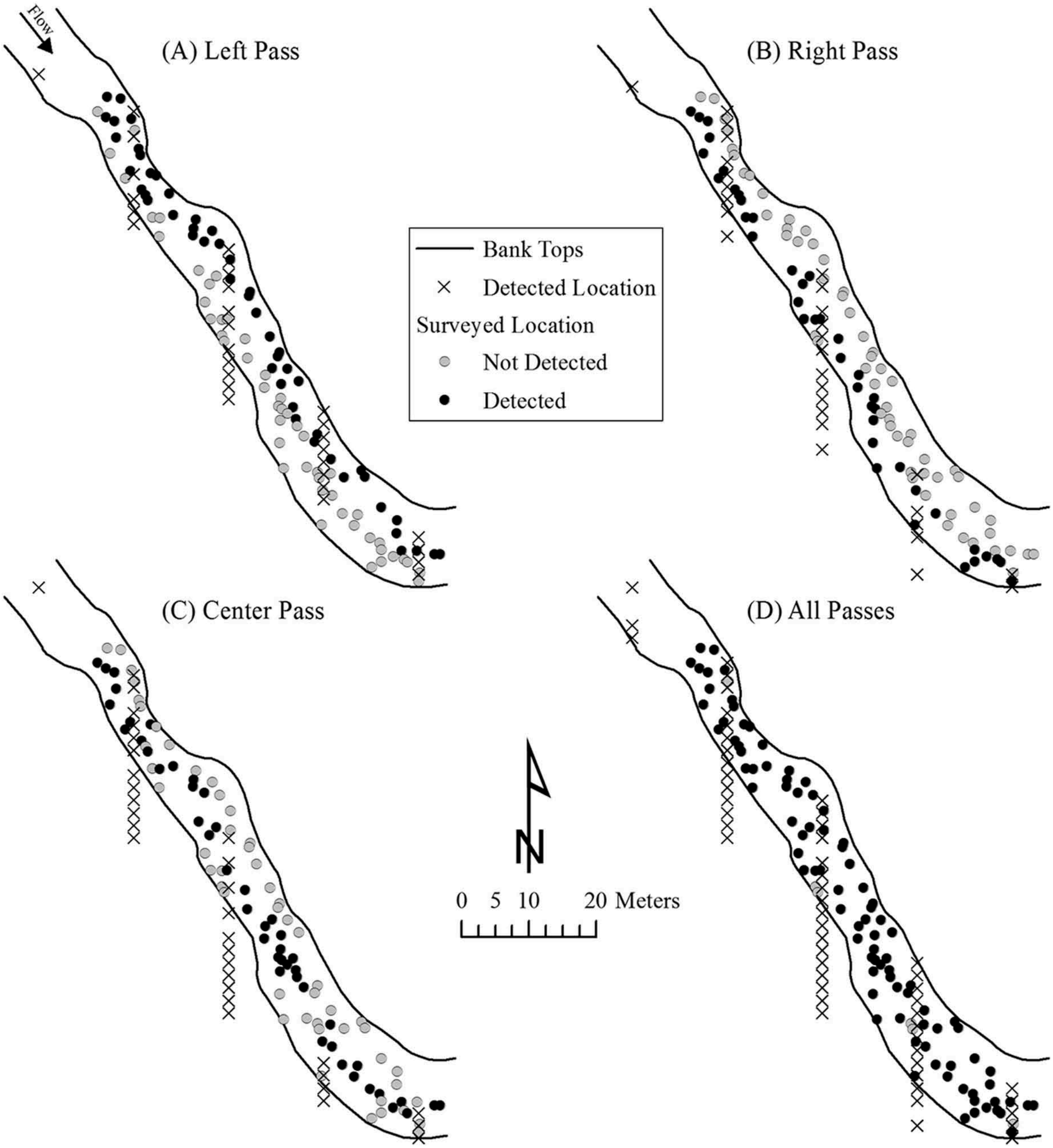

FIGURE 5. Detection results from radio frequency identification–GPS system testing at the stream inlet to Parvin Lake, Colorado, comparing surveyed and detected PIT-tag locations for operator 1 completing **(A)** the left pass, **(B)** the right pass, **(C)** the center pass, and **(D)** all passes combined.

Garo reach during higher flows (Table 4). On average, *p* for Brown Trout was higher in the Tomahawk reach during lower flows (0.85–1.1 m^3/s) than in the Garo reach during higher flows (4.5–4.8 m^3/s), as would be expected with a vertical read range limited by depth. Capture probabilities for cutbow trout and Rainbow Trout were similar between the two reaches even though low numbers of these species were present in the reaches (Table 4). In the Tomahawk reach, *p* was relatively high (≥0.74) despite the complexity of the habitat (i.e., narrow, braided channels). Although Brown Trout *p* was lower in the Garo reach, *p* was 0.57 or greater for Brown Trout, cutbow trout, and Rainbow Trout in that reach. Recapture probabilities were relatively high in both reaches, suggesting that fish remained in a detectable location after the first pass whether the passes were made during the same day (Tomahawk reach) or on consecutive days (Garo reach).

Because of the high capture and recapture probabilities, abundance estimation was not only possible but also relatively

TABLE 3. Summary statistics for GPS position error (m) in northing and easting coordinates as well as absolute error between detected and surveyed locations for PIT-tagged rocks in the stream inlet to Parvin Lake, Colorado.

Statistic	Northing error	Easting error	Absolute error
Maximum	6.8	11.4	12.4
Mean	2.0	3.7	4.5
Median	1.8	3.1	4.2
Minimum	0.0	0.1	0.3
SD	1.4	2.4	2.3

precise in both reaches despite differences in discharge during deployment. Abundance estimates indicated that PIT-tagged Brown Trout were more abundant in both reaches than cutbow trout or Rainbow Trout, and overall trout abundance was higher in the Garo reach than in the Tomahawk reach (Table 4). However, the Garo reach was over twice as long as the Tomahawk reach, indicating that the density of PIT-tagged trout was higher in the Tomahawk reach (33.0 PIT-tagged trout/km) than in the Garo reach (16.4 PIT-tagged trout/km). Unfortunately, no electrofishing surveys were conducted during fall 2014, when the RFID–GPS system was deployed in the Tomahawk reach. However, electrofishing surveys conducted during fall 2015 (i.e., after field deployment of the RFID–GPS system) indicated that significantly more fish were present in the Tomahawk reach than in the Garo reach (Figure 6).

Fish population estimates.—Population estimates from electrofishing surveys were only generated for Brown Trout, as the proportion of Rainbow Trout and cutbow trout captured on the first and second passes was insufficient to estimate those species' population densities with the Seber–Le Cren method (Seber and Le Cren 1967). Brown Trout densities declined significantly between fall 2012 and fall 2013 at both sites sampled (Figure 6), possibly due to mortality or emigration. Population density then increased significantly at two of the three sites sampled during fall 2015. These changes highlight temporal and spatial variability during the study period (Figure 6), when Brown Trout densities ranged from less than 900 fish/km to over 3,800 fish/km. Although the 95% CIs for the highest density estimate were very large (1,820–5,930 fish/km; Figure 6), all other electrofishing surveys resulted in relatively precise population estimates.

The total number of Brown Trout present within each reach was calculated from population estimates and reach lengths. Population estimates were averaged by season for the three sites within the Garo reach, but only one site was used to represent Brown Trout density in the Tomahawk reach (Figure 2). Reach-average trout densities were then multiplied by the reach length to estimate the total number of Brown Trout for each sampling season. The Garo reach was estimated to have 7,520 Brown Trout (95% CI = 7,170–8,010) present during fall 2013 compared to 9,910 Brown Trout (95% CI = 9,590–10,240) during fall 2015. For the Tomahawk reach, the total number of Brown Trout was estimated at 1,900 (95% CI = 1,810–2,000) during fall 2013 and 8,870 (95% CI = 8,618–9,120) during fall 2015. As the RFID–GPS system only detected 67 unique fish in the Garo reach and 70 unique fish in the Tomahawk reach, population estimates indicated that the proportion of the trout population detected with the RFID–GPS system was typically less than 1%.

Habitat utilization.—Habitat utilization was evaluated for all PIT-tagged fish that were detected with the RFID–GPS system during two passes through the Tomahawk reach. Two passes through the reach resulted in 105 total PIT tag detections, with 57 (81%) tags detected on the first pass, 48 (69%) tags detected on the second pass, and 35 (50%) tags detected on both passes. Detected positions were spatially associated with surveyed habitat units in ArcGIS. The difference in spatial extent between the four habitat types that were initially surveyed (i.e., riffle, run, pool, and glide) and the two habitat types (i.e., riffle and pool) used to analyze habitat utilization is illustrated in Figure 7. When the intersect method was used to assign habitat types, over half (52%) of PIT tags were assigned to pools and 9% were assigned to riffles, while 39% of the tags had detected positions within the NWA (Table 5). Similar results were observed when the 4.5-m buffer was placed around each detected position to account for GPS error (Figure 7). The initial buffer analysis placed tags in the habitat class or NWA that had the highest proportion of area within the buffer. For this buffer analysis, 50% of the tags were associated with pools, 9% were

TABLE 4. Model-averaged capture probabilities (p), recapture probabilities (c), abundance estimates (N), and associated unconditional SEs for Brown Trout, cutbow trout, and Rainbow Trout detected with the radio frequency identification–GPS system in the Tomahawk reach (fall 2014; 0.85–1.1 m^3/s) and Garo reach (spring 2015; 4.5–4.8 m^3/s) of the Middle Fork South Platte River, Colorado.

	Tomahawk reach			Garo reach		
Species	p	c	N	p	c	N
Brown Trout	0.74 ± 0.09	0.62 ± 0.07	65.0 ± 4.2	0.57 ± 0.09	0.54 ± 0.07	78.8 ± 8.2
Cutbow trout	0.74 ± 0.13	0.67 ± 0.12	9.8 ± 1.2	0.67 ± 0.24	0.58 ± 0.23	2.3 ± 0.7
Rainbow Trout	0.83 ± 0.14	0.79 ± 0.19	1.1 ± 0.3	0.78 ± 0.22	0.74 ± 0.23	1.1 ± 0.4

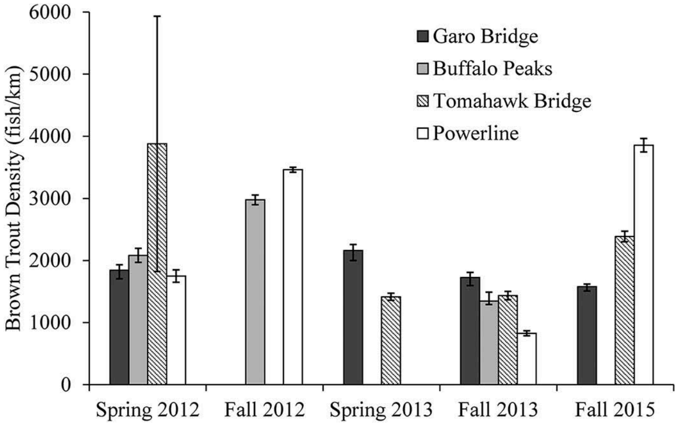

FIGURE 6. Brown Trout population estimates (±95% confidence interval) from electrofishing surveys at three monitoring sites within the Garo reach (Garo Bridge, Buffalo Peaks, and Tomahawk Bridge) and one site within the Tomahawk reach (Powerline) of the Middle Fork South Platte River.

associated with riffles, and 42% were associated with the NWA (Table 5).

Because PIT-tagged fish should not be associated with areas outside of the wetted channel, we attempted to assign all tags detected within the NWA to a pool or riffle by using the closest method in ArcGIS and excluding the NWA from the buffer analysis. The closest method resulted in 80% of the tags being assigned to pools and 20% of the tags being assigned to riffles (Table 5). In the buffer analysis with NWA excluded, 76% of the tags were assigned to pools, and 24% of the tags were assigned to riffles. To place these results in context, 64% and 36% of the surveyed habitat area were classified as pool and riffle, respectively. Despite the GPS error associated with detected position, it appeared that more tags were detected in pools when NWA was excluded (76–80%) relative to the percentage of area classified as pools (64%; Table 5).

The closest method was selected to evaluate habitat utilization in relation to species and fish length because it did not associate detected locations with NWA and was relatively simple to apply compared to the buffer analysis. Although it is logical to assume that the actual position of the fish would occur in the closest habitat unit to the detected position, this may not always be true, which causes some uncertainty when evaluating habitat utilization. To evaluate habitat utilization by fish size and species, frequency distributions for fish TL were compared to habitat type by species (Figure 8). Because only one Rainbow Trout was detected in the Tomahawk reach, Rainbow Trout and cutbow trout were combined into a single group for evaluation of habitat utilization. The average TL of Brown Trout detected in pools was 27.9 cm (SD = 8.6), while the average length for Brown Trout detected in riffles was 36.3 cm (SD = 10.7). All cutbow trout and Rainbow Trout were detected in pools and were typically smaller than Brown Trout, with an average length of 22.4 cm (SD = 3.8). Length frequency distributions also indicated that smaller Brown Trout were detected more frequently in pools than in riffles (Figure 8).

Multiple passes through the same reach did not appear to affect habitat utilization or initiate substantial fish movement between passes. For the 35 fish that were detected on both passes in the Tomahawk reach, the maximum distance between detected positions on the first and second passes was 14.6 m. Ten of the PIT tags detected on both passes had the same GPS coordinates for each pass. Detected positions moved upstream for five of the tags captured on both passes and moved downstream for six of the PIT tags detected on both passes. The average distance between detected positions for tags detected on both passes was 4.7 m (SD = 5.7). For the 25 PIT tags that changed position between passes, 7 of the tags changed easting coordinates, while 18 tags changed northing coordinates. The average change in easting coordinates between passes was 14.5 m, whereas the average change in northing coordinates was 3.5 m.

DISCUSSION

Although our mobile RFID system was deployed from a raft, the system configuration is flexible and could be deployed from a backpack or variety of watercraft to cover areas that are difficult to access by raft, such as logjams or point bars above the water line. The system can accommodate a range of aquatic sensors via the CR1000 datalogger, such as water temperature, dissolved oxygen, turbidity, or photosynthetically active radiation. Components of the system could be incorporated into stationary antenna systems to aid in evaluation and inform operation of fish passage structures. Restoring connectivity at instream barriers would allow fish to migrate in response to unsuitable habitat conditions (e.g., increasing water temperature); preserve behavioral traits inherent to their life histories; and improve resilience to land use, water development, and climate change. An enhanced understanding of the driving factors behind the timing of fish migration (e.g., season, flow, water temperature, and darkness) could provide valuable information for the operation of fish passage structures and could benefit the conservation and management of fish populations.

The area of the detection field generated by the antenna was greater than the average area of a riffle cross-section. However, dimensions of the detection field were deeper and narrower than the typical riffle cross-section, leaving substantial portions of this habitat type outside the field of detection. The RFID–GPS antenna only covered 52% of the cross-sectional area for a typical riffle within the study reach, but detection efficiency increased to 63% in narrower, deeper pools. As pools comprised 64% of the habitat area in the Tomahawk reach, the antenna was designed to maximize the depth at which a PIT tag could be detected. The reduced efficiency in riffle habitat may have affected the proportion of PIT tags detected in different habitat types and may have skewed the habitat utilization results toward pools. Another

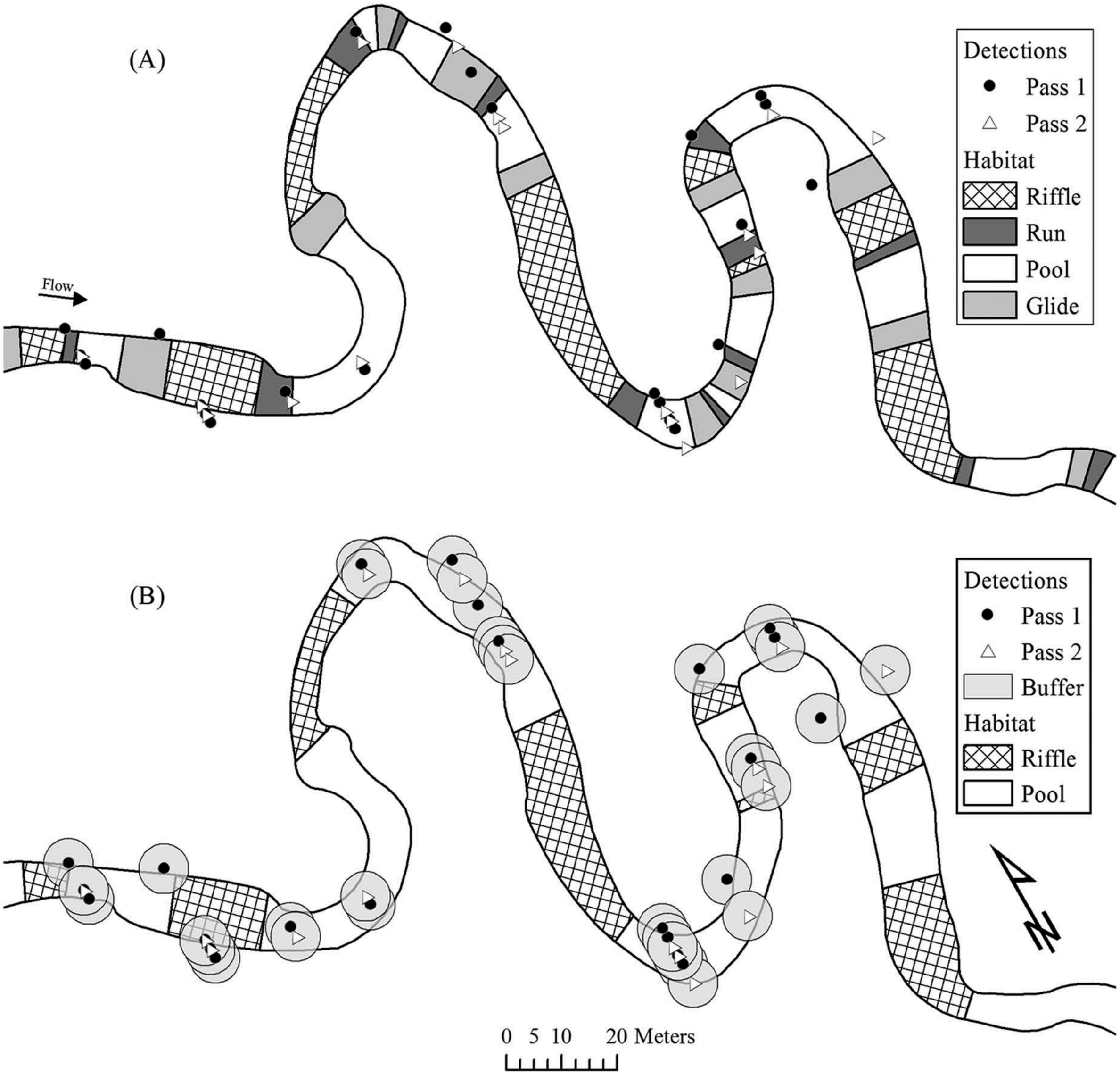

FIGURE 7. Example of detection results from field deployment of the radio frequency identification–GPS system in the Tomahawk reach of the Middle Fork South Platte River, showing **(A)** the detected positions within all four habitat types (riffle, run, pool, and glide) and **(B)** buffered detected positions within two simplified habitat types (riffle and pool).

drawback of optimizing detection distance for maximum depth is that ghost tags—tags buried in the sediment because of tag loss, predation, or natural mortality (O'Donnell et al. 2010)—may be detected and misidentified as tagged fish. Conversely, the ability to detect expelled tags buried in the sediment can provide valuable information regarding the fate of individual fish or the location of spawning redds. Larger detection fields could also result in tag collision (Axel et al. 2005; O'Donnell et al. 2010), where no tags are detected due to the presence of multiple tags within the detection field. Antenna configuration could be varied to optimize detection distances for specific streams or conditions. For example, a wider antenna with less vertical detection distance could be deployed during base flow periods, and an antenna optimized for vertical detection distance could be used to detect tagged fish under snow and ice.

Detection probability increased with multiple passes due to increased coverage of channel area. System testing demonstrated that p was negatively affected by stream width and depth. Distance from the center of the stream channel (DFC) also had an adverse effect on p. Detection probability will therefore decrease as stream channels increase in size. However, the antenna dimensions, number of passes, and location of passes could be selected to parsimoniously optimize p for specific study sites. Studies using mobile RFID antennas should be designed to maximize p by selecting the appropriate number and location of passes to cover as much channel area as

TABLE 5. Habitat utilization results, showing the percentage of trout PIT tags detected in pools, riffles, and nonwetted areas (NWA) by using different spatial association methods (intersect, closest, and buffer; see Methods). The percentage riffle and percentage pool based on habitat surveys are also presented.

Method	Riffle	Pool	NWA
Intersect	8.6	52.4	39.0
Buffer (including NWA)	8.6	49.5	41.9
Closest	20.0	80.0	0.0
Buffer (excluding NWA)	23.8	76.2	0.0
Habitat surveys	35.6	64.4	0.0

possible. If an estimate of *p* or PIT-tagged fish abundance is desired, a minimum of two passes with at least one fish detected on both passes is required to obtain these estimates (White et al. 1982). Multiple RFID–GPS systems could be deployed at the same time to cover more channel area and reduce the number of survey events needed to achieve a target number of passes. If multiple RFID systems are used concurrently, it might be necessary to synchronize them to prevent interference between systems; alternatively, a minimum distance between systems should be maintained to prevent proximity detection errors (Aymes and Rives 2009). Operator did not affect detection probability, suggesting that the design of this system and the ease of deployment could overcome limitations related to a lack of operator experience, which are encountered with other designs (e.g., O'Donnell et al. 2010).

Similar channel dimensions for the stream inlet to Parvin Lake (average width = 8.4 m; average depth = 0.34 m) and the Tomahawk reach (average width = 8.0 m; average depth = 0.55 m) indicate that detection probabilities observed during system development should be similar to those observed during field deployment. However, the PIT-tagged rocks used during system development were stationary, whereas PIT-tagged fish were free to move in avoidance of the antenna and raft, which could further decrease *p*. Although researchers were typically walking on the streambanks behind the raft and antenna, we did observe fright responses by fish that were startled by some component of the deployed system. The direction of response varied, as we observed some fish moving away from the system in the downstream direction, potentially evading detection, whereas some fish swam directly under the antenna and raft in the upstream direction, thus facilitating detection. Ellis et al. (2013) suggested that responses might be exaggerated when conditions are such that the antenna casts shadows (e.g., sunny days). We also observed a number of fish, typically in pools, that were not detected by the system, most likely because they had not been tagged. Detection probability is also dependent on the orientation of the PIT tag relative the antenna. Trout typically face upstream when feeding to search for drifting prey, which would result in an optimal, perpendicular orientation to the vertical plane of the antenna and maximum *p* (Nunnallee et al. 1998; Morhardt et al. 2000; Zydlewski et al. 2006; Compton et al. 2008; Aymes and Rives 2009). Although a trout is more likely to be encountered in a perpendicular orientation to the antenna, it is possible to encounter trout in any orientation between perpendicular and parallel. Orientations that deviate from perpendicular will decrease *p* and may influence tag collision, with PIT tags in perpendicular orientations being detected more frequently than those in parallel orientations.

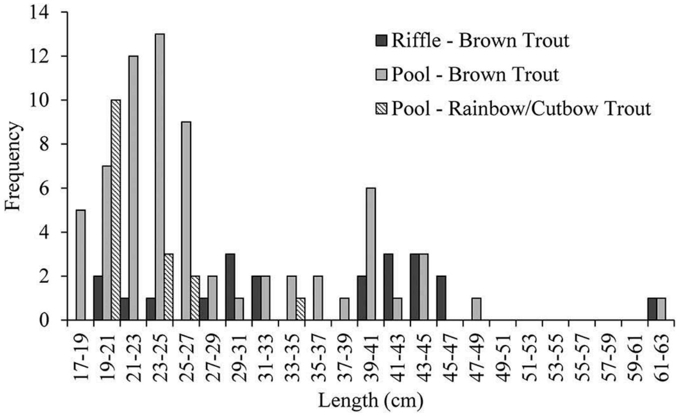

FIGURE 8. Length frequency distribution, showing the proportions of PIT-tagged Brown Trout and Rainbow Trout/cutbow trout detected in pools and riffles. Note that no PIT tags associated with cutbow trout or Rainbow Trout were detected in riffle habitat.

Multiple passes with the RFID–GPS system were used to estimate abundance of PIT-tagged fish in the Garo and Tomahawk reaches by using mark–recapture procedures. Results suggest that the array's performance was relatively similar between the two reaches despite differences in habitat complexity and streamflow. Abundance estimates were not only obtainable but also accurate, suggesting that the RFID–GPS system could be used to determine differences in habitat use at multiple discharges and among seasons. The relative agreement between population estimates of PIT-tagged fish detected with the RFID–GPS system and electrofishing surveys suggests that marked fish detection with the RFID–GPS system can provide a good representation of fish distribution within a stream. Results from electrofishing surveys indicated that trout densities declined between fall 2012 and fall 2013, possibly due to mortality after spawning or due to emigration of fish to the downstream reservoir. After the fall spawning migration, deceased or severely stressed Brown Trout are relatively common along the banks of the Middle Fork South Platte River. These fish exhibit typical traits of increased stress postspawning, including infection with *Saprolegnia* fungus. If the population exhibits high mortality rates after spawning or if a high proportion of PIT tags are expelled during spawning, the likelihood of encountering ghost tags with the mobile array would increase, particularly for longer-duration studies (>1 year). If a significant number of detected tags are no longer inside fish, population estimates for PIT-tagged fish derived from mark–recapture will be overestimated. Based on published mortality rates (e.g., Lobón-Cerviá et al. 2012) and PIT tag retention rates (e.g., Dieterman and Hoxmeier 2009), it is possible that a significant number of PIT-tagged Brown Trout died or expelled their tags during spawning between their initial release in 2013–2014 and their detection with the RFID–GPS system in 2014–2015. The system cannot distinguish between PIT tags that are inside fish and those that no longer are; thus, failure to account for these ghost tags will bias results for movement, survival, and population estimates. Given that mobile RFID systems provide increased spatial coverage for a study reach and GPS coordinates can be used to determine whether detected PIT tags have moved between survey events, the RFID–GPS system presented in this study may provide a novel means for detecting and identifying ghost tags.

The accuracy of GPS sensors depends on a variety of factors, including topographic complexity, the number of satellites available for triangulation, vegetative cover, movement, and receiver quality. The GPS sensor failed to achieve the highest specified position accuracies (<3 m) under DGPS with WAAS correction and operated under SPS or DGPS with USCG/RTCM correction. This limitation suggests that the RFID–GPS system may be more useful for reach-scale studies (>1,000 m) rather than fine-scale habitat evaluations (<10 m). The average area of habitat types in the study reach compared to the average GPS error suggests that detected PIT tags should not be associated with smaller habitat units (<60 m^2), such as runs and glides. However, the average area of habitat types will vary with stream size and type. As such, the relative importance of GPS error for accurate habitat association will generally decrease as channel size increases. In some cases, the observed change in detected position between passes may have been due to GPS error rather than actual fish movement. Because the error in the easting was greater than the error in the northing, higher error and uncertainty should be expected for detected positions in channels flowing along lines of latitude compared to longitude. Accuracy of GPS could be increased by improving the quality of the GPS sensor. However, improvement in GPS accuracy may be limited for mobile RFID systems. Survey-grade GPS requires the receiver to be stationary for 2–3 s before achieving an RTK solution, which is not feasible for mobile systems that are floating downstream.

Salmonid populations have demonstrated dominance hierarchies related to fish size, wherein larger fish select and defend the most profitable habitat while smaller fish associate with less-desirable habitat (Fausch 1984, 2014). Profitable feeding positions are locations where the energy available from drifting prey is greater than the energetic cost of swimming to maintain the position (Fausch 1984). Dominance hierarchy theory suggests that larger fish would be detected in the more desirable, or profitable, habitat. Frequency distributions indicated that smaller fish were relatively more abundant in pools than in riffles (Figure 8). While this observation could indicate that pools were less-desirable habitat compared to riffles, it is also possible that larger fish selected optimal feeding positions in both pool and riffle habitats. Larger Brown Trout (>400 mm TL) were detected with similar frequency in both riffles and pools (Figure 8), suggesting that profitable feeding positions were available in both habitat types. Results also indicated that PIT tags were not randomly detected in pools or riffles because a higher percentage of tags were found in pools compared to the relative area of the pools within the study reach (Table 5). However, as pools accounted for 64% of the total wetted area, the higher proportion of small fish detected in pools could merely be related to the amount of available pool habitat. Retention studies have documented PIT tags in redds and lower retention rates for larger fish (Bateman et al. 2009; Meyer et al. 2011), which could indicate that some of the larger trout detected in riffles were actually spawned-out PIT tags. Detected PIT tag locations should be investigated further to identify ghost tags and evaluate the proportion of detected tags that are no longer inside the fish.

Future research should focus on further development of RFID technology for fisheries management applications. Combining stationary and mobile antenna systems has the potential to elucidate spatial and temporal patterns of fish migration, habitat utilization, and population growth. Tracking individuals throughout their life history would improve our understanding of habitat utilization and prioritize areas for conservation and restoration. This technology could be applied to evaluate the effectiveness of stream restoration projects, including utilization of specific restoration treatments by different fishes. Additional research could reveal the appropriate residency and migration ranges for different species and life stages, providing valuable information for fisheries management and restoration. Due to the ability to cover long river reaches (>5 km) and flexibility in both antenna and sensor configurations, the RFID–GPS system presented here should be useful for a variety of studies related to habitat utilization, fish migration, and population trends.

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