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Tag Type and Location-Dependent Retention Impart Varied Levels of Bias on Mark–Recapture Parameter Estimates

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Abstract

Population parameter estimates from mark–recapture studies are dependent on individuals retaining marks or tags. Therefore, tag retention estimates are needed for different tag types and anatomical tagging locations. Few studies have empirically quantified the bias from tag retention on fish population parameters that are derived from mark–recapture studies. We examined differences in retention between T-bar anchor tags and PIT tags as well as among

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four anatomical locations for PIT tags in Brown Trout *Salmo trutta* in a tail-water fishery in Arkansas, USA. We also estimated the relative bias of tag type and PIT tag location on apparent survival estimates from Cormack–Jolly–Seber models. Tag retention for the anchor tags was 15.1% lower than that for the PIT tags after 1 year and 46.1% lower after 4 years. Greater PIT tag retention resulted in less biased estimates of apparent survival for PIT tags (average -7.1%) than for anchor tags (average -37.8%). However, PIT tags that were placed in different anatomical locations had varying retention rates, so the degree of relative bias that was associated with their apparent survival estimates also varied. Inserting the PIT tags in the cheek or dorsal musculature provided the greatest retention for Brown Trout and may provide the least biased apparent survival estimates from future mark–recapture studies.

Mark–recapture is an important technique in fisheries management that provides quantitative estimates of fish population characteristics and dynamics, including abundance, growth, and survival (Quinn and Peterson 1996; Edwards et al. 1997). When combined with spatial information, recaptures of tagged individuals offer insight into the movement of individuals and population connectivity (Spurgeon et al. 2018). Mark–recapture studies typically require fisheries professionals to attach or insert tags in different anatomical locations (hereafter, “locations”; e.g., jaws, opercula, or dorsal musculature) under varying study designs (e.g., open or closed designs; Pine et al. 2012). An important assumption that is consistent across mark–recapture study designs is that the tags are retained in the locations where they are attached or inserted (Pine et al. 2012). Therefore, selecting the appropriate tag type and a location that maximizes tag retention is an important component of any mark–recapture study design.

The characteristics of tag retention studies may limit the application of previously derived estimates to novel mark–recapture settings. For instance, pilot studies to estimate tag retention may be biased by the study length (e.g., short-term retention rate) or study system (e.g., retention in holding tanks or aquaria) and may not be applicable to field settings (Dieterman and Hoxmeier 2009). Furthermore, ambiguity among tag retention studies can occur, resulting in a need for clarification regarding the appropriateness of tag types and locations in mark–recapture studies. Several tags have been used to identify aspects of salmonid life history, and mixed results have been reported regarding the retention

rates of different tag types and locations (Slatic 1976; Walsh and Winkelman 2004). In general, internal tags (e.g., PIT tags) are thought to have higher long-term retention than do external tags (e.g., T-bar anchor; Buzby and Deegan 1999; Rude et al. 2011). However, the anatomical placement of PIT tags may alter their retention and estimates may vary within a species or family. For instance, PIT tags that are placed in the abdominal cavity of Brown Trout *Salmo trutta* have lower estimated retention rates (<60% to >80%; Acolas et al. 2007; Dieterman and Hoxmeier 2009) than do those that are placed in the dorsal musculature of salmonids (95–98%; Prentice and Park 1985; Dieterman and Hoxmeier 2009). Retention from alternative PIT tag placement locations such as the cheek (83%; Prentice and Park 1985) lack sufficient study for the salmonid family but have been found to exhibit high retention in other species (e.g., >97% for Zander *Sander lucioperca*; Zakeš and Hopko 2013). To the best of our knowledge, retention from other locations has only been quantified once (e.g., 84% in the caudal peduncle; Prentice and Park 1985).

Mark–recapture theory posits that biased population parameter estimates will result when tag retention is not absolute (Arnason and Mills 1981). Moreover, there is limited empirical information regarding the magnitude of effect that reduced tag retention, due to a combination of tag type and location, may have on estimated population parameters, particularly among studies of freshwater fish populations. Therefore, the goal of this study was to assess the influence of tag type (i.e., T-bar anchor tag or PIT tag) and PIT tag location on long-term (i.e., 4 years) tag retention as well as on estimates of apparent survival for Brown Trout in a tailwater fishery. We selected T-bar anchor and PIT tags because they are both commonly used for tagging studies (Pine et al. 2012). T-bar anchor tags are externally visible, making them useful for studies that require angler returns. They require no specialized equipment to read and are lower cost relative to PIT tags, but they are generally more likely to be lost by the fish as study duration increases (Rude et al. 2011; Pine et al. 2012). Conversely, PIT tags are internal tags, which require specialized equipment to read and are more expensive than T-bar anchor tags, but they are generally less likely to be lost by the fish as study duration increases (Buzby and Deegan 1999; Pine et al. 2012). The objectives of this study were to (1) quantify the retention estimates of PIT and anchor tags and the retention of PIT tags in different locations using

instantaneous tag retention models and (2) assess the relative bias in the nonadjusted apparent survival estimates due to tag retention that was associated with tag type and PIT tag location.

Methods

Study site.—Greers Ferry Tailwater is an approximately 48-km segment of the Little Red River below Greers Ferry Dam in Arkansas (TMP and THP 2017). The hypolimnetic discharge from Greers Ferry Dam maintains a mean annual water temperature of approximately 10°C and creates suitable conditions for a trout fishery. The managed fishery consists primarily of Rainbow Trout *Oncorhynchus mykiss* and Brown Trout. Catchable size (279mm TL) Rainbow Trout are stocked year-round, with limited spawning activity (i.e., redd construction) observed for the species (Robison and Buchanan 1988). Brown Trout were stocked in the 1970s (TMP and THP 2017) and undergo annual spawning with consistent recruitment. Brown Trout are not stocked within the Greers Ferry Tailwater. This population is currently one of the most southern self-sustained populations of Brown Trout in the Northern Hemisphere.

Brown Trout sampling.—The Brown Trout were tagged with an individually numbered T-bar anchor tag (51mm TL, color marker length 32 mm; Hallprint) that was inserted between the dorsal pterygiophores, as well as a single PIT tag (12.5 mm, 134.2 kHz; BioMark) that was inserted into one of four anatomical locations by using a Biomark MK25 tag implanter. The PIT tag locations included the (1) abdominal cavity, (2) dorsal musculature, (3) cheek, and (4) caudal peduncle. The original objective of the study was to compare the retention of abdominally placed PIT tags to that of the T-bar anchor tags that were inserted between the dorsal pterygiophores. During the tagging period, we expanded this objective to include a comparison of retention for PIT tags that were placed in different anatomical locations. The decision to expand this objective during the tagging period resulted in more fish with PIT tags placed in the abdominal cavity than with PIT tags placed in the dorsal musculature, cheek, or caudal peduncle (**Table 1**).

Tagging was conducted from the top of JFK Special Regulation area to the bottom of Beech Island and at Rainbow Island between January

Table 1. Number of individuals initially tagged in 2013 (Tagged) and their associated total lengths (Lengths) and wet weights (Weights) during the tagging period. Also included are the numbers of individuals that were recaptured with a PIT tag or T-bar anchor tag still present from 2014 to 2017 and over the whole study (total) and the percentage of recaptured fish with a missing PIT tag or T-bar anchor tag (Observed Losses) during the tagging period (2013) and during recapture sampling (2014–2017). The results for the PIT tags have been summarized using both the four tagging locations and all of the locations for easy comparison with those for the T-bar anchor tags.

Tag type	Tag location	Tagged	Lengths (mm)	Weights (g)	Number of recaptures				Observed losses (%)		
					2014	2015	2016	2017	Total	2013	2014–2017
PIT	Abdominal cavity	494	185–700	66–6,300	21	10	11	2	44	8.3	12.0
PIT	Dorsal musculature	281	191–800	37–8,680	19	5	2	1	27	4.5	3.6
PIT	Cheek	280	264–843	200–8,760	13	8	4	3	28	0.0	3.5
PIT	Caudal peduncle	284	199–744	84–6,300	14	14	5	1	34	0.0	12.8
PIT	All locations	1,339	185–843	37–8,760	67	37	22	7	133	3.7	8.9
T-bar anchor	Dorsal pterygiophores	1,339	185–843	37–8,760	41	18	14	1	74	7.3	49.3

and October of 2013. Recaptures from the initial tagging period were recorded for use in instantaneous tag loss models. Recapture sampling for our mark–recapture model was conducted once at each of the original tagging locations, along with five additional fixed sites that were spatially distributed across the tailwater, during October each year from 2014 to 2017. At each site, 3–5 sequential 10-min electrofishing runs were conducted in a downstream direction. All of the sampling was conducted from fiberglass electrofishing boats that were equipped with Smith-Root 5.0 GPP electrofishing units (Settings: range = high, Amps \sim 1.0, pulses per second = 30, percent of = 100%). The samples were collected at night during periods of no generation by a single netter. The presence or absence of each tag type was recorded during each recapture event.

Angler removal of tags.—Anglers reported removing T-bar anchor tags from 53 fish during the study; however, they were not asked to do so (i.e., no tag reward system was in place). From this voluntary reporting it was determined that 31 of these fish were released back into the tailwater from 2013 to 2017. Four of these individuals were recaptured during our electrofishing surveys. These individuals were included in our analysis because angler reporting rates were not available. For these reasons, the retention estimates for the T-bar anchor tags should be treated as a joint estimate of angler and naturally induced tag loss. We assume that PIT tag retention was unaffected by angler removal, as no PIT tags were reported by anglers.

Data analysis.—Two instantaneous tag retention estimators were used to assess the differences in tag retention between the tag types and among the PIT tag locations. Instantaneous tag retention estimators were selected because discrete tag retention estimators may not track the tag loss process if the fish have been at large for extended periods (Spurgeon et al. 2020). The instantaneous tag retention estimates required information on cumulative days at large and whether or not the tags were retained. The first instantaneous tag retention model was

$$Q(t) = e^{-Lt}$$

where $Q(t)$ is the probability of a fish retaining a single tag if recaptured t days after release and L is a parameter describing the instantaneous

rate of tag shedding (Beverton and Holt 1957; Barrowman and Myers 1996; Adam and Kirkwood 2001; Vandergoot et al. 2012). The second tag retention model was

$$Q(t) = \alpha e^{-Lt}$$

where $Q(t)$ is the probability of a fish retaining a single tag if recaptured t days after release, α is a parameter that describes the probability of immediate tag loss, and L is a parameter that describes the instantaneous rate of tag shedding (Beverton and Holt 1957; Barrowman and Myers 1996). Both instantaneous models (i.e., with and without an immediate tag loss parameter) were generated by minimizing the negative of their log likelihoods, as is described in McCormick and Meyer (2018).

Cormack–Jolly–Seber (CJS) models (Cormack 1964; Jolly 1965; Seber 1965, 1982) were fit to the mark–recapture data to estimate apparent survival (ϕ) and capture probability (p). The recaptures were grouped by tag type for inclusion in the CJS models, which were run using all permutations of apparent survival and capture probability being constant or varying across years. The rjags package (Plummer et al. 2019) was used to fit the CJS models by using a Bayesian approach with Gibbs sampling in JAGS (Plummer 2003), using Program R (R Core Team 2016) as an interface. All of the models were fit using uninformative uniform priors. Each mark–recapture model consisted of three Markov chain–Monte Carlo (MCMC) chains with 10,000 burn-in samples and 50,000 post-burn-in samples at a thinning rate of 20. The MCMC chains were assessed for convergence postsimulation by using visual diagnostic plots and a Gelman–Rubin diagnostic test (convergence was confirmed at $\hat{r} \leq 1.1$; Albert 2009). Model likelihood was ranked using the deviance information criterion (DIC), with the lowest DIC value selected as the top model (Spiegelhalter et al. 2002; Albert 2009). This approach was selected because it has been used previously for model selection when multiple Bayesian mark–recapture models have been fit (Stewart et al. 2017; Haxton and Friday 2018). Parameter estimates were then summarized using the mean \pm SD for the top T-bar anchor tag and PIT tag models.

An additional five CJS models were compared to assess the influence of PIT tag location on apparent survival or capture probability. These models allowed apparent survival and capture probability to vary across

the PIT tag locations, be constant across years, or vary by year. These five models and the four models that were run prior for the PIT tag recapture data were compared using DIC, and the lowest value was selected as the top PIT tag location model (Spiegelhalter et al. 2002; Albert 2009). The parameter estimates for the top model for PIT tag location were summarized using the mean \pm SD.

To quantify the bias that was associated with tag type and location, the mean and SD were estimated for apparent survival using the top candidate models for tag type and PIT tag location. Survival was then adjusted to account for tag loss using the two different instantaneous retention estimates via the following equation:

$$\hat{\phi}_i^c = \frac{\hat{\phi}_i}{\hat{\theta}_i}$$

where $\hat{\phi}_i^c$ is the probability that a fish that is alive at time i survives and is available for capture at time $i + 1$, adjusted for tag loss (i.e., adjusted apparent survival); $\hat{\phi}_i$ is the probability that a fish that is alive at time i survives to time $i + 1$ (i.e., nonadjusted apparent survival); and $\hat{\theta}_i$ is the probability that a fish that is alive at time i retains its tag at time $i + 1$ (i.e., probability of tag retention; Arnason and Mills 1981). The standard deviation of adjusted apparent survival was estimated using,

$$SD(\hat{\phi}_i^c) = \frac{SD(\hat{\phi}_i)}{\hat{\theta}_i}$$

where $SD(\hat{\phi}_i^c)$ is the standard deviation of the probability that a fish that is alive at time i survives to time $i + 1$, adjusted for tag loss (standard deviation of adjusted apparent survival); $SD(\hat{\phi}_i)$ is the standard deviation of the probability that a fish that is alive at time i survives to time $i + 1$ (standard deviation of nonadjusted apparent survival); and $\hat{\theta}_i$ is the probability of tag retention.

We corrected our instantaneous tag loss estimates to account for individuals who may have lost both tags prior to adjusting the apparent survival estimates. This correction was necessary because neither of our instantaneous models accounted for individuals who lost both tags (Barrowman and Myers 1996; McCormick and Meyer 2018). Therefore, to accurately quantify the relative bias due to differences in retention, we

needed to account for the fact that individuals may have lost both tags. This was done in a manner similar to that in Meyer and Schill (2014); however, because we required an estimate of retention and not tag loss, we modified the formula to

$$\hat{\theta}_i = \widehat{Q(t)}_i \times \left[1 - \left(\frac{N_{Ai}}{2N_{AAi}} \right) \right]^2$$

where $\hat{\theta}_i$ is the probability that a fish that is alive at time i retains its tag at time $i + 1$, $\widehat{Q(t)}_i$ is the average of the instantaneous tag retention ($Q[t]$) estimates for the period i to $i + 1$, N_{Ai} is the number of fish observed with a single tag for the period i to $i + 1$, and N_{AAi} is the number of fish observed with both tags for the period i to $i + 1$. The second half of this equation allowed us to account for fish that were never recaptured due to the loss of both tags (Miranda et al. 2002). The discrete correction method was selected because squaring the instantaneous retention estimates (i.e., $Q[t]^2$) resulted in corrected apparent survival estimates that were not possible (e.g., $\hat{\phi}_i^c > 1$) and the data were not collected in a manner that allowed us to fit the time-dependent retention equation that was used by Miranda et al. (2002). Once adjustments were made to the apparent survival estimates for each tag type and PIT tag location using both corrected instantaneous retention rates, we compared the initial and adjusted mean \pm SD apparent survival estimates. These comparisons allowed us to determine the relative bias (i.e., difference between apparent survival and adjusted apparent survival estimates) that was associated with each tag type and each PIT tag location.

Results

A total of 1,339 individual Brown Trout were tagged in Greers Ferry Tailwater during 2013 (Table 1). Across all of the surveys, $\sim 11\%$ of the tagged Brown Trout were recaptured. The total number of recaptured fish decreased for both tag types and PIT tag locations between 2014 and 2017. By the end of the study, 59 more fish were recovered with PIT tags still present and anchor tags missing (Table 1). During the study, Brown Trout were recorded with T-bar anchor tags still attached 10–1,477 d after initial tagging and with PIT tags (at all locations) still

present 10–1,581 d after tagging. Recaptures varied across years for each PIT tag location, ranging from a high of 21 for the abdominal cavity in 2014 to a low of 1 for both the dorsal musculature and caudal peduncle in 2017 (Table 1). Brown Trout were observed with PIT tags still present in the abdominal cavity and dorsal musculature 15–1,581 d and 15–1,580 d after initial tagging, and they were recaptured with PIT tags still present in both the cheek and caudal peduncle 10–1,484 d after initial tagging.

Instantaneous tag retention estimates varied by tag type and PIT tag location. Models with or without the immediate tag loss parameter did not substantially change the tag retention estimates between tag types, except for PIT tags that were placed in the caudal peduncle. The instantaneous tag retention model with the immediate tag loss parameter for PIT tags that were placed in the cheek did not converge. Tag retention for anchor tags was 15.1% lower than that for PIT tags after 365 d (**Figure 1**). Tag retention differences between tag types increased through the length of the study, reaching a maximum average difference of 46.1% after 4 years. After 1 year, PIT tags that were placed in the cheek had the highest retention (98.2%; estimated with no immediate tag loss parameter). Tags that were placed in the dorsal musculature (95.7%), caudal peduncle (92.7%), and abdominal cavity (91.2%) also produced average retention estimates >90.0% for the first year (Figure 1). After the first year, the retention estimates began to diverge, and cheek tags had the highest retention (92.5%; estimated with no immediate tag loss parameter) at the end of the study, followed by PIT tags that were placed in the dorsal musculature (84.0%), abdominal cavity (72.9%), and caudal peduncle (52.5%). The instantaneous tag retention estimate for the caudal peduncle was much lower at the end of the study when an immediate tag loss parameter was included (24.0% versus 81.1%). Not surprisingly, the corrected average instantaneous retention over the entire study period was higher for PIT tags (86.6%) than for anchor tags (52.0%). The corrected average instantaneous retention estimates were highest for the PIT tags that were placed in the cheek (96.2%; with no immediate tag loss parameter), followed by the dorsal musculature (91.4%), abdominal cavity (82.1%), and the caudal peduncle (77.0%).

All of the MCMC chains reached convergence for all of the models based on visual inspection and Gelman–Rubin diagnostic tests (i.e., all

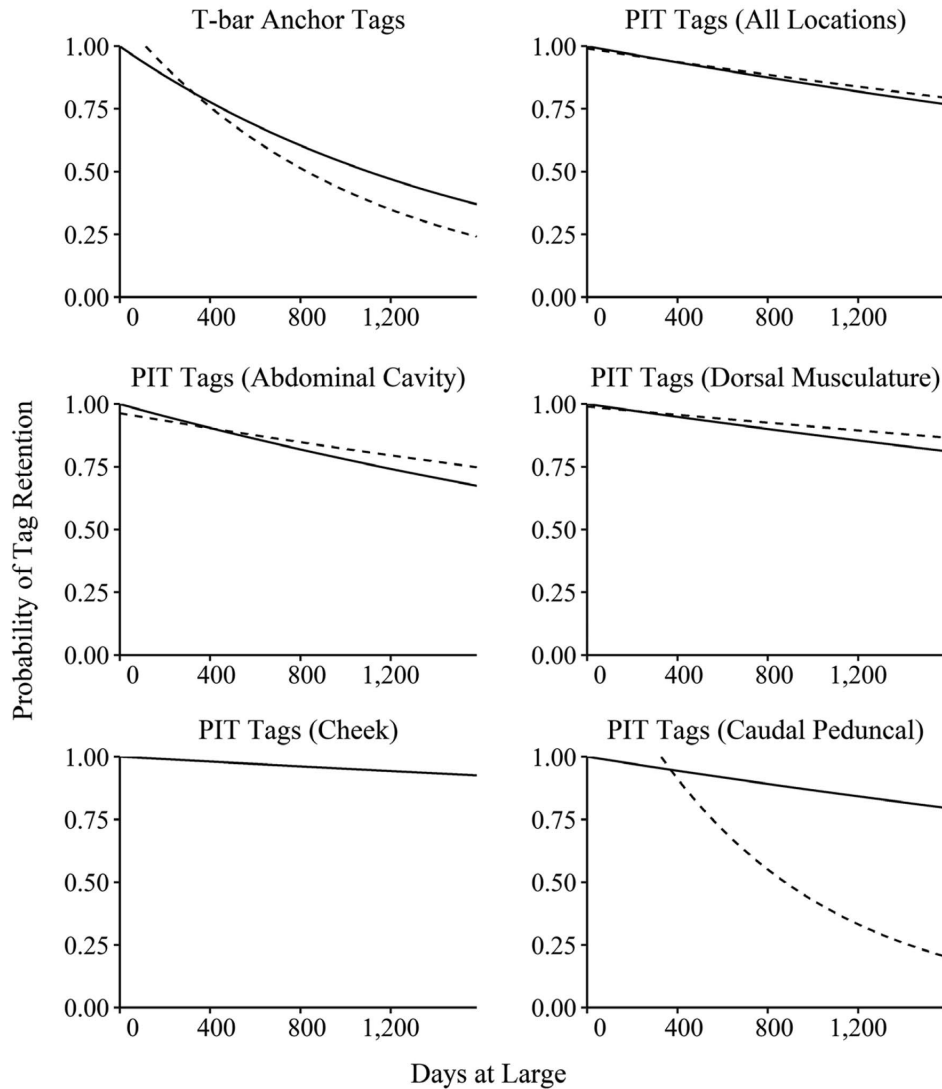


Figure 1. Instantaneous tag retention models including (dashed line) and excluding (solid line) an immediate tag loss parameter plotted against the days at large for T-bar anchor tags and PIT tags, along with each PIT tag location. We were unable to estimate parameters for the instantaneous model when the PIT tags were placed in the cheek.

$\hat{r} \leq 1.1$). The mean parameter estimates varied for the CJS mark-recapture models based on the anchor and PIT tag recaptures. Though capture probability estimates were close, they did not overlap (**Figure 2**). Conversely, apparent survival showed a high degree of overlap between the tag types (Figure 2). The top candidate model for both anchor tags

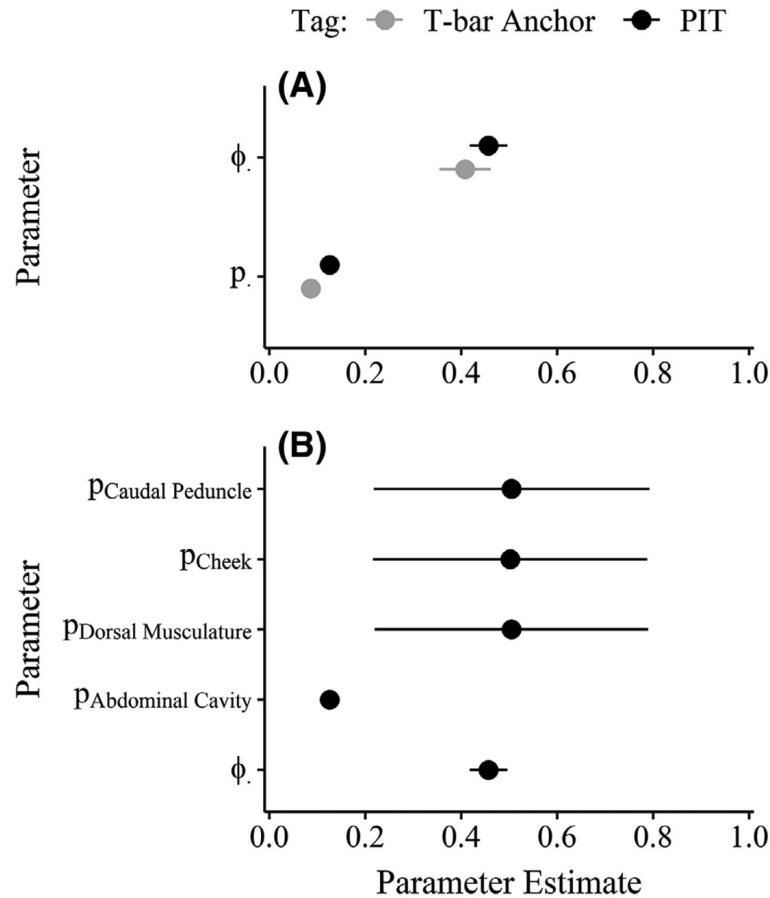


Figure 2. Parameter estimates (mean \pm SD) for apparent survival (ϕ) and capture probability (p) from the top-ranking Cormack–Jolly–Seber mark–recapture models using each **(A)** tag type and **(B)** PIT tag location. The subscripts denote whether the parameters were held constant across years (i.e., \cdot) or varied across PIT tag locations.

and PIT tags included time-constant apparent survival and time-constant capture probability (**Table 2**). The top candidate model for PIT tag location included time-constant apparent survival and location-dependent capture probability (**Table 3**). The capture probability (mean \pm SD) for the PIT tags that were placed in the dorsal musculature (0.51 ± 0.29), cheek (0.50 ± 0.29), and caudal peduncle (0.51 ± 0.29) were similar; however, the capture probability for the PIT tags that were placed in the abdominal cavity (0.13 ± 0.02) was noticeably lower (Figure 2).

Table 2. Model rankings based on DIC scores for each of the four Cormack–Jolly–Seber mark–recapture models ran for both tag types. Included are the number of actual parameters within the model and the number of effective parameters that was used to calculate DIC. The subscripts denote whether the parameters were held constant across year (i.e., \cdot) or varied across year (i.e., year).

<i>Tag type</i>	<i>Model</i>	<i>Model parameters</i>	<i>Effective parameters</i>	<i>DIC</i>
PIT	ϕ_{\cdot}, p_{\cdot}	2	60.90	1,189.87
PIT	$\phi_{\cdot}, p_{\text{year}}$	5	162.10	1,255.05
PIT	$\phi_{\text{year}}, p_{\text{year}}$	8	180.30	1,269.12
PIT	$\phi_{\text{year}}, p_{\cdot}$	5	173.10	1,270.47
Anchor	ϕ_{\cdot}, p_{\cdot}	2	22.40	735.9
Anchor	$\phi_{\cdot}, p_{\text{year}}$	5	83.00	766.3
Anchor	$\phi_{\text{year}}, p_{\cdot}$	5	77.50	771.9
Anchor	$\phi_{\text{year}}, p_{\text{year}}$	8	92.80	777.5

Table 3. Cormack–Jolly–Seber model likelihood rankings based on DIC for all of the PIT tag candidate models. Included are the numbers of actual parameters within the model and the numbers of effective parameters that were used to calculate DIC. The subscripts denote whether the parameters were held constant across years and across PIT tag location (i.e., \cdot), varied across year but were held constant across PIT tag location (i.e., year), or varied across PIT tag location but were held constant across year (i.e., location).

<i>Model</i>	<i>Model parameters</i>	<i>Effective parameters</i>	<i>DIC</i>
$\phi_{\cdot}, p_{\text{location}}$	5	57.50	1,186.82
$\phi_{\text{year}}, p_{\text{location}}$	8	59.80	1,188.70
$\phi_{\text{location}}, p_{\cdot}$	5	60.50	1,189.74
ϕ_{\cdot}, p_{\cdot}	2	60.90	1,189.87
$\phi_{\cdot}, p_{\text{year}}$	5	162.10	1,255.05
$\phi_{\text{location}}, p_{\text{year}}$	8	165.50	1,258.57
$\phi_{\text{year}}, p_{\text{year}}$	8	180.30	1,269.12
$\phi_{\text{year}}, p_{\cdot}$	5	173.10	1,270.47
$\phi_{\text{location}}, p_{\text{location}}$	8	188.60	1,278.02

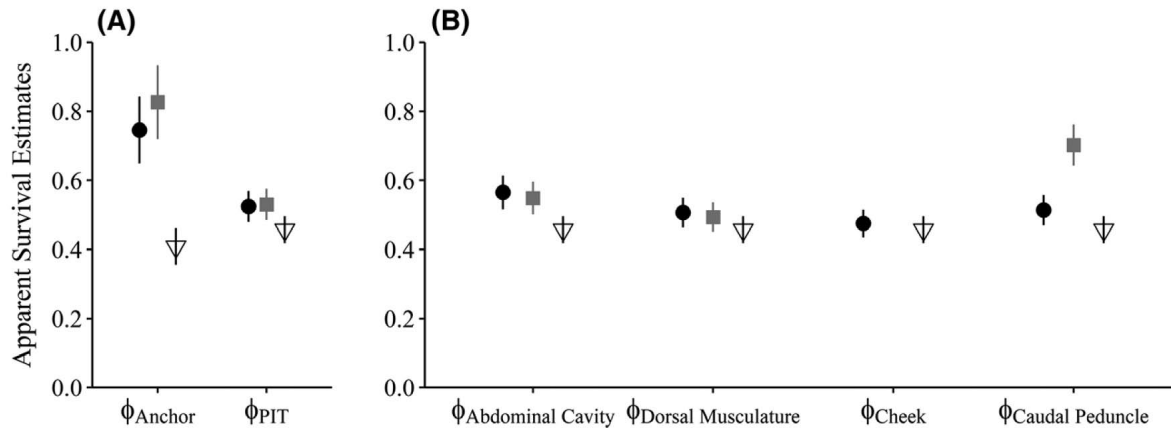


Figure 3. Nonadjusted apparent survival (ϕ [mean \pm SD]) from the top-ranking Cormack–Jolly–Seber mark–recapture model for **(A)** both tag types and **(B)** each PIT tag location (white triangles). Also depicted are the adjusted apparent survival (ϕ) estimates, which were adjusted using the instantaneous tag retention models that included (gray squares) and excluded (black circles) an immediate tag loss parameter.

The model with constant apparent survival across years was selected for both tag types and each PIT tag location to estimate the relative bias of the population parameter estimates when tag retention was not considered. To account for varying retention between periods, the average instantaneous retention estimates were used to correct apparent survival. Nonadjusted apparent survival was, as expected, consistently lower than adjusted apparent survival regardless of tag type or PIT tag location (**Figure 3**). The negative bias in nonadjusted apparent survival when compared with adjusted apparent survival was larger for anchor tags (–37.8%) than for PIT tags (–7.1%). The bias—using instantaneous tag retention models with and without an immediate tag loss parameter—that was associated with the PIT tag locations was –1.8% for the cheek, –4.3% for the dorsal musculature, –10.0% for the body cavity, and –15.1% for the caudal peduncle. The bias that was associated with the apparent survival estimate for the caudal peduncle was similar to that for the other tag locations based on the instantaneous model without the immediate tag loss parameter (–5.7%) but different for the instantaneous model with the immediate tag loss parameter (–24.5%).

Discussion

Based on the results from the instantaneous tag retention models, tag retention of PIT tags was greater than that of T-bar anchor tags in Brown Trout. Although no other long-term comparisons of these two tag types were available for Brown Trout, these findings agree with results from Arctic Grayling *Thymallus arcticus* (Buzby and Deegan 1999). Lower long-term retention of T-bar anchor tags relative to PIT tags has also been observed for Muskellunge *Esox masquinongy* (Rude et al. 2011), Gulf Sturgeon *Acipenser oxyrinchus desotoi* (Clugston 1996), and Common Snook *Centropomus undecimalis* (Boucek and Adams 2011). Our results support the idea that PIT tags may be more suitable for long-term mark–recapture studies.

The tag retention estimates for PIT tags (in all locations) fell within the range from published literature for Brown Trout (i.e., 56–98%; Prentice and Park 1985; Acolas et al. 2007; Dieterman and Hoxmeier 2009; Richard et al. 2013). However, our results suggest that retention will vary based on the location where PIT tags are inserted. We found that the PIT tags that were placed in the cheek or dorsal musculature had the highest estimated average instantaneous retention (both > 90%) relative to those that were placed in the abdominal cavity and caudal peduncle. Dieterman and Hoxmeier (2009) also documented higher PIT tag retention for dorsal musculature placement (95%) when compared with tags that were placed in the abdominal cavity (56%). Interestingly, our results are within the range that has been reported for age-0 Brown Trout and juvenile Coho Salmon (80–89%; Prentice and Park 1985; Acolas et al. 2007; Richard et al. 2013). Based on this, we hypothesize that the lower retention that was observed by Dieterman and Hoxmeier (2009) may have resulted from inserting the tags into the abdominal cavity posterior to the pelvic fins. Retention estimates for PIT tags that were placed in the cheek were higher than those that have been observed for Coho Salmon (80%; Prentice and Park 1985), falling between the ranges reported for Muskellunge (i.e., 90–92%; Jennings et al. 2009; Younk et al. 2010) and Zander *Sander lucioperca* (97–100%; Zakęs and Hopko 2013). Therefore, PIT tags that are placed in the cheek appear to have relatively high retention and may be a suitable method for monitoring Brown Trout populations. However, our instantaneous PIT tag retention model with an immediate tag loss parameter did not converge for cheek placement

of the PIT tags. Due to this, we suggest that future studies that use PIT tags that are placed in the cheek of Brown Trout also assess long-term retention. Our instantaneous retention estimates without an immediate tag loss parameter were 6% lower than that observed for Coho Salmon (84%; Prentice and Park 1985); however, when the immediate tag loss parameter was included, they were approximately 60% lower. We believe this discrepancy is the result of the immediate tag loss parameter representing the data poorly (see McCormick and Meyer 2018) and discuss this in detail below. Regardless, we still observed relatively poor retention for tags that were placed in the caudal peduncle when an immediate tag loss parameter was not included and therefore do not recommend placing tags in this location.

Anglers reported removing T-bar anchor tags during the study despite the fact that no tag reward system was in place. Despite this, our average instantaneous retention estimates after 2 years for T-bar anchor tags fell within the range (66–85%) reported for Brown Trout by Brewin et al. (1995). Furthermore, they were similar (immediate tag loss parameter included), or higher, after 3 years compared to 41%, as estimated by Nuhfer et al. (1996). Given that anchor tag removal by anglers is not addressed in the aforementioned studies, this agreement suggests that either our retention estimates were relatively unaffected by any additional angler removals of anchor tags or angler removal of external tags was unknown and unaccounted for in prior studies on Brown Trout. We are unaware of any retention or bias studies that specifically note and account for anglers removing external tags; however, managers and researchers should note that angler behavior may influence their estimates of retention for external tags. The amount of influence that angler removal has on retention estimates for external tags warrants further study.

The apparent survival estimates for both tag types and all PIT tag locations were negatively biased due to tag loss. Tag loss is known to influence parameters in mark–recapture studies (Arnason and Mills 1981; McDonald et al. 2003; Pollock et al. 1990); however, the magnitude of this bias has received little attention in population assessments of freshwater fish that use mark–recapture. Our findings indicate that apparent survival was negatively biased 2.0% when tag retention averaged 96.0%. Furthermore, our results suggest that as average tag retention went below 90.0%, apparent survival estimates were negatively biased

over 5.0%. This increased to over 11.0% if average tag retention was below 80.0%. There was greater negative bias in the apparent survival estimates for fish with PIT tags that were placed in the caudal peduncle, which was influenced by the low tag retention rate that was estimated from the instantaneous model with an immediate tag loss parameter. We suggest that this occurred because no tag loss was observed for this location in 2013, followed by relatively high tag loss being observed from 2014 to 2017. Further support stems from the fact that we were unable to attain output for the instantaneous model with an immediate tag loss parameter when using data from the PIT tags that were placed in the check (i.e., the other location with no observed short-term tag loss). Given how different the trend line from this instantaneous estimator is relative to that of the model without the immediate tag loss parameter, it is possible that the immediate tag loss parameter represented the data poorly (McCormick and Meyer 2018). An instantaneous tag retention model with an immediate tag loss parameter may not always be the most appropriate model for describing the tag loss process and could result in a possible overcorrection of the population parameter estimates.

Relying solely on anchor tags or PIT tags in locations with less retention would have resulted in adjusted apparent survival estimates that likely did not reflect the actual survival of the tagged population. For example, consistency in the adjusted apparent survival estimates from the tag types and locations with greater retention provided a level of confidence in the adjusted parameter estimates. When we compared the estimates for the tags and locations with greater retention with those with lower retention, we saw a noticeable difference in the corrected estimates. Due to this observed difference, we hypothesize that even adjusted apparent survival estimates may not accurately represent the population if retention is low. Although this phenomenon warrants further study, our results suggest that the use of tags or locations with retention $\leq 70\%$ may impart undo bias into even corrected population parameter estimates. This elucidates the necessity of using tags and tag locations that maximize tag retention to the greatest extent possible.

The similarity of the nonadjusted parameter estimates among the CJS models may demonstrate the robustness that the capture probability parameter provides to apparent survival estimates for open-population models (see Cormack 1964; Jolly 1965; Seber 1965, 1982). It appears that the CJS models accounted for the varying capture probability

that resulted from different tag retention between the tag types and locations. For example, the initial apparent survival estimates for anchor and PIT tags were similar but tag retention was much lower for anchor tags than for PIT tags. The CJS model produced similar apparent survival estimates by lowering the estimated capture probability for anchor tags. A similar example occurred among the PIT tag location models. The most likely model based on DIC showed that apparent survival was equal across tag locations but capture probability was not. Since we estimated differences in retention at various PIT tag locations, this is another example of the CJS model producing a similar apparent survival estimate by varying capture probability. Interestingly, only the PIT tags that were placed in the abdominal cavity had a different capture probability with a credible interval that did not overlap with the others. These findings disagree with the results from our retention estimators, which suggested that all of the tag loss rates were different. The contrasting results may be an artifact of the different number of tags within each location, as nearly double the tags were placed in the abdominal cavity as in other locations (i.e., initial variation in treatments; Hurlbert 1984).

Using tags with poor retention (i.e., T-bar anchor tags) or placing PIT tags in lower-retention areas (i.e., the abdominal cavity or caudal peduncle) can result in underestimates of apparent survival. Using biased demographic data that results from poor tag retention will bias the results that are obtained from any management software or model (e.g., Ricker, Beverton–Holt). This will in turn inaccurately represent the fishery and could lead to detrimental or unnecessary regulation. Therefore, we recommend that tag retention always be monitored during a mark–recapture study and that it be accounted for by adjusting the estimates. At the same time, not all mark–recapture data sets will have information regarding tag retention. If managers or researchers are unable to account for tag retention estimates, an open-population model may be able to account for some of the bias in the parameter estimates due to tag retention by varying capture probability. Finally, our results show that even tags that are thought to be permanent or semipermanent, such as PIT tags, are susceptible to tag loss and can impart bias on parameter estimates—particularly if they are not applied in appropriate locations. Studies that assess the population characteristics and demographic rates

of Brown Trout by using mark–recapture may benefit by using PIT tags that are placed in the dorsal musculature and avoiding the use of PIT tags in the caudal peduncle and body cavity as well as anchor tags for extended periods. However, study design, or objectives, may not allow the use PIT tags or PIT tag placement in the aforementioned locations. Therefore, understanding the objectives of the study and the design for meeting those objectives would be critical when selecting an appropriate tag type or PIT tag location.

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