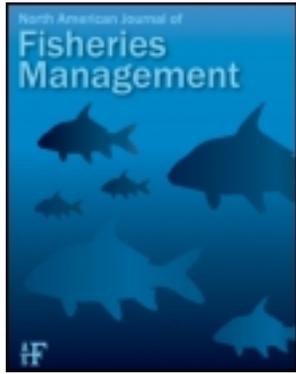


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MANAGEMENT BRIEF

# Estimating Habitat-Specific Abundances of PIT-Tagged Juvenile Salmonids Using Mobile Antennas: A Comparison with Standard Electrofishing Techniques in a Small Stream

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## Abstract

The use of passive integrated transponder (PIT) tags in ecological studies is increasingly common, but evaluations of their performance and range of application in the field are still emerging. Here, we compare habitat unit–scale abundance estimates of PIT-tagged juvenile coho salmon *Oncorhynchus kisutch* and steelhead *O. mykiss* derived from multiple-pass surveys with a submersible pole-mounted PIT antenna and backpack electrofishing in a small coastal California stream. We found high concordance of methods for coho salmon and age-0 steelhead and moderate concordance for age-1 and older steelhead. Regression analysis of PIT antenna estimates on electrofishing estimates indicated an approximately one-to-one relationship between methods. Regression intercepts for coho salmon and age-0 steelhead were significantly greater than zero, but the differences were small (with an effect equivalent to less than one fish). We found no evidence that pool area, cover area, or cover complexity influenced the relationship between methods for coho salmon and age-0 steelhead, but some evidence that electrofishing may be more effective than PIT antennas for estimating the abundance of age-1 and older steelhead in pools with high cover complexity. Our results demonstrate that surveys using submersible PIT antennas can provide habitat unit–scale estimates of juvenile salmonid abundance similar to those derived from electrofishing in small streams. An advantage of using PIT antennas is that they allow fish abundance estimation without fish recapture and frequent sampling can occur without subjecting study animals to excessive handling stress or mortality. This is a particularly important consideration in studies of small populations, sensitive species, or fish listed under the U.S. Endangered Species Act.

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One of the challenges of fish ecology is linking the behavior, growth, and survival of individual fish to population dynamics. A useful method for linking individual- and population-level

ecological processes is to tag and recapture or relocate individuals across a range of environmental conditions and to track the consequences, in terms of growth and survival, of differential habitat selection (e.g., Bell et al. 2001; Harvey et al. 2005; Ebersole et al. 2006). Passive integrated transponder (PIT) tags have become an increasingly common tool in ecological studies, in part because they provide an efficient and relatively inexpensive method for tagging and tracking large numbers of individual animals. Passive integrated transponder tags consist of a small computer chip, capacitor, and antenna coil encapsulated within 11–32-mm-long glass tubes that are typically implanted within the peritoneal cavity of small fish (Guy et al. 1996; Roussel et al. 2000). When passed near an external energy source, PIT tags transmit a unique numeric code that can be recorded and stored by a data logger. In the last decade, application of PIT technology to ecological studies has helped field researchers gain detailed insight into key processes affecting survival and growth rates of animal populations (e.g., Zydlewski et al. 2006; Brakensiek and Hankin 2007).

Although studies using PIT tags are increasingly common, evaluations of PIT tag performance and their range of application in field studies are still forthcoming. Here, we test whether PIT technology can be adapted to obtain habitat-specific estimates of tagged fish abundance in streams by using multiple-pass surveys with submersible antenna systems. In fall 2005, we began a study of the seasonal abundance, habitat use, and movements of juvenile coho salmon *Oncorhynchus kisutch* and steelhead *O. mykiss* in a small coastal California stream (Stillwater Sciences 2008). We hypothesized that winter conditions would

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cause a recruitment bottleneck for juvenile salmonids within the study stream and that the response to flood disturbance would be mediated by stream cover complexity at the habitat unit scale. To test these hypotheses, we tracked the change in abundance of PIT-tagged fish across a range of habitats over relatively short (e.g.,  $\leq 1$ -month) time intervals during winter. In support of the ecological objectives of our study, we conducted a methodological evaluation to determine whether PIT techniques could estimate in situ fish abundance using relocation data from submersible antennas. This evaluation involved comparing population estimates from multiple-pass surveys with a submersible pole-mounted mobile PIT tag antenna and those obtained by backpack electrofishing. Specifically, our objectives were to determine whether relocation data from a mobile PIT tag antenna could provide abundance estimates of PIT-tagged fish similar to those obtained by multiple-pass electrofishing at the habitat unit scale, and whether the agreement between methods varied by species, age-class, or physical habitat features such as habitat size and instream cover complexity.

## STUDY AREA

We conducted this study in Devil's Gulch, a third-order tributary to Lagunitas Creek that drains into Tomales Bay on the central California coast. The study area receives precipitation as rainfall from November through March (mean annual rainfall  $> 100$  cm) and is typified by a mild Mediterranean climate, dominated by dry summers and wet winters punctuated by periods of intense rainfall. The 1.2-km study reach lies within Samuel P. Taylor State Park at an elevation of  $\sim 50$  m and with a drainage area of approximately  $7 \text{ km}^2$ . The wetted channel averages 3.5 m wide in winter and alternates between shallow riffles and pools (maximum depth,  $\sim 1.0$  m) over gravel and cobble substrate. The stream is confined within a steep valley and has a mean channel gradient of 2%. Winter stream temperatures average approximately  $10^\circ\text{C}$ , with daily minima remaining above  $6^\circ\text{C}$ . Habitat units included in the study had a mean surface area of  $46 \text{ m}^2$ . All work was conducted at base flow levels between approximately  $0.05\text{--}0.08 \text{ m}^3/\text{s}$ , although peak flows between sample events sometimes exceeded  $25 \text{ m}^3/\text{s}$ . Large wood, undercut banks, and unembedded cobble and boulder substrate provided varying degrees of cover within study units. Riparian vegetation provides more than 80% canopy cover and is dominated by California bay laurel *Umbellularia californica*, white alder *Alnus rhombifolia*, oaks *Quercus* spp., bigleaf maple *Acer macrophyllum*, and Oregon ash *Fraxinus latifolia*.

Coho salmon and steelhead are the only salmonids present within the study stream. Coho salmon predominantly smolt after 1 year of freshwater residency within the region (Shapovalov and Taft 1954) and were represented by a single age-class in the study stream. Steelhead predominantly smolt after 2 years of freshwater residency (Shapovalov and Taft 1954) and several age-classes were present. Prickly sculpin *Cottus asper* and

California giant salamanders *Dicamptodon ensatus* were the only other aquatic vertebrates present.

## METHODS

*Field surveys.*—In October 2005, we selected 28 study units and used multiple passes with a backpack electrofisher to capture fish from each habitat unit. We blocked the upstream and downstream ends of each unit with 6-mm mesh netting prior to electrofishing. All captured fish were anesthetized and identified to species, and the fork length (FL) to the nearest millimeter and wet weight to the nearest 0.01 g were recorded. Juvenile salmonids greater than 60-mm FL were tagged with sterilized PIT tags. We used either full-duplex (FDX) or half-duplex (HDX) PIT tag types during the study, both of which emitted a signal at 134.2-kHz radio frequency (Allflex USA, Dallas, Texas). Full-duplex tags measured 11 mm and were used for fish from 60- to 99-mm FL, which included all coho salmon and age-0 steelhead. Half-duplex tags measured 23 mm and were used for all steelhead 100-mm FL and longer. The size range we chose for applying the different tags in steelhead corresponded to the size break separating age-0 from age-1 and older steelhead during fall, as determined by scale analysis. Overall, the size of tagged fish ranged from 60 to 223 mm. All tags were inserted into the body cavity anterior to the pelvic fin with a hypodermic needle. A subsample of 148 fish (104 coho salmon and 44 steelhead) were tagged and held for 24 h before release to assess short-term survival and tag retention, which was 100% for both. Otherwise, we released all fish into their original habitat units immediately after recovery from handling.

Beginning 40 d after the initial tagging event, we estimated the abundance of PIT-tagged fish within a subsample of 13 of the 28 study units using multiple passes with both a mobile PIT tag antenna and backpack electrofisher. We selected the subset of study units to span the range in habitat size and complexity observed within the original 28 study units. We sampled four units on December 8, 2005; five units on January 25, 2006; and four units on February 24, 2006. The initial population of PIT-tagged fish in the 13 units was 533 coho salmon, 432 age-0 steelhead, and 91 age-1 and older steelhead, but owing to movement, mortality, or both after the initial tagging, a smaller (but unknown) number of the initial tagged population was present at the time of sampling.

We used a commercially available mobile PIT tag antenna system (Biomark FS2001-ISO data logger with a 30-cm triangle waterproof multidirectional antenna) capable of detecting both FDX and HDX PIT tags. The antenna consisted of a sealed coil mounted on a retractable pole (adjustable length of 2–3 m) that was designed to be moved through the water column to search for tagged fish. Under our study conditions, the antenna had a detection range of approximately 30 cm and was connected to a data logger that automatically recorded the unique numeric tag code as well as the time and date of detection for each tagged fish encountered. To match the data logger records to the appropriate

study unit and pass number, we recorded the beginning and ending time of each pass within each unit and matched those times with the downloaded PIT detection records. We conducted all fish surveys after dark when juvenile salmonids are less likely to be concealed in cover during winter (Contor and Griffith 1995) and detection probabilities were expected to be greater. Study units were blocked with netting at the upstream and downstream end, and a single surveyor made three passes with the antenna while an observer recorded the beginning and end time of each pass. To complete a pass, the surveyor waded upstream, systematically moving the antenna over the entire wetted area of the study unit. We used headlamps and handheld flashlights to provide light over the sampled area. Passes were separated by 10–15 min to allow study units to return to ambient conditions. The same person conducted all PIT antenna surveys to avoid surveyor bias (O'Donnell et al. 2010). All sampling took place during stable low-flow periods. Stream stage at the time of each survey did not differ by more than 6 cm, as measured by a pressure transducer installed in the midpoint of the study reach.

Immediately following the PIT antenna survey, we conducted three electrofishing passes. The electrofishing crew consisted of the electrofisher operator and two netters. To complete an electrofishing pass, the crew moved upstream, systematically sampling the entire study unit. We used pulsed direct current (30 Hz at 300 V) to capture fish. A separate crew of two people anesthetized, measured, weighed, and scanned all captured salmonids for PIT tags according to the methods described above. Fish were held in live cars within the stream outside of the sampled units until the final electrofishing pass was completed, and all fish were returned to their original capture location. The total time from start to finish of electrofishing each habitat unit was recorded to compare the effort required for each gear type.

We measured the habitat characteristics of all units prior to the December surveys and, owing to flood-induced habitat changes in late December, we repeated these measurements after the February fish sampling. To characterize habitat in the sampled units, we measured wetted width at 4–10 equally spaced, orthogonal transects and the total habitat length. We measured cover within each habitat unit by counting the number of object surfaces in a 0.25-m-wide cross-sectional cell (Kinsolving and Bain 1990). Cover types included wood, cobble–boulder, and undercut banks. Solid objects 10 cm or larger in any cross-sectional dimension and more than 3 cm from the stream substrate (e.g., unembedded wood or boulders) were considered three surfaces. Objects 10 cm or larger that did not provide overhead cover for fish (e.g., embedded boulders) and objects smaller than 10 cm in any cross-sectional dimension but more than 3 cm from the substrate were considered single surfaces. We used the product of cover area and mean number of surfaces as an index of cover complexity within the study units.

*Data analysis.*—Prior to data analysis, we screened the data set to identify potentially shed tags. Tag loss after 40 d was approximately 4% based on examination of secondary marks (M. R. Sloat, unpublished data). Because shed tags may re-

main active after they are lost, they can result in false detection by PIT antennas and could bias the comparison of methods. Consequently, we examined the tag history for any tag that was detected during the antenna survey but not found in fish captured immediately afterwards by electrofishing. If fish with these tags were captured at a later sampling date, or if subsequent or previous relocations with the antenna indicated movement from an original tagging location, we considered the tag to be valid. According to these criteria, we could not confirm the validity of 12 out of the 225 detected tags (5%) and they were excluded from subsequent analysis. Of the detections we judged valid based on movement patterns, eight (4%) were based on downstream movement, and it is possible that some of these detections were shed tags that moved passively during high streamflows occurring in late December. However, we retained these records for analysis because their small number was unlikely to influence the results.

For both gear types, separate estimates were calculated for each species and age-class strata (i.e., coho salmon, age-0 steelhead, and  $\geq$ age-1 steelhead) for each of the 13 units sampled. Surveys with the two gear types produced data that lent themselves to different statistical population estimators. Estimates from PIT antenna surveys were calculated using the multiple mark–recapture, multinomial model for closed populations of Seber (1982), the capture probabilities treated as independent samples from the beta distribution  $B\left(\frac{1}{2}, \frac{1}{2}\right)$ . This produces a likelihood function for the total population,  $N$ , proportional to

$$\frac{N!}{(N-T)!} \prod_{i=1}^r B\left(m_i + \frac{1}{2}, N - m_i + \frac{1}{2}\right),$$

where  $m_i$  ( $1 \leq i \leq r$ ) is the number of PIT-tagged fish detected in the  $i$ th sample event, and  $T$  is the total number of distinct PIT-tagged fish detected in all samples. The abundance estimate is the posterior median value, assuming a uniform prior distribution on  $N$ . In this model, we assume that all fish within a species and age-class stratum have the same probability of capture within a given pass. We do not necessarily assume that the probability of capture is the same in all passes. We chose this estimator among multiple candidate models, including maximum likelihood models, because in simulations it outperformed other estimators in terms of accuracy (i.e., root mean square error) and proportional bias given the range of capture efficiencies and population sizes we were likely to encounter (P. F. Baker, unpublished data).

Estimates of PIT-tagged fish captured by electrofishing were calculated using the robust jackknife estimator of Pollock and Otto (1983) with bias-correction following unpublished data from M. S. Mohr and D. G. Hankin, Humboldt State University, expressed as

$$\hat{y}_j^* = \sum_{i=1}^{r-1} c_i + \frac{c_r}{\hat{q}},$$

where  $\hat{y}_j^*$  is the estimate of PIT-tagged fish abundance for unit  $j$ ,  $c_i$  is the number of PIT-tagged fish captured on the  $i$ th pass,  $r$  is the total number of passes,  $c_r$  is the number of PIT-tagged fish captured on the final pass, and  $\hat{q}$  is the estimated capture probability.

To examine the relationship between PIT antenna and electrofishing estimates, we used linear models. Fish abundance estimates were square-root transformed to standardize variances and normalize residuals (Zar 1996). Analysis of covariance (ANCOVA) was used to test for differences in regression slopes and intercepts among species and age-class strata. Concordance of methods was analyzed using Lin's concordance coefficient ( $\rho_c$ ), which evaluates agreement between methods by measuring variation from a 45° line through the origin (Lin 1989). The concordance correlation coefficient has a possible range from -1 to 1, a value of 1 having perfect concordance (i.e.,  $\alpha = 0$ ,  $\beta = 1$ ), a value of -1 having perfect contraposition, and 0 indicating no association between methods. To determine if the two sampling methods differed in their size selectivity within the species and age-class strata, we compared the initial lengths of PIT-tagged fish detected with the PIT antenna with those captured by electrofishing using a two-sample Kolmogorov–Smirnov test (Zar 1996). The Kolmogorov–Smirnov test is a nonparametric test of the null hypothesis that samples are drawn from the same probability distribution. The effect of habitat characteristics on the relationship between methods was determined through linear regression of the difference in PIT antenna and electrofishing estimate pairs on measures of pool size and instream cover characteristics. Measures of cover included cover area and cover complexity (the product of cover area and mean number of cover “surfaces”).

## RESULTS

We relocated a total of 26 coho salmon, 119 age-0 steelhead, and 19 age-1 and older steelhead using the mobile PIT tag antenna within the 13 study units (Table 1). This compares with a total of 31 coho salmon, 120 age-0 steelhead, and 36 age-1 and older steelhead captured by electrofishing within the same study units (Table 1). Mean capture efficiencies exceeded 75% for both gears in all species and age-class strata (Table 1). Seventy-three percent of all relocated individuals were detected by the PIT antenna, and 83% of all relocated individuals were captured

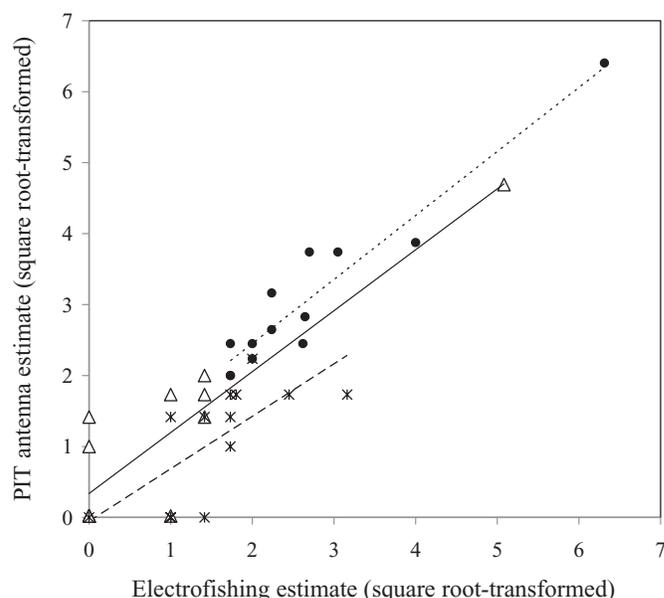


FIGURE 1. Comparison of abundance estimates of PIT-tagged age-0 coho salmon (open triangles, solid line), age-0 steelhead (closed circles, short-dashed line), and age-1 and older steelhead (stars, long-dashed line) obtained from a mobile PIT antenna and electrofishing. The estimates were square-root transformed to standardize variances.

via electrofishing. The length distributions of fish vulnerable to each gear type were not significantly different for any species and age-class strata (coho salmon: PIT antenna mean = 70 mm, electrofishing mean = 71 mm,  $D = 1.005$ ,  $P = 0.99$ ; age-0 steelhead: PIT antenna mean = 72 mm, electrofishing mean = 74 mm,  $D = 0.0735$ ,  $P = 0.90$ ;  $\geq$ age-1 steelhead: PIT antenna mean = 127 mm, electrofishing mean = 131 mm,  $D = 0.1611$ ,  $P = 0.86$ ).

Estimates derived from the PIT antenna and electrofishing were similar over a broad range of fish abundances (range of untransformed fish abundances = 0–41 fish; equivalent fish densities = 0–1.8 fish/m<sup>2</sup>; Figure 1). Lin's concordance correlation coefficient ( $\rho_c$ ) indicated strong concordance between methods for coho salmon ( $\rho_c = 0.89$ , 95% confidence interval [CI] = 0.33–0.98) and age-0 steelhead ( $\rho_c = 0.91$ , 95% CI = 0.45–0.97) and moderate concordance for age-1 and older steelhead ( $\rho_c = 0.59$ , 95% CI = 0.30–0.78). Regression of square-root-transformed data indicated that electrofishing

TABLE 1. Combined abundance estimates (SEs in parentheses), total numbers of fish detected by PIT antennas or captured by electrofishing, and associated capture efficiencies for juvenile coho salmon and steelhead in 13 study pools in Devil's Gulch.

Species and age-class	Combined PIT antenna estimate	Number of fish detected by PIT antenna	Mean PIT detection efficiency	Combined electrofishing estimate	Number of fish captured by electrofishing	Mean electrofishing capture efficiency
Coho salmon	39 (8.6)	26	0.83	34 (2.5)	31	0.98
Age-0 steelhead	140 (11.0)	119	0.89	122 (2.4)	120	0.99
$\geq$ Age-1 steelhead	24 (3.6)	19	0.79	39 (0.6)	36	0.86

TABLE 2. Linear regression models of fish abundance estimates derived from mobile PIT antenna (PIT) and electrofishing (EFISH) in 13 study pools in Devil's Gulch. The estimates were square-root transformed to standardize variances.

Species and age-class	Regression equation	$R^2$	$F_{1,11}$	$P$
Age-0 coho salmon	$\text{SQRT}(\text{PIT}) = 0.34 + 0.86 \text{SQRT}(\text{EFISH})$	0.80	43.76	<0.001
Age-0 steelhead	$\text{SQRT}(\text{PIT}) = 0.59 + 0.96 \text{SQRT}(\text{EFISH})$	0.91	118.29	<0.001
$\geq$ Age-1 steelhead	$\text{SQRT}(\text{PIT}) = -0.11 + 0.81 \text{SQRT}(\text{EFISH})$	0.50	11.14	0.007

abundance estimates explained a large portion of the variance in PIT antenna estimates for age-0 salmonids (i.e.,  $\geq 80\%$ ) and a moderate portion of the variance in age-1 and older steelhead PIT antenna estimates (Table 2). The slopes of the regression lines were not significantly different among species and age-classes (ANCOVA:  $F_{2,36} = 0.23$ ,  $P = 0.80$ ), nor did they differ from a slope of one (coho salmon:  $t_{24} = -1.23$ ,  $P = 0.23$ ; age-0 steelhead:  $t_{24} = -0.790$ ,  $P = 0.44$ ;  $\geq$ age-1 steelhead:  $t_{24} = -1.277$ ,  $P = 0.21$ ). The  $y$ -intercepts for coho salmon and age-0 steelhead were significantly greater than 0 (coho salmon:  $t_{24} = 2.02$ ,  $P = 0.05$ ; age-0 steelhead:  $t_{24} = 3.04$ ,  $P < 0.01$ ), but the differences were small, the effect being equivalent to less than one fish (Table 2). The intercept for age-1 and older steelhead was not significantly different from 0 ( $t_{24} = -1.29$ ,  $P = 0.20$ ). The coho salmon intercept was not significantly different from age-0 steelhead (least-squares means comparison:  $P = 0.16$ ) but was different from age-1 and older steelhead ( $P = 0.02$ ). The statistical similarity of regression lines for coho salmon and age-0 steelhead indicates that there was no between-species difference in the relationship between PIT antenna and electrofishing estimates for age-0 salmonids, but that age-0 salmonids had an elevated intercept relative to age-1 and older steelhead. Overall, the analysis of regression lines indicated that, besides slightly positive intercepts for age-0 salmonids, there was a roughly one-to-one relationship between estimates derived from the PIT antenna and electrofishing for all species and age-class strata.

We found no evidence that pool area (mean = 46.0 m<sup>2</sup>, range = 20.5–78.4 m<sup>2</sup>), cover area (mean = 10.0 m<sup>2</sup>, range = 0–34.3 m<sup>2</sup>), or cover complexity (mean = 47, range = 0–288) influenced the relationship between sampling methods for age-0 salmonids (Table 3). Likewise, those habitat variables did not influence the relationship between sampling methods for age-1 and older steelhead when all pools were considered (Table 3). However, one pool with a large wood jam had much greater

cover complexity than other sampled units (Figure 2). When this pool was removed from the analysis, there was a negative linear relationship between cover complexity and the difference in estimated abundances for age-1 and older steelhead ( $F_{1,10} = 8.89$ ,  $P = 0.01$ ,  $R^2 = 0.47$ ), indicating that electrofishing estimates of age-1 and older steelhead tended to be greater than those from PIT antennas in pools with higher cover complexity (Figure 2). Removing the high-complexity pool from the analysis did not change patterns related to any other species, age-class, or habitat variable.

Electrofishing was more labor intensive than surveys with the mobile PIT antenna. On average, electrofishing took a five-person crew 31 min per habitat unit. During electrofishing, the labor was divided between a three-person crew operating the electrofisher and netting fish while two people simultaneously processed captured fish. Mobile PIT antenna surveys took a two-person crew an average of 25 min per habitat unit.

## DISCUSSION

Our results demonstrate that surveys with mobile PIT antennas can provide habitat unit-scale estimates of tagged-fish abundance similar to those derived from electrofishing. We found strong concordance between methods for age-0 steelhead and coho salmon, and moderate concordance for age-1 and older steelhead. The analysis of regression lines indicated that there was a roughly one-to-one relationship between estimates derived from PIT antennas and electrofishing. These results suggest that PIT techniques can be adapted to reliably estimate juvenile salmonid abundance at the habitat unit scale in small streams. In the only other comparison of multiple-pass mobile PIT antenna and electrofishing of which we are aware, O'Donnell et al. (2010) also found that PIT antenna and electrofishing estimates were similar for juvenile Atlantic salmon

TABLE 3. Parameter estimates for the variables used to test for effects of stream habitat on agreement between mobile PIT antenna and electrofishing estimates in linear regression models. None of the variables were significant at  $\alpha = 0.05$  (df = 12).

Variable	Coho salmon			Age-0 steelhead			$\geq$ Age-1 steelhead		
	Coefficient	$t$	$P$	Coefficient	$t$	$P$	Coefficient	$t$	$P$
Pool area	-0.0069	-0.73	0.48	0.0045	0.78	0.53	0.0012	0.12	0.98
Cover complexity	-0.0005	-0.20	0.84	-0.0021	-1.56	0.14	-0.0035	-1.55	0.14
Cover area	-0.0008	-0.04	0.97	-0.0156	-1.43	0.18	-0.0282	-1.57	0.14

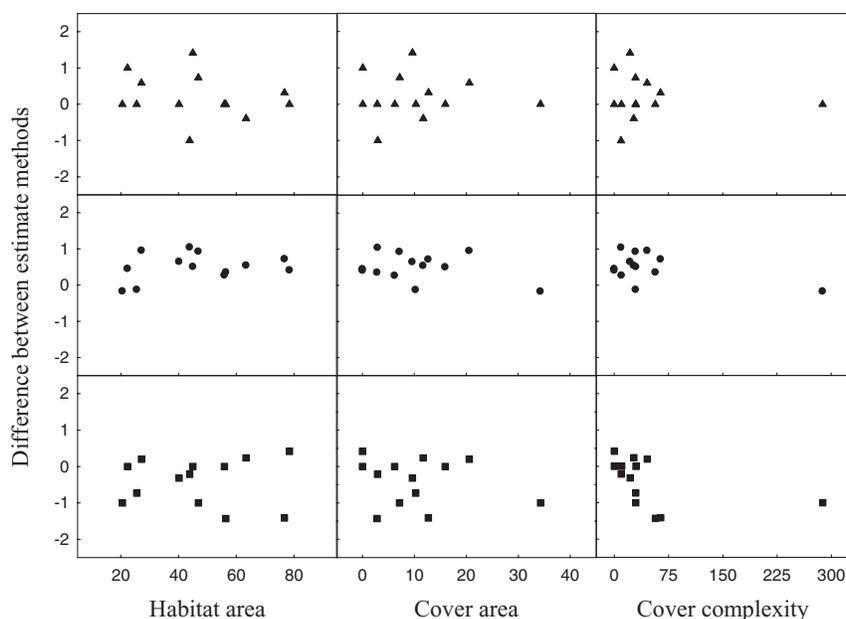


FIGURE 2. Agreement between mobile PIT antenna and electrofishing abundance estimates of age-0 coho salmon (triangles), age-0 steelhead (circles), and age-1 and older steelhead (squares) in relation to habitat area, cover area, and cover complexity in 13 study pools in Devil's Gulch. Positive values indicate that mobile PIT antenna estimates exceeded electrofishing estimates, negative values the reverse. The estimates were square-root transformed to standardize variances.

*Salmo salar* in a 60-m-long reach of a small Massachusetts stream.

Although we found no difference in the size of fish vulnerable to either gear type within each species and age-class stratum, we observed lower concordance between methods for age-1 and older steelhead than for age-0 steelhead and coho salmon, probably because of differences in body size among the age-class strata. Previous studies have found that detection probabilities with mobile PIT antennas are higher for age-0 salmonids than age-1 and older salmonids (Cucherousset et al. 2005; O'Donnell et al. 2010). This difference has been attributed to the greater swimming ability of larger fish (e.g., Thomas and Donahoo 1977), which may enable them to better evade passive relocation. Conversely, smaller fish are less likely to be captured during electrofishing because of their lower voltage gradient and possibly because they are less visible to netters (Reynolds 1996). Despite their increased swimming ability, larger fish may be more vulnerable to capture during electrofishing because of their increased voltage gradient. Consequently, the slight negative bias of PIT antenna estimates relative to electrofishing for older, larger fish is not surprising. Larger discrepancies between methods may occur when sampling populations with a larger range of fish size and age than we encountered in our study.

Pool area, cover area, and cover complexity did not influence the relationship between sampling methods for age-0 salmonids, but we found evidence that cover complexity influences estimates for age-1 and older steelhead. Passive integrated transponder antenna estimates for age-1 and older steelhead tended to be lower than electrofishing estimates in pools with higher cover

complexity. However, this linear trend only became statistically significant when a pool with exceptionally high cover complexity was removed from the analysis. With the highly complex pool removed from consideration, cover complexity explained nearly half of the variation in agreement between methods, suggesting that PIT antenna estimates of age-1 and older fish could be improved by incorporating measures of habitat complexity. However, improvements to  $\geq$  age-1 steelhead estimates may be minor since most discrepancies between the two methods were within two fish.

Techniques that do not require recapture of study animals for estimating population abundance have several potential advantages over capture techniques. First, information on fish movement, habitat use, and abundance can be collected with PIT antenna surveys in less time and with fewer personnel than are required for electrofishing. One trade-off, however, is that information on fish condition (e.g., length, weight) is not obtained from passive relocations. Second, because passive techniques do not require fish capture, they may be more suitable than more-common methods (e.g., snorkeling, electrofishing) during periods of poor water clarity. Third, and perhaps most importantly, because passive techniques minimize disturbance to study animals, they may allow more frequent sampling than might be desirable with capture techniques that can injure fish. Electrofishing is the most commonly used tool for estimating the abundance of stream fish, but potential lethal and sublethal effects of this technique on fish are well documented (e.g., Dalbey et al. 1996; Reynolds 1996; McMichael et al. 1998). While effects of electrofishing can be minimized by using

trained personnel and appropriate equipment settings for environmental conditions, repeated sampling over relatively short time intervals may result in unacceptable injury or altered behavior of study animals. This is an especially important consideration when studying physiologically sensitive species, small populations, or species listed under the U.S. Endangered Species Act (Nielsen 1998). Frequent sampling is often desirable, however, because ecological events, such as flood disturbance, can alter the local abundance of fish over short time scales (e.g., Harvey 1987; Nislow et al. 2002). The mobile PIT antenna methods described here may be well suited for the frequent sampling necessary to identify population responses to discrete ecological events such as floods or other disturbances.

A potential limitation of using mobile PIT antennas to estimate population abundance is that this method can only detect previously tagged fish. When information on total fish density is necessary to meet study objectives, complimentary sampling techniques will be necessary. In our study, the abundance of PIT-tagged fish was a good indicator of total fish abundance (including tagged and untagged fish) estimated by electrofishing within the study units, even though the units were open to movement between sample events. The estimated number of PIT-tagged fish was strongly correlated with the total number of tagged and untagged fish estimated from electrofishing ( $r = 0.94$ ,  $P < 0.001$ ). However, movement rates of untagged fish will undoubtedly be context dependent, and when immigration rates of untagged fish into the study area are high, estimates derived from mobile PIT antennas will underestimate total fish density. When precise estimates of total fish density are required, estimates based on passive detection should be calibrated against active capture techniques.

The results of our study should encourage further comparisons of PIT techniques and traditional sampling methods. Because our study units were open to movement between sampling events, we did not have a known number of fish with which we could compare our abundance estimates. Consequently, we relied on a "paired-gear" approach for comparing estimates derived from a mobile PIT antenna and standard multiple-pass electrofishing techniques (Peterson and Paukert 2009), focusing on the concordance between methods. However, electrofishing removal methods can underestimate true fish population abundances in many situations (e.g., Riley and Fausch 1992; Rogers et al. 1992; Peterson et al. 2004; Rosenberger and Dunham 2005) and do not necessarily constitute an unbiased standard for comparing mobile PIT antenna performance. In our study, electrofishing estimate bias is likely to be low because we conducted three removal passes (Riley and Fausch 1992), observed high detection and capture efficiencies, and used bias correction methods that reduce potential bias associated with jackknife estimators (M. S. Mohr and D. G. Hankin, Humboldt State University, unpublished). Nevertheless, improvements to future comparisons could be made by incorporating alternative study designs that were not logistically feasible here. Estimating population abundances after releasing known numbers of tagged fish

into enclosed areas would allow independent capture probability estimates for each gear type, thereby explicitly accounting for factors that may affect bias or selectivity of sampling gear (Peterson and Paukert 2009). This approach was taken by O'Donnell et al. (2010) in a series of trials using either known numbers of PIT tags encapsulated in vials placed in stream substrate or live PIT-tagged Atlantic salmon. They found that detection probabilities with mobile PIT tag antennas varied by observer, time of day (day versus night), fish age-class, and stream discharge. We standardized our sampling to minimize or eliminate variation in these factors, and they are not expected to have been a factor in our study. However, we suspect that other factors known to influence electrofishing capture probabilities, such as stream size and habitat complexity (Peterson et al. 2004; Rosenberger and Dunham 2005), are likely to influence PIT detection probabilities when sampling over a broader range of conditions than we encountered. Additional studies using known numbers of tagged fish should be conducted over a wider range of stream habitats to further evaluate the performance of mobile PIT antennas.

In summary, managers of imperiled species face the dilemma of needing to identify the mechanisms regulating populations while minimizing the impacts of sampling on the target species. The PIT tag techniques we describe can provide a wealth of information on fish movement, habitat use, and abundance with minimal handling stress after the initial capture event. While we strongly encourage local calibration of PIT tag estimates against traditional capture techniques, calibrations can be made in a subset of the habitats sampled, similar to two-phase sampling methods (e.g., Hankin and Reeves 1988) or paired-gear sampling (Peterson and Paukert 2009). Because passive relocation techniques with PIT antennas can reliably estimate fish abundance, frequent sampling of populations can occur during critical life stages and reveal the mechanisms controlling population abundance.

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