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ARTICLE

Comparison of Methods to Verify Upstream Passage by Trout at Remediated Culverts in Four Rocky Mountain Streams

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Abstract

The removal or remediation of thousands of culverts at road–stream crossings to restore connectivity is a major conservation investment in aquatic systems in North America. Effectiveness monitoring is necessary to confirm that passage has been restored for the species of interest and to justify project costs. We compared the performance of (1) recapture of batch-marked fish by backpack electrofishing, (2) recapture of PIT-tagged fish by electrofishing, (3) detection of PIT-tagged fish by a mobile antenna, and (4) detection of PIT-tagged fish at stationary antennas for verifying upstream passage of native Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi* (WCT) and nonnative Brook Trout *Salvelinus fontinalis* at remediated culverts in four Rocky Mountain streams. Generally, detection probability at stationary antennas was higher (range = 0.74–0.97) than capture by electrofishing (range = 0.24–0.77) or detection by the mobile antenna (range = 0.47–0.66). All four methods confirmed upstream passage by trout that were originally marked or tagged below the culvert, although overall recapture rates were low (≤20%). During summer and early fall, the continuously sampling stationary antennas detected more than twice as many PIT-tagged trout moving upstream through the culvert than either the mobile antenna or the electrofisher. Upstream movement by PIT-tagged trout was first detected by stationary antennas 1–10 d after tagging. For all methods, upstream passage was most frequently detected for fish that were marked or tagged in the 100-m reach adjacent to the culvert. The relative cost of the four mark–recapture methods to evaluate upstream passage of age-1 and older WCT was compared with the cost of "sib-split," a genetic method based on pedigree analysis, which was used previously to evaluate passage of age-0 WCT in the study streams. Stationary antennas, the mobile antenna, and sib-split were comparatively expensive for a single-year study because of PIT equipment and laboratory costs, respectively, and electrofishing was less than half the cost.

Habitat fragmentation is a well-recognized threat to aquatic organisms (Wilcove et al. 1998; Olden et al. 2010), and fish in stream systems are at particular risk given the dendritic structure of these networks (Fagan 2002). Passage barriers at road–stream crossings are a major cause of this fragmentation in stream networks (Chelgren and Dunham 2015). In forested watersheds of the USA, there are tens of thousands of structures—in particular, culverts—at road–stream crossings that may restrict the movement of amphibians, invertebrates, and fish (GAO 2001; Hendrickson et al. 2008; Januchowski-Hartley et al. 2013). Effects of culvert barriers on fish populations are now well documented. Culvert barriers may contribute to the extirpation of populations above the barrier (Peterson et al. 2014), limit species distribution (Nislow et al. 2011; MacPherson et al. 2012), restrict access to spawning and rearing habitat (Sheer and Steel 2006), reduce genetic diversity (Wofford et al. 2005; Whiteley et al. 2013; Neville

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and Peterson 2014; Torterotot et al. 2014), and lead to lower abundance in the above-barrier segment of the population (Nislow et al. 2011).

Given the prevalence of culverts and other passage barriers and their (generally) negative effects on aquatic species, it is not surprising that the removal of passage barriers in streams represents a major conservation investment in aquatic systems of the USA (GAO 2001; Bernhardt et al. 2005) and Europe (Kemp and O'Hanley 2010 and references therein). The average cost of individual fish passage projects on small streams may be modest, ranging from tens to a few hundred thousands of U.S. dollars (Bernhardt et al. 2005; Gillespie et al. 2014; Fitzpatrick and Neeson 2018), but the cumulative costs of removing or replacing these structures can be tens to hundreds of millions of dollars across river basins (e.g., Tillamook–Nestucca River basin, Oregon; D. Shively, U.S. Fish and Wildlife Service [USFWS], and S. Pilson, U.S. Forest Service [USFS], unpublished data) or with the purview of a land or natural resource management agency (GAO 2001; WSDOT 2017).

After culverts identified as fish passage problems have been remediated, the question of biological effectiveness remains. In general, postproject and effectiveness monitoring for river restoration projects (including fish passage) is infrequent (e.g., ~10% of projects include monitoring; Bernhardt et al. 2005). The (re)colonization of unoccupied habitat after barrier removal can occur rapidly for highly migratory species like those in the family Salmonidae, making effectiveness monitoring relatively simple (e.g., Roni et al. 2002; Shrimpton et al. 2008; Pess et al. 2014). Where the target species are already present above the barrier, demonstrating a biological response to barrier removal can be more difficult and requires monitoring for multiple generations (Neville and Peterson 2014; Neville et al. 2016). Though population-level responses, such as increased abundance and distribution and diverse life history expression, are generally recognized as the objective of the barrier removal (Dunham et al. 2011; Hoffman et al. 2012; Chelgren and Dunham 2015), simply verifying that individual fish and other aquatic organisms can pass remediated culverts is still an important short-term monitoring objective and interim indicator of a successful conservation action. Confirming passage by monitoring individual movement is especially relevant given that culvert remediation can fail to achieve the fundamental objective of restoring connectivity for aquatic organisms, even when such projects are permitted under design standards to ensure passage (e.g., Price et al. 2010). Monitoring also assists with the continuing need to validate, calibrate, and refine existing models or widely used software packages (e.g., FishXing; https://www.fs.fed.us/biology/nsaec/fishxing/) that predict passage success.

Empirical evaluation of fish passage at culverts has often utilized mark–recapture with batch marks (Warren and Pardew 1998; Coffman 2005; Burford et al. 2009; Norman et al. 2009), short-range telemetry with PIT tags (Solcz 2007; Mahlum et al. 2014; Goerig et al. 2015), or both in combination (e.g., Roghair et al. 2014). These methods are effective but may be expensive in terms of labor (field crews) or specialized equipment (PIT tags and readers), and they can be plagued by small numbers of recaptures (Dunham et al. 2011; Hoffman et al. 2012). Genetic methods for verifying individual-level movement of aquatic organisms can be used to verify fish passage at culverts (Hudy et al. 2010; Neville and Peterson 2014; Whiteley et al. 2014), but these approaches are also expensive (e.g., genetic marker development and laboratory costs) and may require a subject matter expert (geneticist) to analyze and interpret the data (Hoffman et al. 2012; Heredia et al. 2016). Biologists who are tasked with verifying individual-level movement through remediated culverts (i.e., first-order biological effectiveness monitoring) would benefit from knowing which monitoring method would be most efficient and cost effective for their purposes.

To that end, we compared the relative performance and cost of four different approaches to verifying upstream fish passage through recently remediated culverts in four streams in Montana and Idaho during summer and early fall 2011. Target species were native Westslope Cutthroat Trout *Oncorhynchus clarkii lewisi* (WCT) and nonnative Brook Trout *Salvelinus fontinalis* (BKT)—hereafter collectively referred to as “trout”—present above and below the culverts. We used a combination of PIT tags and reach-specific batch marks to reference initial capture location and then assessed movement through culverts by using physical recapture of batch-marked or PIT-tagged trout via electrofishing (methods 1 and 2), detection at stationary PIT tag antenna arrays within and adjacent to culverts (method 3), and detection using a mobile PIT tag antenna (method 4). We summarize upstream movement at the four sites and then characterize the performance of the four methods in terms of various detection metrics (e.g., individuals detected, frequency of detection, and time to first detection), relative cost, strength of inference, and accessibility of results to field biologists and practitioners. We also contrast these findings and costs with those of a related study that used a novel genetic method to assess the movement of young-of-the-year WCT through culverts in these same streams (Neville and Peterson 2014).

METHODS

Study Sites

Study sites were four high-elevation headwater streams in U.S. national forests along the Idaho–Montana border, where culverts had been replaced to improve upstream passage of fish and other aquatic organisms (Figure 1; Table 1). Prior to remediation, culverts at the study locations had been rated as partial or total barriers to upstream fish passage based on a USFS assessment protocol (Clarkin et al. 2005; Hendrickson et al. 2008). Undersized culverts at the four study sites were eventually replaced with larger, squashed-pipe- or pipe-arch-style culverts filled with natural substrate (i.e., stream simulation culverts). Two of the sites were unnamed tributary streams to East Fork Lolo Creek in the Lolo National Forest, Montana; the sites were designated Stream523 and Stream521 in reference to the USFS culvert tag numbers that existed prior to culvert replacement. The two sites in the Clearwater National Forest, Idaho, were both tributaries to the Crooked Fork of the Lochsa River: an unnamed tributary (CrookedFkTrib) and Haskell Creek.

Culvert locations are nonrandom (e.g., Chelgren and Dunham 2015), and the four sites were selected based on both objective and subjective criteria. Two of the sites (Stream521 and Stream523) were part of an ongoing study to measure population-level effects of culvert remediation (Neville and Peterson 2014; D.P.P. and H.M.N., unpublished data). Additionally, we canvassed USFS biologists within the western portion of the Northern Region (Region 1) for a list streams with recently replaced culverts and filtered that information by those locations having similar fish communities and physical characteristics. With that information, we conducted site visits at eight culvert replacement projects in three different national forests during June 2011 to select the final two streams (CrookedFkTrib and Haskell Creek) included in the study.

Study streams were small (1.5–2.3-m wetted width), cold (8.0–10.4°C in August), first-order tributary streams with low to moderate channel slopes (4.3–15%) at similar elevations (1,377–1,623 m) and drained small catchments upstream from the culvert locations (250–333 ha; Table 1). Westslope Cutthroat Trout were present at all sites, whereas BKT were present and abundant in Stream521 and Stream523. Bull Trout *Salvelinus confluentus* were rare in Haskell Creek but common in CrookedFkTrib.

Approach to Verifying Upstream Movement through Remediated Culverts

Study design.— The basic experimental design was to mark and tag trout in proximity to culverts and then intensively sample to recapture or detect fish that moved upstream through the culverts. We focused on upstream passage because culvert remediation for fish passage usually focuses on removing constraints for fish to enter (e.g., jump height at the pool outlet) and move through (e.g.,

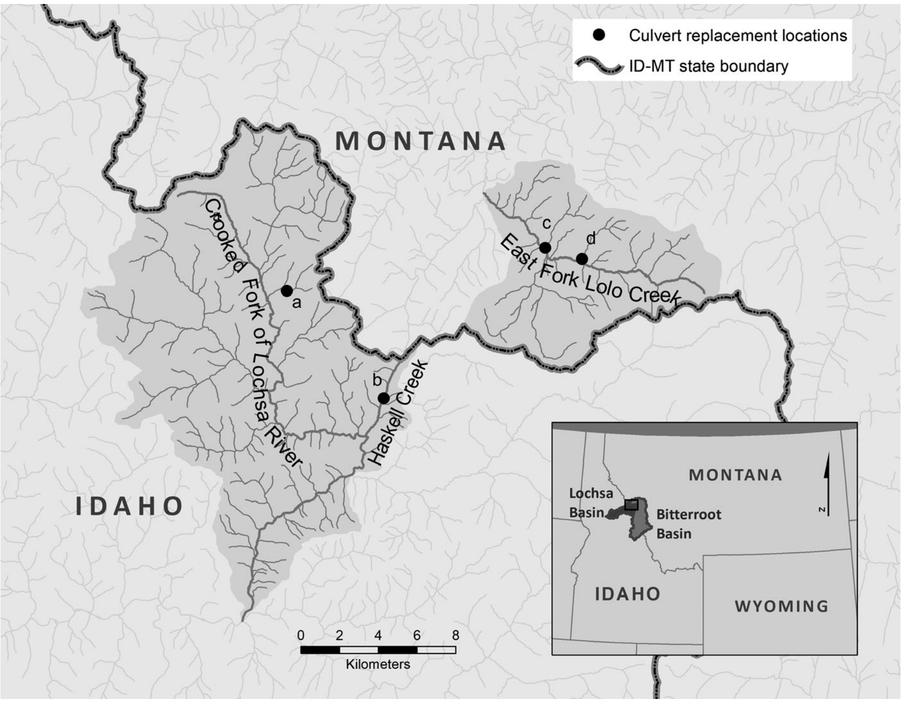

FIGURE 1. Locations of four study streams in Idaho and Montana that had remediated culverts. Streams included two tributaries to the Crooked Fork of the Lochsa River, Idaho (an unnamed tributary, CrookedFkTrib [a]; and Haskell Creek [b]), and two unnamed tributaries of East Fork Lolo Creek, Montana (Stream521 [c] and Stream523 [d]).

TABLE 1. Physical habitat, culvert characteristics, and fish communities at the four study streams (two tributaries to the Crooked Fork of the Lochsa River, Idaho [Haskell Creek and an unnamed tributary, CrookedFkTrib]; and two unnamed tributaries of East Fork Lolo Creek, Montana [Stream521 and Stream523]) during summer 2011.

	Stream			
Attribute	CrookedFkTrib	Haskell Creek	Stream521	Stream523
Elevation at culvert (m)	1,623	1,393	1,377	1,436
Wetted width (m)[a]	2.3	2.2	1.8	1.5
Slope of upstream segment (%)[b]	15.0	4.3	6.9	7.5
Mean August water temperature (°C)[c]	8.0	8.8	10.2	10.4
Catchment area above culvert (ha)	250	333	310	265
Culvert dimensions (m)[d]	3.3 × 2.1 × 18.3	3.8 × 2.4 × 17.5	2.6 × 1.8 × 12.2	2.6 × 1.8 × 10.4
Year of culvert replacement	2004	2010	2008	2008
Fish community[e]	WCT, BLT	WCT	WCT, BKT	WCT, BKT

[a] Wetted width is averaged over the study area, 300 m above and 300 m below the culvert, except in Stream521, which had only an 80-m main channel and a 100-m side channel below the culvert and before its tributary junction with East Fork Lolo Creek.

[b] Slope calculations are based on a digital elevation model for the National Hydrography Database Plus segment upstream from the culvert.

[c] Mean temperatures are from 48–60 daily readings using a TidBit thermograph (Onset Computer Corporation). Stream temperature data for Stream523 are from 2012 because the thermograph battery failed in May 2011 and was not replaced until October 2011.

[d] Dimensions of the replacement culvert designed for aquatic organism passage are presented as span × rise × length.

[e] WCT = Westslope Cutthroat Trout; BKT = Brook Trout; and BLT = Bull Trout. An individual BLT was captured twice in Haskell Creek during 2011.

velocity barrier) culverts in the upstream direction. Initial fish marking and tagging were concentrated in the 300-m stream segment downstream from the culvert, which was delineated into three 100-m reaches. Recapture or detection events were focused on the 300-m segment upstream from the culvert (also subdivided into three 100-m reaches), and sampling was either periodic (electrofishing and mobile antenna) or continuous (stationary antennas). The individual methods are described in greater detail below.

The study was designed to be executed within a single field season to approximate the time and logistical constraints facing a biologist attempting to validate fish passage at multiple sites within a specific area of concern (e.g., forest district, management zone, project area, etc.). Within the intermountain western USA and northern Rocky Mountains, a typical field season for fishery biologists working in higher-elevation forested watersheds starts in June, when streamflows begin to decline after snowmelt runoff, and ends in October, when stream temperatures drop below 4°C and the first significant winter storm is likely to occur.

Fish marking and tagging.— Multi-pass closed-site electrofishing was used to capture trout and provide a sample of marked and tagged fish from which to measure movement through remediated culverts. The initial marking and tagging were conducted in early July and early August 2011, shortly after sites became accessible and snowmelt runoff had subsided and well after WCT had spawned (typically late April to early June at these elevations). In short, 100-m reaches were enclosed with block nets (5-mm nylon mesh) and sampled in an upstream direction by a three- or four-person crew using a backpack electrofisher (operated at 30–40-Hz, 250–350-V pulsed DC). The duration of sampling was recorded. Captured fish were anesthetized (tricaine methanesulfonate [MS-222]), measured (TL; nearest mm), and weighed (nearest 0.1 g). Trout larger than 40 mm TL were given a visual implant elastomer (VIE) batch mark (Northwest Marine Technology) in the dentary tissue that was specific to their original capture location. In addition to the VIE batch marks, WCT larger than 75 mm TL and BKT larger than 50 mm TL were also fitted with 12-mm half-duplex (HDX) PIT tags (Oregon RFID), which were implanted into the body cavity through a small incision in the ventral body surface. Thus, some fish only received VIE batch marks, whereas others received both VIE marks and PIT tags. Captured fish were allowed to recover from anesthesia and handling and were then released within the original 100-m capture reach.

Recapture of batch-marked and PIT-tagged trout by electrofishing.— To detect batch-marked and individually tagged fish that moved upstream through the culvert, we used single-pass, upstream-directed backpack electrofishing to sample the 300-m-long segment (i.e., three 100-m reaches) upstream from the culvert. The entire 300-m segment was enclosed by block nets. Recaptures began roughly 1.0–1.5 months after initial tagging and were repeated about every 2 weeks thereafter for a total of two to three recapture events in each stream between late August and October (see Supplement A available in the online version of this article).

Captured fish were inspected for the presence of VIE batch marks and were scanned for PIT tags by using hand-held PIT tag readers (Agrident Model APR350 or

Allflex Model RS200-3). Electrofisher settings, crew sizes, and fish handling methods were the same as those used for fish marking and tagging (see above). For the comparison of methods, we treated the tally of VIE batch marks and PIT tags as independent, even though trout above a certain size could bear both a VIE mark and a PIT tag. For evaluation of upstream movement, we pretended that batch-marked fish were not individually identifiable in batch mark tallies even if they also contained a PIT tag, because that would be the case if only batch marks had been used. We did, however, use the double-marking to inform whether VIE marks or PIT tags were being lost or not recorded.

Detection of PIT-tagged trout by the mobile antenna.— We used a mobile PIT antenna to repeatedly sample the 300-m segment upstream from the culvert to detect tagged fish that were originally marked downstream. Surveys began about 1.0–1.5 months after initial tagging and generally were repeated every 7–10 d thereafter, with a few exceptions, for a total of three to five recapture events in each stream between late August and October (Supplement A). The mobile antenna system consisted of an HDX transceiver powered by a lithium-ion battery and connected to an antenna housed within an oval loop of polyvinyl chloride tubing (see Supplement B for additional details). The mobile antenna system was analogous in form to a backpack electrofishing unit, with the transceiver held in a backpack worn by the operator who also held the antenna (similar in appearance to an electrofishing anode handle) and scanned the water in front for PIT tags (Hill et al. 2006). Mobile antenna inductance was 38 microhenries (μH), and the maximum perpendicular read distance for 12-mm HDX tags was 46–48 cm. A hand-held personal data assistant (Meazura Model MEZ1000) connected to the transceiver was intended to provide real-time information during surveys but proved to be unreliable. All detections were hand recorded during surveys, and detections stored in the transceiver's memory were subsequently downloaded to a laptop computer and cross-checked against the hand records.

During mobile antenna detection events, a two-person crew (consisting of an operator and data recorder) conducted closed-site surveys in a downstream direction within the 300-m segment above the culvert. The operator walked slowly downstream while moving the antenna so that its detection field covered the wetted channel, and the data recorder paralleled the operator from the streambank. An audio transducer (buzzer) indicated a PIT tag detection, and crew recorded the tag code, time, and location (sample reach and GPS coordinates) for each detection. Survey duration was recorded. Two passes were conducted during site visits, but for the analysis, we focused on detections from the first pass for consistency with single-pass electrofishing.

Detection of PIT-tagged trout at stationary antenna arrays on culverts.— To detect the movement of PIT-tagged trout through the culverts continuously, we installed PIT tag interrogation systems (stationary arrays) having at least two antennas at each culvert site. The stationary arrays in Stream521 and Stream523 had four antennas: two just inside the culvert, with one at either end (inside antennas); and one upstream and one downstream from the culvert, approximately 2–3 m from the culvert opening (outside antennas). The stationary arrays in CrookedFkTrib and Haskell Creek each had two inside antennas.

Each array consisted of rectangular, pass-through antennas with individual tuning capacitors and a multi-antenna HDX transceiver and data logger (Oregon RFID) powered by a pair of 12-V, deep-cycle marine batteries connected in parallel (see Supplement B for additional details). Antennas were constructed on-site and were 2.0–4.0 m long × 0.75 m high. Antenna inductance ranged from 46 to 78 μH, and individual antennas drew 1.8–2.8 A. With 12-mm HDX test tags, the maximum read distance perpendicular to the plane of the antenna was 10–20 cm.

Arrays were installed between late June and late July and operated continuously into October (Supplement A). Arrays were visited by a two-person crew every 3–7 d to change batteries (estimated to last for a maximum of 7 d for the two-antenna arrays), confirm antenna function, and download detection data from the transceiver by using a serial cable connection to a laptop computer running a terminal emulator. Crews recorded the time required to complete these activities.

Raw detections at stationary arrays were processed into movement events through a series of scripts implemented in R version 3.2.3 (R Core Team 2015). To avoid repeatedly counting detections in which a fish might have been near the edge of the antenna's magnetic field (i.e., a stuttering tag), multiple detections at the same antenna within 60 s were treated as a single detection. Detections occurring within 10 min of a crew visit (e.g., to inspect antennas, change batteries, and download data) were excluded to help ensure that movements by trout were volitional rather than a flight response. Direction of movement and passage through the culvert was judged by evaluating the sequence of consecutive detections at multiple antennas. We focused on movement based on detections at the two inside antennas, as this antenna configuration was common to all four study streams. The detections at the outside antennas in the two streams with the four-antenna stationary arrays were used to estimate antenna detection probabilities for the inside antennas (see below).

Capture and detection probabilities of backpack electrofishing, the mobile antenna, and stationary antennas.— The probability of detecting upstream movement with electrofishing and the mobile antenna depends on the capture or detection probability, assuming that marked and tagged fish are present at the sample site. For electrofishing, we estimated capture probability for the depletion sampling during fish marking/tagging electrofishing (see previous section) using the Huggins closed-captures model implemented in Program MARK version 8.1 (White and Burnham 1999). We subsequently assumed that these per-pass or first-pass capture probabilities applied to the single-pass electrofishing recapture surveys conducted above the culverts. Removal methods typically overestimate capture efficiencies compared to mark–recapture methods (e.g., Peterson et al. 2004b). We judged it better to accept this potential bias rather than to subject fish to additional stress by electrofishing and handling, as fish were already being subjected to repeated electrofishing during recapture sampling.

Detection efficiency of the mobile antenna was estimated by a series of eight capture–detection trials. During the final electrofishing recapture event in all four streams, we randomly selected two reaches for closed-site detection trials. Trout that were captured by electrofishing were released back into the selected 100-m reaches enclosed by a block net; on the following day, we performed two passes with the mobile antenna in the downstream direction to detect PIT-tagged trout. We assumed that PIT-tagged trout released into the block-netted reach did not escape and were available for detection. We fitted a series of closed-capture models to the detection data using Program MARK to evaluate whether detection probability depended on pass, survey position relative to the culvert (above versus below), and stream.

Detection probabilities at individual stationary antennas located inside the culvert were estimated using detection data from the two streams with four-antenna arrays. To do this, we filtered the detection data to identify cases in which PIT-tagged fish were detected at both of the outside antennas (indicating that fish moved through the culvert), and we tabulated whether they were also detected at the antennas located inside the culvert. The efficiency of the inside antennas was of interest because that antenna configuration was common to all four study sites. We then fitted a set of Cormack–Jolly–Seber open-population models in Program MARK to estimate these detection probabilities and to evaluate whether they varied by antenna, stream, and direction of fish movement.

Analyses to Verify Upstream Passage and Gauge Relative Performance of Methods

Summary of upstream trout movement.— We summarized upstream movement events by sampling approach, in terms of whether upstream movement through the remediated culvert was confirmed (for each combination of species × stream), the total number of confirmed detections of upstream movement and the frequency of such movement, and whether movement by individually tagged trout was missed by one or more sampling method. We also identified how much time or how many sampling events it took to confirm upstream passage by each method; we assumed that this would be of interest to biologists who want to confirm passage at one site and then move to additional sites and do the same. We used asymptotic 95% confidence intervals (CIs) to compare the proportion of individually tagged trout released downstream that moved upstream or were detected upstream for each sampling method within each stream.

Capture and detection probabilities.— We evaluated the capture probability and detection probability models by ranking them with model weights from Akaike's information criterion corrected for small sample size (AIC_c) and the relative likelihood of models containing particular factors (Burnham and Anderson 2002). We used a single model for estimation if it had at least 50% of the AIC_c weight. The different detection methods were analyzed independently, and contrasts generally were based on the comparison of 95% CIs.

Comparative cost of electrofishing, stationary antennas, the mobile antenna, and a novel genetic method.— We conducted a comparative cost analysis for the different approaches described herein. Although it focused on a different age-class and so was not *directly* comparable, for heuristic purposes and emphasis of its potential utility for assessing age-0 movement, we also included results from a related study (Neville and Peterson 2014) that we conducted concurrently with the present study. Our prior study (Neville and Peterson 2014) used a novel genetic method, termed “sib-split” (Whiteley et al. 2014), to assess the movement of young-of-the-year trout across culverts. To implement the sib-split method, we (Neville and Peterson 2014) sampled age-0 WCT on either side of each culvert in three of the streams used in the present study (Haskell Creek, Stream521, and Stream523; we were unable to evaluate CrookedFkTrib due to reproduction failure), conducted a pedigree analysis to determine family groups, and inferred movement across the culvert based on the presence of full siblings on either side of it (hence the term sib-split; Whiteley et al. 2014). “Majority rule” was used to inform inferences about the direction of movement such that the side of the culvert where more siblings were captured was assumed to be the natal (redd) location.

We tabulated expenses for labor, equipment, supplies, and laboratory work for each of the four mark–recapture detection methods and for sib-split from the previous study. Standard fish survey equipment and supplies, such as a backpack electrofisher, nets, and anesthetic, were not included in cost estimates because we assumed that they would already exist in the inventory of an agency or organization that conducts fishery monitoring in streams.

Instead, we focused on the expenses that were specific to the particular monitoring methods we studied (Supplement C). We first tabulated the start-up cost to implement each method at one site, by type of cost, and we then calculated an average cost per site (up to four sites), including the start-up cost only once to show how this average cost scaled by the number of sites. We assumed that that costs for field labor, genetic lab work, PIT tags, VIE, and hardware that could not be shared among sites (e.g., stationary PIT systems) were a simple multiple of the number of sites, and the sites themselves were treated as spatially independent for travel times and fuel costs. Average costs of hardware that could be shared across sites (e.g., mobile antenna, hand-held PIT tag reader, and field computer) were calculated based on the number of sites. The cost of data analysis was assumed to increase by 20% for each additional site.

RESULTS

Upstream Passage by Trout

During fish marking, we released a total of 368 VIE batch-marked trout and 246 PIT-tagged trout in the reaches downstream of the culverts in four streams (Tables 2, 3). Most of the trout that were captured during initial marking and tagging were age 1 and older (mean TL of marked or tagged trout = 87.6 mm; maximum TL = 183 mm). Overall, the proportion of marked or tagged fish that were recaptured or detected by the four methods was very low, and there were no statistically significant differences in these proportions among streams based on binomial CIs, but upstream passage by trout was confirmed for all four culverts. Recapture of VIE batch-marked trout by single-pass electrofishing confirmed upstream movement through the culvert for the species present in each stream, even if the confirmation was based on a single fish (in two cases; see Table 2). The frequency of detection for batch-marked trout was comparatively high in Stream521, with eight total detections, whereas there were no more than three detections in any other stream (Table 2). Recapture (by single-pass electrofishing) or detection (by the first pass of the mobile antenna) of PIT-tagged fish consistently confirmed upstream passage except for WCT in Stream523 (Table 3). In Haskell Creek, PIT tags confirmed that some batch marks were lost, overlooked, or not recorded properly; only one of four PIT-tagged WCT recaptured above the culvert during electrofishing, which should also have carried VIE batch marks indicating that they were originally captured below the culvert, did bear such a mark. The inside stationary antennas recorded upstream passage in every case (Table 3) and also indicated that some trout transited the culvert more than once (Table 3).

Thirteen of 14 PIT-tagged trout detected by single-pass electrofishing upstream from the culvert on any recapture event were also detected at least once during the mobile antenna surveys (Table 3). During this same time, the stationary antennas detected upstream movement by all 14 fish plus an additional 5 individuals that were never detected by the other methods (see Table 3). If the time period when stationary antennas were operating before the first and after the last electrofishing or mobile antenna survey is also considered (Supplement A), then stationary antennas detected an additional 11 individuals (30 total) that moved upstream through the culvert at least once (see Table 3).

Batch-marked trout that were originally released below the culvert were captured above the culvert on the first recapture event in three streams (Table 2). At least one PIT-tagged trout from below the culvert was captured above on the first recapture event in all streams, although we did not necessarily recapture both WCT and BKT on the first recapture event (Table 3). One or more PIT-tagged trout were detected on the initial pass of the first mobile antenna survey in two streams, and it wasn't until the third survey when upstream passage was confirmed in all four streams (Table 3). Of the 19 PIT-tagged trout that were detected by stationary antennas during the electrofishing and mobile antenna survey period, 8 were also captured during the first electrofishing recapture event, and 4 were detected during the initial pass of the first mobile antenna survey (Table 3).

The first upstream movement of any newly tagged trout through the stationary antennas was always recorded prior to the first electrofishing or mobile antenna survey. Within each stream, these movements were detected 1 d after release in CrookedFkTrib (fish identification code WCT-367), 2 d after release in Stream521 (BKT-109), 4 d after release in Stream523 (WCT-852), and 10 d after release in Haskell Creek (WCT-048; see Table 3). Upstream movement through the culvert was most frequently detected based on fish that were originally marked or tagged within 100 m of the culvert (Tables 2, 3).

Capture and Detection Probabilities

The electrofishing capture probability in reaches above the culverts (i.e., the target areas for the recapture events) ranged from 0.580 in Haskell Creek (95% CI = 0.535–0.690) to 0.766 in Stream521 (95% CI = 0.637–0.859), except for WCT in Stream521, where capture probability was only 0.242 (95% CI = 0.099–0.485; Supplement D). Detection probability with the mobile antenna varied by stream and was greater in Haskell Creek (0.660; 95% CI = 0.520–0.777) than in the other three streams (0.469; 95% CI = 0.401–0.539; top model with 60% of AIC_c weight; Supplement E). The detection probability at individual stationary antennas situated inside the culverts varied

TABLE 2. Counts of batch-marked trout (WCT = Westslope Cutthroat Trout; BKT = Brook Trout) that were captured and released below a culvert and detected above the culvert (i.e., detected as moving upstream) based on recapture by single-pass backpack electrofishing in four streams (two tributaries to the Crooked Fork of the Lochsa River, Idaho [Haskell Creek and an unnamed tributary, CrookedFkTrib]; and two unnamed tributaries of East Fork Lolo Creek, Montana [Stream521 and Stream523]). The same individual could be recaptured during more than one recapture event. Six of the eight trout detected during the first recapture event were originally marked in the 100-m reach closest to the downstream end of the culvert. Similarly, 16 of 22 total detections were from fish marked in the 100-m reach closest to the downstream end of the culvert. The first recapture event in CrookedFkTrib was cancelled because of wildfire in a nearby watershed. (In addition to batch marks, trout above a certain size also received an implanted PIT tag; however, for this summary, they are only treated as if they had batch marks. Detections of trout treated as individually identifiable are presented in Table 3).

Stream	Species	Number released below culvert	Single-pass electrofishing recapture event		
			1	2	3
CrookedFkTrib	WCT	71		0	1
Haskell Creek	WCT	150	1	1	1
Stream521	BKT	39	2	1	4
	WCT	23	4	1	2
Stream523	BKT	15	1	1	1
	WCT	70	0	0	1

among the streams and was 0.967 in Stream521 (95% CI = 0.904–0.989) and 0.742 in Stream523 (95% CI = 0.624–0.833; top model with 83% of AIC$_c$ weight; see Supplement F). If these values are representative of average stationary antenna performance across all streams, then the probability of being detected by at least one antenna in a two-antenna PIT array would range from 0.933 to 0.999 (from $1 - [1 - 0.742]^2$ to $1 - [1 - 0.967]^2$).

In general, within a stream, the probability of detecting PIT-tagged trout by individual stationary antennas was higher than by either electrofishing or use of the mobile antenna (Supplements C–E). The probability of detection by the mobile antenna and the probability of capture by electrofishing were nearly the same in Haskell Creek, but generally electrofishing had a higher probability within a stream, with the exception of WCT in Stream523. The point estimates for electrofishing ranged more widely across streams than did those for the mobile antenna.

Comparative Cost of Five Methods to Evaluate Upstream Movement

Across all streams and marking and recapture events, the average time to electrofish a 100-m reach was 61 min (95% CI = 57–65 min). For the purposes of the cost analysis for recapture events, we assumed that it took 4.5 h to conduct single-pass electrofishing in a 300-m reach and to process any fish captured. The average time to survey 100 m with a mobile antenna was 29 min (95% CI = 28–31 min), so we assumed that it took 1.5 h for a 300-m survey. The average time to check a stationary antenna array was 13 min (95% CI = 11–15 min), which we rounded up to 15 min for analyses.

The stationary PIT arrays, mobile antenna method, and sib-split method were the most expensive to implement, with a single-stream or start-up implementation cost of about US$15,000, $11,000, and $10,700, respectively, whereas electrofishing to recapture fish with VIE batch marks or PIT tags cost around $3,500 and $4,800 (Figure 2A; see also Supplement C). A large proportion of the total cost of sib-split came from laboratory costs to extract DNA and genotype samples (35.4%) and the geneticist's time to analyze the data (69.5% of all labor costs and 44.7% of the total cost). Specialized equipment (e.g., PIT readers and a rugged field computer) was the largest cost component for the mobile antenna (64.7%) and stationary antenna (56.1%) methods. The stationary PIT antenna method had comparatively high field labor and fuel costs due to the need to frequently visit the site and change batteries. The average cost per site declined most rapidly for the mobile antenna method, as much of the required equipment (mobile antenna, laptop computer, etc.) could be used at every site (Figure 2B), and was less than half the single-site cost when all four sites were considered. Averaged across four sites, the cost for electrofishing recapture of PIT-tagged trout decreased by 32% to about $3,300; the cost of sib-split decreased by 25% to about $8,000; the cost of stationary antennas decreased by 28% to about $10,600; and the cost of electrofishing for VIE batch marks decreased by about 16% to $2,900.

DISCUSSION

Fish passage at culverts has been studied by using recapture of batch-marked fish (e.g., Warren and Pardew 1998; Coffman 2005; Burford et al. 2009; Norman et al.

TABLE 3. Individual trout identified by species code (WCT = Westslope Cutthroat Trout; BKT = Brook Trout) that were originally captured and PIT-tagged below a culvert and recaptured or detected above the culvert or detected as moving upstream in four streams (two tributaries to the Crooked Fork of the Lochsa River, Idaho [Haskell Creek and an unnamed tributary, CrookedFkTrib]; and two unnamed tributaries of East Fork Lolo Creek, Montana [Stream521 and Stream523]). The reach origin indicates the location below the culvert where the trout was originally tagged. The letter "U" denotes recapture or detection by event, either during a single pass or during the first pass if multiple passes were conducted on the same occasion. The frequency of movement by direction is noted for stationary PIT antennas. Gray shading indicates when an individual trout was not detected by a particular method when the fish was believed to have been above the culvert and available for detection by one or more method. Movement events detected by stationary antennas but that occurred before or after the survey dates for electrofishing and the mobile antenna are identified by footnotes. Some sampling events in CrookedFkTrib were cancelled or delayed because of wildfire in a nearby watershed (denoted by "–"). Numbers of PIT-tagged trout released below culverts during initial marking were as follows: 63 WCT in CrookedFkTrib; 92 WCT in Haskell Creek; 10 WCT and 35 BKT in Stream521; and 32 WCT and 14 BKT in Stream523.

Species code	Reach origin (m) below culvert	Electrofishing recapture event			Mobile antenna detection event					Stationary antenna by direction (frequency)	
		1	2	3	1	2	3	4	5	Upstream	Downstream
CrookedFkTrib											
WCT-F25	100	–	U		–	–	U		U	2	1
WCT-44A	100	–		U	–	–			U	3	2
WCT-367	100	–		U	–	–	U	U	U	5	4
WCT-44B	100	–	U	U	–	–	U		U	2	1
WCT-F0B[a]	200									1[a]	1[a]
WCT-550[a]	100									4[a]	4[a]
WCT-670[a]	100									2[a]	2[a]
WCT-83F[a]	100									1[a]	1[a]
Haskell Creek											
WCT-51B	100		U				U			6	7
WCT-04B	100	U				▨	▨	▨	▨	1	
WCT-007	300	▨	▨	▨		▨	▨	▨	▨	1	
WCT-B75	200	▨	▨	▨		▨	▨	▨	▨	2	1
Stream521											
BKT-109	80			U		U		U		1	
BKT-217	80	U				U		U	U	1	
BKT-F64	80	U		U		U	U	U	U	1	
BKT-245	80	U	U	U					U	3	2
BKT-70A	80	▨	▨	▨		▨	▨	▨	▨	1	1
BKT-612	80	▨	▨	▨		▨	▨	▨	▨	1	1
BKT-A55[b]	180									3[b]	2[b]
BKT-F76[b]	180									1[b]	
BKT-117[b]	180									6[b]	6[b]
BKT-365[b]	180									1[b]	
BKT-252[b]	180									1[b]	
WCT-70F	80	U	U						U	1	
WCT-B1D	80			U	U	U	U	U	U	1	
WCT-24D[a]	80									7[a]	7[a]
Stream523											
BKT-51E	100		U			U	U	U		3	2
BKT-421	300	U	U	U		U	U	U		1	
WCT-D0F	100	▨	▨	▨		▨	▨	▨	▨	6	6
WCT-852[a]	100									5[a]	5[a]

[a] Passive integrated transponder-tagged trout detected by stationary antennas prior to the first electrofishing or mobile antenna survey in that stream.

[b] Passive integrated transponder-tagged trout detected by stationary antennas after the final electrofishing or mobile antenna survey in that stream.

2009), remote sensing of PIT-tagged fish via stationary antennas (e.g., Solcz 2007; Mahlum et al. 2014; Goerig et al. 2015), or a combination of these two methods (e.g., Roghair et al. 2014). The potential for pedigree-based genetic analyses to detect fish passage has been recognized for some time (e.g., Hudy et al. 2010), and a pedigree-

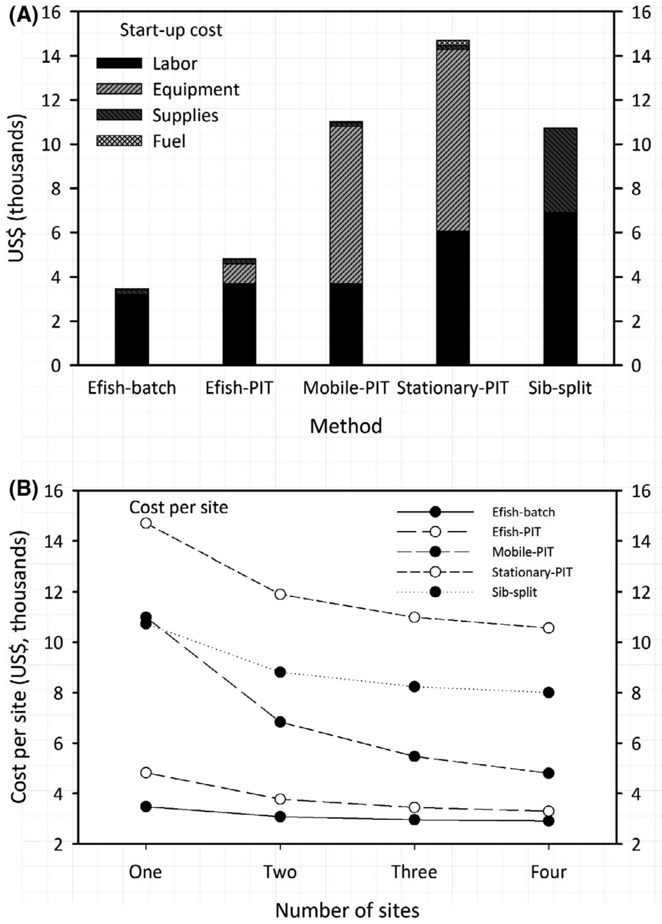

FIGURE 2. Plots of (**A**) average start-up costs, by category, for the five methods used to detect upstream movement by Westslope Cutthroat Trout at remediated culverts in Idaho and Montana streams during 2011 (Efish = electrofishing) and (**B**) average cost per site for each method scaled to the number of sites. In panel (A), bars represent the average of four streams for every method except sib-split (with an average for three streams), and labor includes data collection and data analysis. For sib-split, the supplies category includes the laboratory cost of genotyping fish. In panel (B), the cost per site represents the scaling that can occur for some cost categories; for example, the mobile antenna can be used at all four sites, whereas other cost categories are fixed per site, such as labor to mark and tag fish or equipment for stationary antennas. In panel (B), analysis costs are assumed to increase by 20% with each additional site.

based method was implemented in the same streams used in the present study (Neville and Peterson 2014). To our knowledge, this is the first attempt to use four different mark–recapture methods and a genetic method to evaluate upstream fish passage at the same set of culverts. Population-level responses, such as increased abundance and distribution or full life history expression, are the overarching objectives of fish passage projects, but they can be difficult, expensive, and time-consuming to measure (Hoffman et al. 2012). Our focus on individual movement and contrasting methods is predicated on the need to quickly and unambiguously confirm that an individual culvert remediation project was successful—both to justify project costs and to provide a first-order metric that should lead to a population-level response. Successful upstream passage was confirmed by VIE batch marks and for each PIT-tag-based method (mark–recapture, stationary antennas, and the mobile antenna) for at least one trout species at all four streams. The pedigree-based genetic approach, sib-split, also appeared to confirm upstream movement by age-0 WCT in three of the four streams (Neville and Peterson 2014). Below, we discuss the limitations of the study design, the differences in information content and strength of inference among the different methods (including sib-split), and how those differences can be aligned with monitoring objectives. We also provide some suggestions for biologists who are tasked with postproject effectiveness monitoring of remediated road–stream crossings.

Validating Fish Passage at Remediated Culverts: Objectives, Design, and Information Content

Our study primarily was methodological and was intended to provide a direct, efficient answer to whether trout can pass a culvert; it differs in some significant ways from other studies of fish movement at culverts, in which the primary objective was to (1) estimate the probability of passage or (2) relate passage to culvert characteristics or biological covariates. We used multiple monitoring methods at a few culverts (see also Roghair et al. 2014), whereas other studies have used a single method at a dozen or more culverts judged to differ in their passability (e.g., Coffman 2005; Burford et al. 2009). The “false culvert” or reference reach (e.g., Dunham et al. 2011) design has been used to quantify the barrier effect of a culvert or contrast the fish passage rates between a reference point in a natural stream channel (i.e., false culvert) and one or more culverts exhibiting a range of hydraulic or physical characteristics or passability ratings (e.g., Burford et al. 2009; Norman et al. 2009; Mahlum et al. 2014). Our choice to focus intensively on a few sites and not use a reference reach reflects the likelihood that a biologist implementing such monitoring faces significant time and cost constraints and might stop sampling at a site once passage is confirmed.

This study measured passive movement, where fish are released at their original capture location after marking or tagging and their subsequent behavior is monitored (e.g., Norman et al. 2009; Mahlum et al. 2014). Others have captured fish in one location (upstream of a culvert) and released them in another (downstream from the culvert) and presumed that the fish would be motivated to move (translocation–displacement; e.g., Burford et al. 2009; Goerig et al. 2015). We did not translocate fish because doing so might confound an ongoing study in two of the streams (D.P.P., unpublished data). Unsurprisingly, we observed low recapture rates, yet the passive movement approach verified upstream passage by trout.

Our inferences are limited to several trout species in small headwater streams of the northern Rocky Mountains, but the methods tested are relevant for evaluating culvert passage by less vagile fish species. A case study in southeastern U.S. streams with small-bodied cyprinids and percids (Roghair et al. 2014) concluded that stationary antennas provide more information (e.g., timing of movement and relative passability) than mark–recapture, but those authors noted, qualitatively, the significant cost to acquire and maintain PIT antenna systems.

Monitoring objectives and methods should always be well matched, and we recognize that the ecological setting or practical considerations might support one fish passage monitoring method over another. For example, if the objective is to validate the passage of multiple fish species or multiple age-classes of one or more species at individual crossings (e.g., Coffman 2005; Roghair et al. 2014), then mark–recapture with batch marks can be cost-effective (Figure 2) and may be preferred over sib-split, which requires species-specific genetic markers and where the evaluation may realistically be constrained to only to one age-class (e.g., Neville and Peterson 2014; Whiteley et al. 2014). If the objective is to detect movement by young-of-the-year fish—with the assumption that verifying passage by the weakest swimming individuals of a population would mean that older, larger individuals can also pass the structure (e.g., Whiteley et al. 2014)—then sib-split may be the only viable option given the difficulty in otherwise tagging and tracking the movement of individuals in that age-class.

The mark–recapture methods we assessed could be implemented with a "stopping rule" wherein once the passage of the target species or a particular age-class or size-class is detected or recaptured, then sampling at that site will cease, and the field crew can begin evaluating passage at another site. Field sampling for sib-split may require only a single site visit, but the answer is only revealed some time later after laboratory work and time-consuming analysis by a subject matter expert. Thus, if field crew resources are limited but there is ready access to and resources for a genetics laboratory and geneticists, then sib-split would certainly be a viable approach to assess passage at dozens of sites within a field season.

Information content varied considerably among the mark–recapture methods we tested. The stationary PIT antennas arguably provided the most detailed information and insight about trout behavior at culverts, as sampling was mostly continuous and detection probability was comparatively high (0.74–0.97 per antenna) for a two-antenna array. Although it was not our specific objective here, the detection data from the stationary antennas can provide the means to evaluate diel movement and relate passage to important environmental covariates, such as discharge and temperature (e.g., Solcz 2007; Goerig et al. 2015), or even to characterize when fish approach but do not pass a road–stream crossing (e.g., Mahlum et al. 2014). The stationary antennas also detected upstream movement by some individual trout that went undetected by mark–recapture or the mobile antenna, which implies a lower type II error rate (missing a movement that did occur). Many of these cases involved fish making multiple upstream and downstream movements across the culvert (e.g., Solcz 2007; Dunham et al. 2011) and may be examples of station-keeping behavior (i.e., repetitive movements within a home range; Dingle 2014). The additional information about fish movement potentially gleaned from detections on both stationary and mobile antenna systems did, however, cost additional staff time (Figure 2A).

Inference about Passage and Movement Direction

There was a clear distinction between the strength of inference about the direction of fish movement between the mark–recapture methods and sib-split. Physical recapture of a marked or tagged fish provides definitive evidence of passage and the direction of that movement. Detection of PIT-tagged trout by using mobile and stationary antennas also provides strong evidence of movement (and its direction), but there are some potential sources of error in interpretation or inference. Translocation of a PIT tag by a predator could lead to incorrect inferences about movement by study fish. We have no evidence that this occurred, but we note that repeated detections of an individual tag through time and at different locations would be evidence that it did not. The detection field of stationary antennas extended approximately 10–20 cm on either side, so a tagged fish that entered the antenna field but did not actually pass could possibly be confused with one that passed through. Generally, a fish detected in a stationary antenna's field is assumed to have passed (e.g., Hodge et al. 2017), but deploying multiple antennas, which was done here, helps to remove any doubt. Here, we focused on movement detected at the two inside antennas, which were common to all sites, but we observed that in two streams (Stream521 and Stream523), the two outside antennas detected the same number of individuals moving upstream as did the inside antennas. The deployment of four antennas is likely excessive unless the monitoring objectives also include a detailed understanding of fish behavior in and adjacent to culverts or unless they are needed for estimating detection probabilities, as in the present study. Given a more limited budget, simply placing a single antenna some distance (e.g., >2 m) upstream of the culvert inlet could suffice to confirm the upstream passage of fish tagged or released below the culvert outlet, with a type II error rate equivalent to 1 minus the estimated single-antenna detection efficiency.

In contrast, confirming movement—and, in particular, the direction of movement—by use of the sib-split method relies on several important analytical and inferential assumptions. Inference about movement using sib-split depends on the correct discrimination of family groups, which in turn depends on the number of loci genotyped, the underlying family structure of the target population(s), and the algorithm (e.g., COLONY) used to construct the pedigree (Neville and Peterson 2014; Whiteley et al. 2014). For instance, it is possible to infer movement when it did not occur (type I error), arising from falsely assigning an individual found on one side of the culvert to an identified family on the other side (Neville and Peterson 2014). Similarly, COLONY's occasional tendency to split members from a true family leads to the possibility of not detecting movement that did occur (type II error), arising from not relating a disperser to its family on the other side of the culvert. Increasing the number of loci that are genotyped can reduce both types of error but of course also increases the expense. Using the majority rule to infer that age-0 WCT moved upstream is also problematic because other plausible mechanisms, such as *downstream* dispersal of (the majority of) fish spawned upstream from the culvert, could produce a similar pattern of more siblings on the downstream side of a culvert. A tendency for downstream dispersal of age-0 fish has been noted for WCT (e.g., McIntyre and Rieman 1995), BKT (e.g., Hunt 1965; Hudy et al. 2010; Hoxmeier and Dieterman 2013), and other stream-dwelling salmonids (Raleigh 1971). Differential survival of siblings above versus below the culvert might also produce such a pattern in age-0 trout, especially given that this age-class can experience comparatively high rates of mortality (e.g., Elliott 1986; Peterson et al. 2004a; Hoxmeier and Dieterman 2013). Extending the pedigree analysis to include older individuals or parents may provide additional insight and improve the strength of inference about movement (Neville and Peterson 2014) but may be hampered by mortality and greater movement for these age-classes (potentially out of the study area) and entail additional sampling effort and laboratory costs relative to targeting a single age-class. Thus, although sib-split can be quite effective at simply detecting movement, the possibility of falsely concluding that *upstream* movement occurred by (mis)applying majority rule (type I error), combined with the possibility of missing movement because of COLONY's tendency to split off related individuals when family size is small (type II error), suggests that the sib-split method should be applied cautiously to infer directional movement.

The benefit–cost comparison for the different methods must consider the strength of inference as well as the number of sites and number of years in which monitoring will occur. Based on sib-split, 36 age-0 WCT moved upstream through the culvert in Stream521 (Neville and Peterson 2014), which would equate to \$222 per individual detected based on the per-site average across four sites (Figure 2B). The corresponding cost per PIT-tagged age-1 and older WCT detected as moving upstream in Stream521 was \$1,651 for electrofishing, \$2,405 for the mobile antenna, and \$5,280 for the stationary antennas if restricted to the time period when sampling overlapped for all methods (Table 3; Figure 2B). At face value, this makes the sib-split method appear comparatively more cost effective than mark–recapture, assuming that the majority rule is accurate. In this example, the cost per individual detected for the stationary antennas was 2–10× higher than the costs for the other methods (including sib-split). In a situation where movement is rare, the lower probability of a type II error with stationary antennas might justify the higher cost.

The calculated average cost per site for each method (Figure 2B) was roughly equivalent to the cost to confirm passage (i.e., obtain an answer) at up to four sites during a single year. If similar surveys were conducted at different sites in subsequent years, then the mobile and stationary antennas would be even more cost effective if the readers and antennas could be re-used. In contrast, fixed costs in field labor (marking and recapturing fish and collecting fin clips) or laboratory work (genotyping) constitute a larger portion of the overall cost estimates for electrofishing and sib-split (Figure 2A; see also Supplement C), so the cost per site for those methods should not change dramatically in subsequent years. Irrespective of cost, a practitioner deciding which of these monitoring methods to use may also make an implicit sociopolitical calculation about which data are easier to explain to decision makers.

Practical Guidance for Different Methods

We have discussed how selection of a method to verify passage can depend on a number of factors, including information content, strength of inference, and relative cost. We doubt that one method will be selected uniformly by all practitioners; therefore, we offer some practical suggestions to improve the utility of each. First, for the mark–recapture–detection approach, it can be advantageous, where practical, to use translocation–displacement to enhance recapture rates (e.g., Burford et al. 2009; Goerig et al. 2015) and improve the statistical power of fish models relative to the passive movement design we implemented.

Second, though it is of course difficult to know a priori, it is useful to note that for all methods evaluated in our study, sampling could have been limited to shorter stream reaches (e.g., within 100 m of the culvert) without affecting the conclusions about upstream movement. Most of the fish that were recaptured or detected as moving upstream through the culvert were originally marked in the 100-m reach immediately downstream (Tables 2, 3), and other researchers have observed a similar pattern (Norman et al. 2009; Roghair et al. 2014). Similarly, in our previous work, we (Neville and Peterson 2014) noted that sib-split sampling could have been restricted to within 60 m on either side of the culvert. This knowledge could have reduced the labor costs for fish marking, electrofishing, and mobile antenna surveys by up to two-thirds (Figure 2).

Third, given unlimited funds for equipment and PIT tags, the stationary antennas would presumably be the biologist's first choice because of the comparatively high detection probabilities and continuous sampling, which greatly increase the likelihood of detecting upstream movement. The stationary antennas' detections also showed that upstream movement by PIT-tagged trout occurred within a few days after their release. This suggests that a biologist seeking to confirm passage quickly by using electrofishing or mobile antennas could move up the timing of the first resampling event compared to the periodic resampling in this study. The stationary antennas also showed that the other methods sometimes missed movement (Table 3), and this was the only method that could discriminate when a fish moved upstream and then back downstream (and would thus be unavailable for detection by the other methods). If we assume that the fish that moved upstream remained in the study area, then it is self-evident that the lower detection rates obtained by electrofishing or the mobile antenna could be offset, in part, by making multiple passes. Here, our data suggest that it would be more cost effective to do so for mobile antennas, as three passes could be conducted in the same time it took to complete one pass with the electrofisher. For example, the lowest detection probability we estimated for the mobile antenna was about 0.47, so three passes would result in an effective detection rate of about 0.85 (assuming equal detection probability for each pass). For comparison, the highest single-pass electrofishing detection probability we observed was 0.78.

Fourth, double-marking or both tagging and marking may be important to reduce the likelihood of type II errors. We observed one case in which the count of PIT tag recaptures exceeded the recorded number of VIE batch marks (see Tables 2 and 3), which implies that some cases of upstream movement would have been missed without the complementary tag. We do not know whether the VIE batch marks were lost or simply not observed, but we note that tag and mark retention is a fundamental assumption for capture–recapture models (White et al. 1982). Tag or mark loss can be problematic where low recapture rates might be anticipated, such as with monitoring at road–stream crossings (Norman et al. 2009; Dunham et al. 2011).

Fifth, wherever possible, we recommend collecting tissue samples during mark–recapture monitoring even if genetic approaches to assessing fish movement are not the initial focus, as archived specimens could be used subsequently for additional comparative tests of the sib-split approach or retrospective evaluation of new genetic-based methods. Some other genetic methods currently exist, including genetic assignment (e.g., Wood et al. 2018) and environmental DNA (Wilcox et al. 2016), that may prove useful in detecting fish movement through culverts.

Finally, the use of electronic tags and telemetry systems to monitor aquatic species may hold tremendous promise (Lennox et al. 2017) and PIT technology itself is relatively simple (Gibbons and Andrews 2004), but the platforms are still evolving, and component integration can sometimes prove challenging. The PIT systems like those we deployed require integration of transceivers, power supplies, data storage devices, and computers (e.g., Zydlewski et al. 2006; Connolly et al. 2008). The PIT systems we built were relatively straightforward, yet there was considerable trial and error involved in antenna design. We found also that communication between PIT system transceivers and computers was not always reliable. Biologists who are new to this technology may want to consult with an experienced practitioner or the product vendor's technical specialists before committing to a field deployment.

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SUPPORTING INFORMATION

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