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Growth, survival, and tag retention of steelhead trout (*Oncorhynchus mykiss)* and its application to survival estimates

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Abstract Steelhead trout, *Oncorhynchus mykiss*, are known to expel acoustic tags which can negatively bias population survival estimates. Tag burden may also affect the development and behavior of smolts, thereby impacting the results of population and behavioral studies. We monitored the growth, condition, and tag expulsion rate of steelhead trout in similar-sized individuals and used these data to adjust survival rates from an acoustic telemetry study conducted in the Sacramento River. Eighty fish were surgically implanted with tags—40 with cylindrical tags of 9 mm diameter and 21 or 24 mm length (V9, Vemco Ltd) and 40 with a 7 mm diameter and 20 mm length tag (V7, Vemco Ltd)—to examine the impact of tag size on peritoneal retention and survival rate of juvenile steelhead trout. A total of 20 % (16/80) of all tags were expelled by smolts during the 143-day study. Ten V9 tags were expelled between day 18 and day 66. Six V7 tags were expelled between day 21 and day 143. A statistical difference was found for retention rate by surgeon even though the surgeons were of equal experience and received the same training. There were no significant differences in the tag retention rate in relation to the tag/body weight ratio, or in growth (weight or fork length) among the control, V7 or V9 treatment groups over the duration of the study. All individuals survived throughout the experiment. Two methods were used to adjust the survival estimates of an acoustic telemetry data set from the Sacramento River based on the tag retention study. First, a simple individual censorship approach in Program MARK was utilized and next ATLAS, a software program designed to compensate for bias in survival estimates caused by tag failures was used. The results of the adjusted survival estimates were not significantly different from the unadjusted rates suggesting that it may be more important to focus on improving surgical techniques to reduce tag expulsion rather than adjusting survival estimates dependent on the study. The surgical techniques utilized in this study did not have significant impacts on the growth rates of either of the tag treatment groups compared to the control. However, tag retention was an issue regardless of the size and weight of the implanted tag and the size of the steelhead.

Keywords *Oncorhynchus mykiss* · Tag retention · Surgical procedure · Telemetry · Survival

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Introduction

Miniature acoustic tags have opened new areas of research for fisheries scientists, particularly among salmon researchers. These tags allow researchers to gather more detailed data on the survival, movement, and behaviors of tagged fish than previous techniques. Coded wire tags or other mass marking methods often require having to sacrifice or handle a fish post-release. Because of these advantages, researchers have relied upon acoustic tags in a growing number of investigations. Acoustic tag studies have been conducted to estimate survival (Melnychuk et al. 2007; Chittenden et al. 2008) and route selection of juvenile salmonids in rivers (Perry et al. 2010), estuaries (Moore et al. 1995), and the coastal ocean (Welch et al. 2004; Chittenden et al. 2010) throughout the Pacific Northwest (McMichael et al. 2010).

The shift from coded wire tags to acoustic tags has not diminished the need to assess tag retention rates or the physiological impact of the tag/tagging procedure. Several tag effect studies and reviews (Jepsen et al. 2002; Bridger and Booth 2003) have been conducted on various species, such as pumpkinseed, *Lepomis gibbosus* (Stakenas et al. 2009), mullet, *Myxus petard* and *Mugil cephalus* (Butler et al. 2009), largemouth bass, *Micropterus salmoides* (Cupauto et al. 2009), carp, *Cyprinus carpo* (Daniel et al. 2009), sea bass, *Dicentrarchus labrax* (Arnas et al. 2003), and other marine fish (Fabrizio and Pessutti 2007; Seitz et al. 2010) as one species is not an adequate surrogate for another even if they are closely related (Ebner 2009). A number of studies on salmonids have examined tag and surgical procedure impact on smolt growth (Greenstreet and Morgan 1989; Lucas 1989), swimming performance (Zale et al. 2007), behavior (Moore et al. 1990; Wagner and Stevens 2000), and predator avoidance (Anglea et al. 2004). Researchers have primarily utilized tag length to body length ratios or tag weight to body weight as standardized metrics when researching tag impacts. A range of maximum tag to body weight ratios have been recorded for salmonids including conservative estimates of 2 % (Winter 1983) and 6.7 % (Anglea et al. 2004) to more liberal estimates of <7.3 % and <11.5 % for 7 mm and 9 mm diameter tags, respectively, for Chinook salmon smolts, *Oncorhynchus tshawytscha* (Rechisky and Welch 2009). The tag to body ratio has also been suggested to be as high as 16 % of the fork length (FL) to tag length and 8 % of the mass for Atlantic salmon, *Salmo salar* (LaCroix et al. 2004), and 7-8 % for pre-smolt coho salmon, *O. kisutch* (Chittenden et al. 2009).

In addition to the physical burden added by the surgically implanted tag there is also the potential for smolts to shed or expel surgically implanted tags (Summerfelt and Mosier 1984). Although other studies have considered the impact of surgically implanting smolts with acoustic tags and tag retention rates in relation to body size ratios (Moore et al. 1990; Welch et al. 2007), it is equally important for researchers to understand the impact of applying a tag retention rate to a study population (Nelson et al. 1980; Wetherall 1982; Conn et al. 2004).

It is important to provide an accurate representation of tag retention rate and potential impact of the tagging procedure when conducting examinations of individual fish survival and behavior. Failure to attend to these components may inadvertently or unintentionally violate assumptions of Cormack-Jolly-Seber (CJS) models (Cormack 1964; Jolly 1965; Seber 1965) and lead to erroneous interpretation of the data. Mark recapture experiments have been conducted using various marking methodologies throughout the years such as CWT (Baker et al. 1995), PIT tags (Clarke et al. 2011), visible implant elastomers (Jensen et al. 2008), acoustic tags (LaCroix and McCurdy 1996), and radio tags (Spicer et al. 1995). Regardless of the study objective (e.g., growth, survival, or movement rates), retention of the mark given to the individual is crucial to minimize result bias, and thus, numerous studies have been conducted to estimate tag loss or failure rates (Xiao 1996; Zhou 2002; Brenden et al. 2010; Younk et al. 2010).

CALFED, a state-federal program assessing management options for the Sacramento-San Joaquin Delta in California's Central Valley, funded a study to examine the movements and survival of juvenile steelhead trout and Chinook salmon through the use of acoustic telemetry. Several other agencies working on other rivers in the Sacramento River watershed also began studies examining the survival and movement of steelhead (Del Real et al. 2011; Steel et al. 2012; Michel et al. 2012). More than 15 government, academic, and private groups collaborated to put together an extensive array of acoustic receivers to monitor the survival and movement patterns of various fish species. The CALFED study intended to examine reach-specific rates of survival and movement to identify potential problematic reaches for smolts. In acoustic tagging studies where smolts are released into a river, it is often difficult to determine whether a smolt has chosen to remain in freshwater (residualized) rather than migrate to sea, been consumed by a predator, or shed the tag. Each of these issues becomes significant when making survival estimates and has the potential to bias results and incorrectly identify a reach as an area with lower survival.

The purpose of the study was to determine: 1) the tag retention rate of steelhead trout smolts, 2) the impact of the tagging procedure on the growth and survival of tagged individuals, and 3) the effect of tag retention rates on estimates of survival. We considered tag size, smolt size, suture material, and surgeon when examining tag retention and the tag retention rate was applied to the population under two different methodologies.

Materials and methods

Three hundred juvenile steelhead trout, ~80 mm FL, were taken from Coleman National Fish Hatchery (CNFH) in Anderson, California and transported to the Center for Aquatic Biology and Aquaculture (CABA) on the University of California, Davis, campus. At CABA, the smolts were reared to a size of 180–225 mm FL over a period of 3 months. Smolts were similar to the size of individuals being implanted with acoustic tags at CNFH to monitor movement and survival in the Sacramento River for the larger CALFED study.

One hundred twenty steelhead were separated into three primary treatment groups of forty individuals each: 1) untagged control, 2) tagged with V7 (V7-4 L-R64K, with an average off time 60 s, power output 136 dB, 7×22.5 mm, 1.8 g in air, Vemco Ltd Halifax, Nova Scotia, Canada), and 3) tagged with V9 (V9-2 L-R64K, with an average off time 30 s, power output 146 dB, 9×29 mm, 4.7 g in air, Vemco Ltd.) (Table 1). Monodox 4-0 violet FS-2 (Absorbable) and Supramid® II 4-0 white FS-2 (non-absorbable) suture material was used in equal proportions for each of the tag treatment groups in order to asses differences in healing and suture retention of tagged smolts. While some studies support tagging individuals with larger tags, we chose to implant only smolts with acoustic tags if their tag/body weight ratio was less than 5 %. Smolts were starved for 24 h prior to the surgical operation. Next, smolts were captured from the large round 4 m diameter by 1 m depth tank and moved into the tagging facility adjacent to the tanks. Each smolt was anesthetized with a 90 mg/l MS-222 which was buffered with 360 mg L^{-1} sodium bicarbonate. Once a smolt was fully anesthetized, defined as having lost equilibrium/reflexes/re-activity with slow opercular movements, stage 4/5 (Summerfelt and Smith 1990), it was removed from the anesthesia, weighed (g), measured (FL in mm), photographed, and the condition of its eyes, fins, and scales were qualitatively scored as good, fair, or poor so that any change in the physical condition of the smolt could be documented during the course of study. After these procedures were completed, each smolt was placed in the surgical cradle where a lower dosage of 30 mg L^{-1} MS-222 buffered by 120 mg L^{-1} sodium bicarbonate was pumped over its gills and the individual was operated upon. Surgical procedures were completed by one of two surgeons with the same training and prior experience working with juvenile salmonids. Steelhead smolts in the two tag treatment groups were placed in the surgical cradle where a small incision of ~10 mm in length was made parallel to and just off the ventral midline anterior to the pelvic girdle. The tag was inserted vertically and positioned horizontally within the peritoneal cavity of the individual. The incision was closed using two simple interrupted stitches with one of the two suture materials. A Passive Integrated Transponder (PIT) tag was inserted into each individual. PIT tags are small tags with electronic microchips that encode a unique ID that can be read by handheld units (Gibbons and Andrews 2004). Acoustically tagged fish received their PIT tags through the same incision where the acoustic tag was

Table 1 Average sizes and ranges of three tag treatment groups of 40 fish each (control, V7, V9) at the beginning of the study

	Weight (g)	Range	FL (mm)	Range	% Body Weight	Range
Control	107.8	83.4–142.0	204	191–225	N/A	N/A
V7	108.0	77.0–140.6	203	183–222	1.7	1.3–3.0
V9	111.7	71.0–138.3	205	185–218	2.3	2.0–4.4

implanted. This enabled us to identify all individuals quickly throughout the course of the study. The amount of time each individual spent in the anesthesia, in surgery, and took to recover from the surgery were all recorded. Anesthetic and surgical bath water were frequently replaced during surgical procedures. The temperature and dissolved oxygen levels were closely monitored with a YSI.

Smolts in the control group were anesthetized and placed in the surgical cradle in the same manner as the smolts implanted with the acoustic tags; however, only a PIT tag was injected into the smolt rather than having an acoustic tag implanted.

Post surgery we held smolts in a small recovery tank (1 m diameter x 0.5 m depth) where a spray bar created a flow of fresh aerated water. Smolts recovered quickly, and were subsequently transferred to the large outdoor holding tank for the duration of the study. The holding tank was visually inspected for shed tags on a daily basis. The smolts were monitored over a period of 143 days. Each subject was subsequently removed from the holding tank 31, 64, 101, and 143 days post surgery for examination. Smolts were anesthetized prior to examination. The mass, FL, and condition of the eyes, fins, scales, the number of sutures present, the presence or absence of inflammation, and tag bulge were all recorded. Inflammation was scored on a scale of 0–2, with 0, 1, and 2 meaning no inflammation, light inflammation, and high inflammation, respectively. Light inflammation was classified as little to moderate swelling and grayish coloration, and high inflammation was classified as prominent swelling and red appearance near the incision/suture site. Tag bulge of smolts implanted with acoustic tags was scored on a scale of 0–3 with 0) representing no tag bulge, 1) tag bulge is slightly noticeable, 2) bulge is highly noticeable, the shape of the tag is noticeable in the body wall or the incision site, and 3) tag bulge is highly noticeable and is protruding from the fish, a discoloration or necrosis may be associated with the bulge (Fig. 1).

Data analysis

Our analyses focused on three areas: Tag retention, the impact of the surgical procedure, and the impact of applying the tag retention rate from the captive steelhead study to a data set of acoustically tagged juvenile steelhead trout. When considering tag retention we examined the effect of suture material (absorbable/non-absorbable), tag size (V7/V9), and surgeon. The impact of the surgical procedure was assessed by difference in growth rate between groups. We defined our significance level as $P< 0.05$ for all statistical tests.

Tag retention

We used the Fisher's Exact test to examine differences in the two tag treatments tag retention rates. The Fisher Exact test uses a contingency table and is typically utilized when sample size is small and expected numbers are low. It operates in the same way as a Chi square test. We also used ANOVAs to examine the impact of initial FL of smolts on tag retention by classifying individuals into one of three groups (<200 mm, 200–209 mm, and >209 mm), date of tag loss by size group, and finally the date of tag loss and corresponding number of sutures present. A *t*-test was used to test for differences in mean date of tag loss between the two tag treatment groups and tag/body weight ratio of smolts that retained their tags for both the V7 and V9 treatment groups. An ANOVA was completed to look at the date of tag loss and number of sutures present. We also used a Chi square test to test for differences in the tag retetention rate of fish implanted by the two surgeons.

Impact of the surgical procedure

We examined several aspects of the surgery post operation. The primary goal was to assess differences in growth or healing based on the near monthly examinations. An ANOVA was used to verify that there was not a significant difference in the FL or weight in any of the treatment groups. Changes in FL and weight over the study duration were tested with an ANOVA to determine if there were significant differences between the control, V7, or V9 treatment groups. In addition to examining the growth of smolts from FL and weight we also calculated relative daily growth rate (RDGR) following Kaemingk et al. (2011). We used an ANOVA to determine if there were differences in RDGR of the three treatments. We also used a *t*-test to examine differences between the duration of suture retention by material, the impact or retention of the suture on inflammation, and the proportion of fish encapsulating their tag by the end of the study. An ANOVA was used to elucidate any differences in the

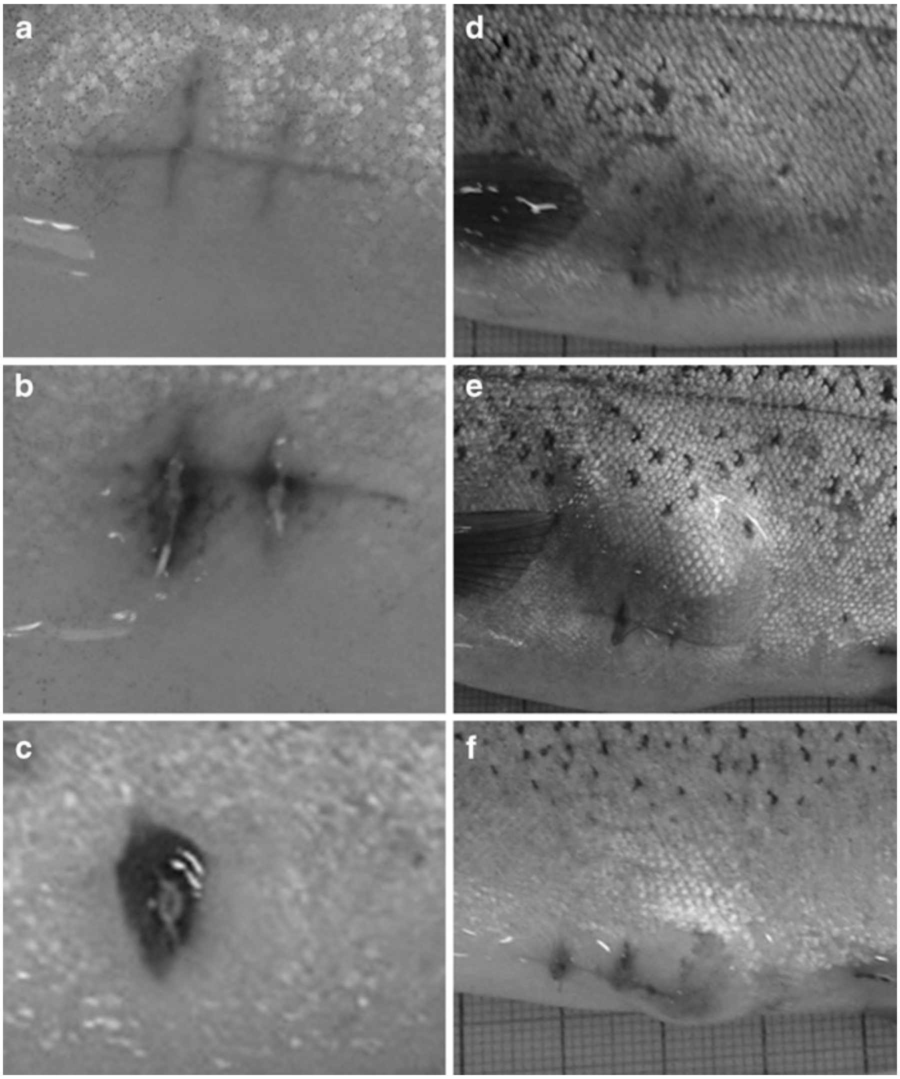


Fig. 1 From top to bottom on the left hand side are examples of how the level of inflammation an individual is exhibiting would be scored: **a** inflammation level of 0 as there is no sign of irritation or redness, **b** inflammation level of 1, there is redness and mild irritation around the incision, and **c** level 2 inflammation, there is a high degree of irritation the tissue around the incision is a red/gray coloration. The photos on the right from top to bottom **d**-**f** show the different levels of observed tag bulge during the study: **e** tag bulge of 1, there is small bump beginning to form/is slightly visible, tag bulge of 2, the tag is clearly visible in the body wall or near the incision, and tag bulge of 3. The tag is protruding from the individual. There may be a loss of scales r necrosis near the potential expulsion site

time in anesthetic and recovery time of all treatment groups. A *t*-test was used to test for differences in the surgical procedure times for the V7 and V9 treaments.

Survival estimates and adjustments

In order to apply a tag retention rate to survival estimates two main assumptions must be made to deal with potential CJS assumption violations: 1) all tag shedding occurs in a specified period of time, applied as a proportional loss over time, and 2) smolts that shed their tags behave the same as smolts who retain their tags. For *O. mykiss*, which can either stay in freshwater (residualize) or go to sea (become a steelhead), this means individuals that will shed their tag have the same probability as individuals that retain their tag to residualize or out-migrate from the system.

We used Program MARK (White and Burnham 1999) to complete a Cormack-Jolly-Seber (Cormack 1964; Jolly 1965; Seber 1965) analysis and adjust the survival estimates with the tag retention rate data gathered in this study. Program MARK survival estimates are based on maximum likelihood estimates and takes detection probability into account when making survival estimates. A data set of 50 individuals from an acoustic tag study conducted in 2008 with steelhead trout from CNFH was used for all survival estimates (Sandstrom et al. unpubl. data). V9 tags were surgically implanted into individuals as described. Smolts ranged in size from 204 mm FL and 87.9 g to 254 mm FL and 170.6 g (Average FL: 229.82± 12.95; Average Weight: 123.91±22.28).

More than 200 acoustic receivers were deployed throughout the Sacramento River watershed to detect these smolts implanted with acoustic transmitters (Fig. 2). The GPS location of each monitor was recorded and the distance in river kilometers (RKM) from the Golden Gate, considered RKM 0, was calculated. The system can be broken up into reaches, the area between two selected monitoring locations. For our study we separated the system into 15 reaches beginning at Butte City (RKM 363) and ending at the Golden Gate Bridge.

All smolts were released at the Butte City boat ramp on 24 January 2008. For each individual detected at a given monitor, datum consisted of a unique acoustic tag ID, specific latitude and longitude for the monitor, and a time of detection. All detections of an individual in the Sacramento River watershed were compiled to create a detection history specific to each smolt. The detection histories were transformed into a series of ones and zeros for survival estimates in Program MARK used for the CJS mark–recapture analysis.

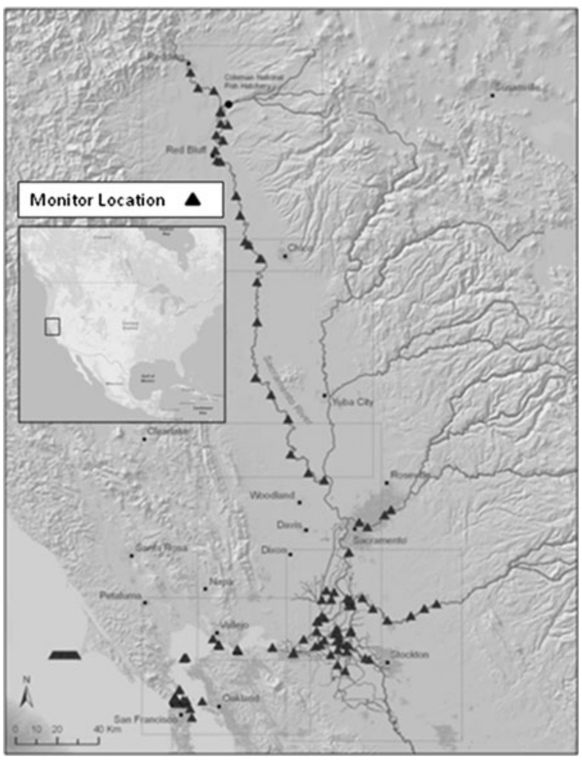


Fig. 2 More than 200 hundred acoustic receivers have been deployed throughout the Central Valley. The majority of monitors deployed by the California Fish Tracking Consortium are in the Sacramento River, Delta, and San Francisco Bay Estuary. There are also sites maintained in the Feather River, Yuba River, American River, Mokelumne River, and San Joaquin River. Map from California Fish Tracking Consortium (2009)

Once the unadjusted CJS model estimates were completed in Program MARK for the 15 reaches, we began to adjust the estimates by censoring smolts from the population based on their detection history. Individuals could be selected for censorship from the survival estimates if they were deemed to have the potential to shed their tag based on the last detection. Smolts that successfully migrated out of the system (RKM 0) or were detected after the final tag of a treatment group had been shed were considered to have retained their tags. For the V9 treatment group any fish retaining their tag for more than 66 days was considered to retain their tag since no smolts tagged with a V9 tag shed a tag past that date. The remaining fish were considered to have the potential to shed their tag. Steelhead smolts fell into one of four movement patterns: 1) upstream migration following release, 2) detected only in the 55 RKM downstream of the release site, 3) successful migration to the lower river (detected >55 RKM downstream), and 4) successful migration to the delta/estuary (detected >175 RKM away). We excluded the fish that migrated upstream and the three fish that successfully migrated to sea.

Smolts survival estimates were adjusted according to V7 and V9 tag retention rates. Any fish that was considered to have shed their tag for the survival estimate was selected from the pool of smolts which could potentially shed their tag. The pool of potential smolts differed for the V9 and V7 treatment based on the difference in date of last tag shed event recorded in the retention study. Smolts were selected from the pool using a random number generator. All smolts were assigned a number (1–50) and a random number generator was used to select which smolt to remove from the population following their final detection. The tag retention rates were applied to the survival estimates under three different scenarios. These three scenarios were selected to illustrate how adjusting survival estimates with different methodologies impact the outcome, as well as how our assumptions shape the results. 1) Individuals only detected near the release site (<55 RKM) were considered to have shed tags. In this case no smolts detected downstream of the third site could be removed from the population. 2) Smolts were selected at random. Any smolt in the pool of potential tag shedders could be selected for removal from the population following their final detection. 3) Finally, the tag retention rate was applied proportionally to smolts detected near the release site (<55 RKM), detected in the lower river (>55 RKM away), and in the delta/estuary (>175 RKM from the release site). The number of smolts in a given category was multiplied by the tag shed rate to determine the number of smolts that would be censored. If a higher proportion of the tagged population was detected in the lower river while few smolts were last detected in the estuary or near the release site, then a higher number but equal proportion of tag expulsions would be assigned to that part of the study population.

In addition to examining the impact of correcting for tag loss through removal of smolts believed to shed tags in Program MARK, survival estimates were also adjusted with ATLAS (Lady et al. 2010). The software was designed to model tag failure with the encounter history of tagged individuals and correct negative bias from a tag life curve derived from a set of tags held back from the study. In our case we used the tag retention curve as a substitute for the tag life curve. Failure of a tag to function is essentially the same as a fish shedding a tag. In both instances the fate of the smolt is unknown and it negatively biases survival estimates. The adjusted survival estimates in ATLAS follow the methods of Townsend et al. (2006). Our tag retention curve was fitted with a non-parametric function for both the V7 and V9 curves. This second methodology of tag loss correction was completed to compare to the results of the survival estimates in Program MARK adjusted by removal of individuals as described earlier.

All survival estimates were made with a CJS for the same reaches using Program MARK and ATLAS. Survival estimates were adjusted according to the tag retention rates of the V7 and V9 treatment as described above. The survival estimates were not considered to be significantly different if the adjusted survival estimates was within the range of unadjusted survival estimates±SE.

Results

Tag retention

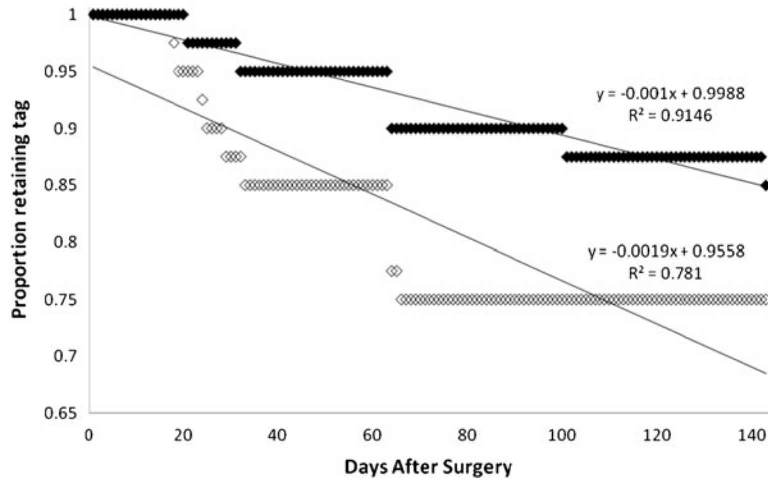
All smolts that expelled their tags survived and showed few visible signs of ill effects at the end of the study. Overall, 10 out of 40 (25 %) of the larger V9 tags implanted in smolts were expelled over the 143 day study, while 6 of 40 (15 %) of the smaller V7 tags implanted in smolts were expelled. There was no statistically significant difference in the retention rate of smolts tagged with a V7 versus a V9. There was also no statistical difference in the tag/body weight ratio of smolts that retained their tag or smolts that expelled their tag for the V7 treatment or V9 treatment.

Tag shedding began at approximately the same time for the V9 and V7 tags, at 18 and 21 days after the surgical procedure, respectively. While a higher number of V9 tags were shed than V7 tags, the V9 tags were also shed over a shorter time period, 48 days compared to 122 days for the V7 tags (Fig. 3). No V9 tags were shed >66 d post surgery. One smolt implanted with a V7 was documented to have lost the tag during the final examination, 143 d post surgery. There was no statistical difference in mean date of tag shed between the V7 and V9 treatment groups.

Based on the timing and visual inspection of smolts, it appears that individuals exhibited one of two methods of tag expulsion. The first is tag expulsion at or near the site of incision. This type of tag shedding occurred more readily during the initial part of the study. The second type of observed tag shedding occurred through the body wall of the individual. Fifty-seven and a half percent (57.5 %) of all tagged individuals were documented with tag bulge during the course of the study. Twenty-five (25) individuals implanted with V9 tags and 21 individuals implanted with V7 tags showed tag bulge during the study. Some individuals were able to successfully pass the tag through their body wall while others retained the tag and tag bulge, which decreased in size over the duration of the study. Seven individuals that shed their tags were not documented to have any tag bulge during the study. Four of the seven individuals shed the tag prior to the first examination period at day 31, while an additional smolt shed a tag the day following the examination. The remaining two smolts were not documented to have lost their tags until almost 1 month later.

Smolts did not shed tags relative to their size. There was no difference in the proportion of tags shed based on size class. The date at which smolts were first documented to have lost their tag was also unrelated to smolt size. There was no statistical difference

Fig. 3 The graph above shows the tag retention rate of hatchery juvenile steelhead trout over the course of 143 day experiment. The solid diamond represents the retention rate of V7 acoustic tags and the open diamond represents the retention rate V9 acoustic tags. Steelhead expelled 6 of 40 (15 %) V7 tags, and 10 of 40 (25 %) V9 tags. The majority of tag expulsion occurred between 20 and 65 days after tagging



between the dates at which a smolt of a given size shed its tag. There was also no statistical difference between the number of tags shed in the three size classes for the V7 treatment group or the V9 treatment group. Fifteen percent (n=13) from the <200 mm, 12 % (n=17) from the 200–209 mm, and 20 % (n=10) from the >209 mm size class in the V7 treatment group shed their tags. The V9 treatment group also had similar number in each size class shed tags with 23 % (n=13) from the <200 mm, 27 % (n=15) from the 200–209 mm, and 25 % (n=12) from the >209 mm size class shedding their tags (Tables 2 and 3).

Retention of sutures appeared to be unrelated to retention of the tag, as smolts that retained their tags shed sutures at similar times as fish that shed their tags. There was a significant difference between the date of tag loss and the number of sutures retained by smolts (ANOVA, $P< 0.05$). Smolts that shed their tags early typically had two sutures, as suture retention appeared to be a function of time. Two of individuals that shed their tags prior to the first examination period expelled the tag at the incision site between two intact sutures. As the study progressed smolts that were observed to shed their tags had one or zero sutures.

Although only a small number of fish, 26, were handled by the second surgeon, and the number of expelled tags are similar for both surgeons, there was a significant difference in the tag retention rate of the two surgeons (X^2, $P< 0.05$) (Table 3). When the two tag treatment groups are examined by surgeon there is a significant difference in the retention rate of the larger V9 treatment group, but not the smaller V7 treatment group (X^2, $P< 0.05$).

Impact of the surgical procedure

The average time from removal of individual smolt from anesthesia to placement in the holding tank post surgery was approximately 2 min, and the average recovery time until the smolt began to swim and regained orientation was approximately 45 s. There was a significant difference among groups for the time in anesthetic (ANOVA, $P< 0.01$). Smolts in the V7 tag treatment group were in the anesthesia for a shorter period than smolts in the V9 treatment group (Tukey's Test: HSD=25.15 $P< 0.05$). However there was not a significant difference in the surgical times of the two tag treatment groups, or the recovery times of any treatment group (Table 2). Surgical incisions on the smolts were inspected on four occasions during the study.

Three inspection periods during the study and a final examination provided helpful information about post-surgical healing and tag shed timing of smolts.

Table 2 Average anesthetic, surgical, and recovery times in minutes and seconds (with standard deviations in parentheses) for each treatment group. The surgical times include the time taken to weigh, measure, and take a photo of the individual in addition to performing the surgical procedure. Recovery of the fish was classified as the smolt regaining equilibrium and actively swimming

	Anesthetic	Surgical procedure	Recovery
Control	01:57 (00:48)	01:01 (00:23)	00:50 (00:33)
V7	01:43 (00:44)	02:36 (00:36)	00:46 (00:49)
V9	02:17 (00:50)[a]	02:36 (00:41)	00:43 (00:22)

[a] statistically significant difference

Table 3 The percent of fish from size class shedding tagging with the corresponding feature and the average number of days until tag shedding occurs with the range shown in parentheses

Size class (FL)	Tags shed	V7	V9	Absorbable	Non-absorbable	Surgeon 1	Surgeon 2	Avg. days to shed
<200 mm	19.23	15.00	23.00	16.67	14.29	20.00	16.67	64 (18–143)
200–209 mm	18.75	12.00	27.00	12.50	25.00	11.11	60.00	36 (19–64)
>209 mm	22.73	20.00	25.00	25.00	30.00	12.50	50.00	58 (29–101)

The sutured incisions of some individuals healed with no visible signs of the surgery at the end of the study. Others showed a bulge outward from their body before expelling tags. Several of the smolts showing signs that they might shed their tag early in the study retained their tag for the duration. It was common for smolts that retained tags to encapsulate tags in a thin membrane or tissue adhered to the body wall or embedded in body fat (Fig. 4). At the end of the study, 84 % of the steelhead retaining tags had encapsulated individual tags. Steelhead that shed their tag later in the study exhibited tag bulge prior to expelling the tag 81.8 % of the time.

The tagging procedure did not have a statistically significant impact on the growth rate of any treatment group over the course of the study for FL or weight (Fig. 5). Average smolt FLs at the start of the study were 204 (± 9.87), 203 (± 8.46), and 204 (± 9.03) for the control, V7, and V9 groups, respectively (Table 4). There was no statistically significant difference in starting size among the three groups. Smolts in the control group had a higher relative daily growth rate (RDGR) in FL than the two tag treatment groups during the first 30 days (ANOVA $P< 0.01$) (Fisher's Protected *T*-test: $df_{wn}=113$ t_{crit}:2.617 $t_{V7, C}=7.1$ $t_{V9, C}=8.4$)(Table 5). There was no significant difference in the RDGR by FL or weight when only the initial and final measurements are examined. Six smolts shed PIT tags during the study. These smolts were not included in the analysis after the date at which we were no longer able to identify them. There was no difference in the survival of tagged and untagged fish, as no mortality of any individual was observed during the course of the study.

The majority of smolts, 97 %, had no remaining sutures at the end of the study. Half of all tagged individuals had lost at least one if not both sutures by the first sampling period, 31 d post surgical procedure. Nearly all smolts, 93 %, regardless of the suture material, had lost one or both sutures by the second sampling period, 64 d post surgical procedure. Ninety-seven percent of smolts with the non-absorbable material retained at least one suture for 31 days, and 45 % retained at least one suture for more than 64 days. No smolts with absorbable sutures retained any sutures past day 64 of the study. Seventy-five percent of the smolts with absorbable suture had lost one or both sutures 31 days after the surgical procedure (Table 6). However, smolts whose incisions were closed with non-absorbable suture material retained the sutures for a greater period of time than those whose incision was closed with absorbable suture material (*t*-test, $P< 0.01$). Retention of suture material was often correlated with inflammation near the incision site. Juvenile steelhead that retained sutures for a longer time exhibited inflammation more frequently and to a higher degree than smolts that had lost their sutures. Smolts that retained sutures until the second sampling period, 64 days after the surgical procedure, showed a higher degree of inflammation (ANOVA, $P< 0.01$).

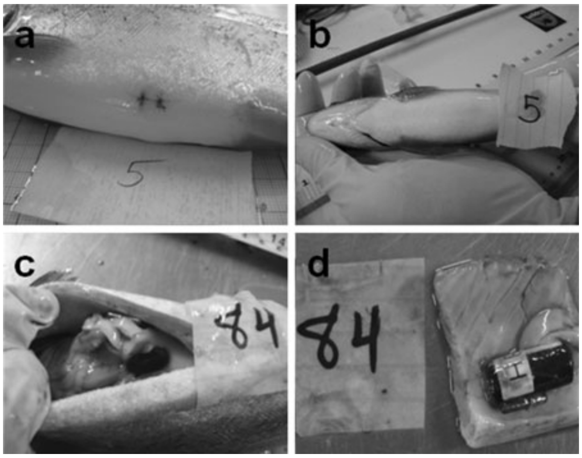


Fig. 4 Fish 5 shown above 31 days **a** and 143 days **b** after the surgical implantation of the smaller acoustic tag (V7). Fish 84 shows the encapsulation of the larger acoustic tag (V9) into the fat and body wall of the individual after 143 days **c** & **d**

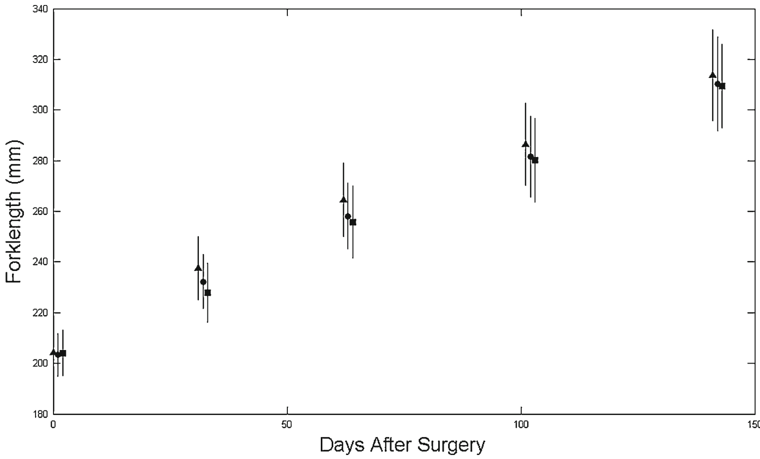


Fig. 5 The graph above shows the growth, in fork length (mm), of the three different treatment groups. The control group is represented with a solid triangle, the V7 tag group is represented by the solid square, and the V9 tag group is represented by the solid square. Each group consisted of 40 individuals, and the values above are the average fork length of all individuals within a treatment at a given time in days after surgery. The

Survival estimates and adjustments

Detection data from 50 steelhead smolts implanted with V9 tags, and released at Butte City, CA (RKM 363; Fig. 1) were utilized to examine the impact of correcting for tag retention rates under two different methodologies. Only three of the 50 individuals released at Butte City successfully migrated from the river to the ocean. Two individuals were last detected as moving upstream from the release site, and two other smolts were never detected post release. Twenty-five smolts were only detected at the release site or the subsequent downstream site less than 15 RKM away. The remaining 18 smolts were last detected at a site between 325 and 14 RKM.

The application of a tag retention rate has impacts on the survival estimates made in Program Mark at several points. It is most noticeable in the areas of lower survival; however, none of the adjustments were considered to be significant (Table 7). When the tag retention rate is applied only to fish detected at sites near the release location, the greatest impact on the survival estimates in the first three reaches. There were no significant differences between the values of the adjusted and unadjusted survival estimates for either of the treatments (Table 7).

The application of the tag retention rate to smolts only detected near the release site had the greatest impact on the initial reach specific survival estimates, although these differences were not significant (Fig. 6a). When the tag retention rate was applied randomly to the population of potential smolts that expel their tag the impact on the point estimates for survival were more spread out over the reaches. The application of the tag retention rate at random to the population changed the shape of curve for the V9

Table 4 Average size of each treatment group, fork length (mm) and weight (g), sorted by date with standard deviation in parentheses. Sizes remain similar to one another throughout the study as and smolts grow and the standard deviations increase

Date	Control		V7		V9	
	Avg. FL (mm)	Avg. weight (g)	Avg. FL (mm)	Avg. weight (g)	Avg. FL (mm)	Avg. weight (g)
9/8/2008	204 (9.9)	109.5 (17.1)	203 (8.5)	108.0 (16.5)	204 (9.0)	109.9 (13.9)
10/8/2008	238 (12.4)	180.5 (31.4)	232 (10.6)	167.0 (26.8)	228 (11.7)	162.0 (25.8)
11/10/2008	265 (14.6)	235.5 (42.3)	258 (12.9)	215.4 (38.3)	256 (14.3)	212.1 (38.0)
12/17/2008	287 (16.2)	299.4 (56.4)	282 (15.9)	279.2 (54.4)	280 (16.6)	279.9 (54.3)
1/28/2009	314 (18.0)	367.5 (74.8)	310 (18.6)	353.8 (73.0)	309 (16.5)	353.7 (59.8)

Table 5 Relative Daily Growth Rates and SE of each treatment by increments in days throughout the study and for the entire study

Treatment	*N*	1–30	31–64	65–101	102–143	1–143
RDGR FL						
Control	35	0.00550 (0.00093)	0.00344 (0.00066)	0.00225 (0.00048)	0.00219 (0.00062)	0.01653 (0.00386)
V7	39	0.00414 (0.00058)	0.00338 (0.00059)	0.00244 (0.00051)	0.00243 (0.00046)	0.00368 (0.00046)
V9	36	0.00385 (0.00100)	0.00371 (0.00092)	0.00264 (0.00047)	0.00262 (0.00071)	0.00368 (0.00066)
RDGR Weight						
Control	35	0.0221 (0.0056)	0.0093 (0.0021)	0.0073 (0.0018)	0.0051 (0.0018)	0.0165 (0.0039)
V7	39	0.0176 (0.0034)	0.0089 (0.0023)	0.0080 (0.0024)	0.0066 (0.0021)	0.0159 (0.0032)
V9	36	0.0145 (0.0053)	0.0096 (0.0032)	0.0093 (0.0021)	0.0067 (0.0021)	0.0158 (0.0050)

treatment in comparison to that of the survival curve with no adjustment for tag retention rates. Although there were changes in the shape of the survival curve estimates, there were no significant differences between the unadjusted and adjusted survival estimates (Fig. 6b). The last methodology by which the tag retention rate was applied in Program MARK was by looking at the encounter history for each individual and assigning them to one the three groups based on the final location where they were detected. The application of the retention rate proportionally to the population had the greatest impact in the lower reaches of the study region. Individual corrections lower in the system have a greater impact as the sample size has been reduced (Fig. 6c). Only one of the survival estimates, in the V9 proportionally adjusted, was significantly different from the unadjusted CJS model.

We also adjusted survival rates by increasing the percentage of tags shed. The V7 and V9 treatments shed 15 % and 25 % of tags respectively, but we also completed estimates of survival by applying a shed rate of 35 and 45 % proportionally to the study population. When the rate of tag shed was increased adjusted survival estimates fell outside of the unadjusted survival estimate SE's (Fig. 7).

The results from the application tag retention rates in ATLAS were slightly different from those made in Program MARK through censorship. The survival estimate adjustments are based on the individual capture histories of smolts and the tag life curve, or in our case tag retention curve. The retention curve and capture histories help inform which fish have a higher probability of shedding their tag. Ideally, all smolts would pass a location prior to the start of tag shedding. A high proportion of our fish reach locations prior to the first occurrence of tag shedding for either group, but as smolts move further downstream the proportion of individuals reaching a given location prior to the occurrence of tag shedding decreases (Fig. 8a, b, c).

The application of the tag retention data in ATLAS yielded higher reach specific survival estimates for all but two reaches. The observed differences between the adjusted and unadjusted estimates were not significantly different (Table 7). The results from the survival estimates in ATLAS were also not largely different than what we observed when censoring individuals from Program MARK by proportionally applying the tag retention rate to the three different spatial groups of smolts. The V9 adjustment had a larger impact than the V7 adjustment and the effect was spread out over all reaches, but was most notable at low and high points of survival. The shape of the survival curve was different between ATLAS and the proportional application in Program MARK in the estuary reaches.

Table 6 The number of smolts with the corresponding number of sutures (absorbable/non-absorbable) remaining by day after the surgery

Days after Surgery	Absorbable			Non-absorbable		
	0	1	2	0	1	2
0	0	0	40	0	0	40
31[a]	9	20	10	1	8	29
64[a]	39	0	0	21	12	5
101	40	0	0	33	6	1
142	40	0	0	38	2	0

[a] Not all fish were accounted for on day 31 and day 64. One individual was unaccounted for during both time periods for the absorbable treatment, and two individuals were unaccounted for during both periods for the non-absorbable treatment

Table 7 Survival estimates in Program MARK and ATLAS from steelhead trout released in 2008. The survival estimates were adjusted to compensate for the observed V7 and V9 tag retention rates

Reach	Environment	Length(RKM)	Program MARK Survival (±SE)			ATLAS Survival (±SE)		
			Unadjusted	V7 Adjusted	V9 Adjusted	Unadjusted	V7 Adjusted	V9 Adjusted
1	Upper River	0.304	0.960 (±0.028)	0.960 (±0.028)	0.960 (±0.028)	1.010 (±0.010)	1.013 (±0.013)	1.013 (±0.012)
2	Upper River	14.015	0.818 (±0.104)	0.867 (±0.097)	0.854 (±0.093)	0.838 (±0.116)	0.841 (±0.117)	0.843 (±0.117)
3	Upper River	23.352	0.601 (±0.116)	0.654 (±0.119)	0.683 (±0.121)	0.579 (±0.129)	0.591 (±0.131)	0.598 (±0.136)
4	Lower River	16.677	0.889 (±0.105)	0.889 (±0.105)	0.889 (±0.105)	0.857 (±0.132)	0.849 (±0.131)	0.850 (±0.140)
5	Lower River	49.743	1.000 (±0.000)	1.000 (±5.0E-9)	1.000 (±1.7E-8)	1.000 (±0.000)	1.002 (±0.006)	1.002 (±0.019)
6	Lower River	19.272	0.955 (±0.106)	0.930 (±0.097)	1.000 (±9.4E-8)	0.867 (±0.078)	0.875 (±0.079)	0.881 (±0.083)
7	Lower River	15.507	1.000 (±0.000)	1.000 (±2.0E-8)	1.000 (±0.000)	1.122 (±0.154)	1.115 (±0.153)	1.109 (±0.155)
8	Lower River	35.166	0.554 (±0.126)	0.634 (±0.132)	0.654 (±0.117)	0.544 (±0.140)	0.549 (±0.141)	0.554 (±0.143)
9	Delta	20.464	0.900 (±0.095)	09.00 (±0.095)	0.900 (±0.095)	0.900 (±0.095)	0.890 (±0.094)	0.885 (±0.97)
10	Delta	70.889	0.700 (±0.145)	0.700 (±0.145)	0.700 (±0.145)	0.800 (±0.126)	0.800 (±0.126)	0.801 (±0.127)
11	Delta	28.111	0.857 (±0.132)	0.857 (±0.132)	1.000 (1.8E-8)	0.750 (±0.153)	0.757 (±0.154)	0.763 (±0.156)
12	Estuary	17.81	0.667 (±0.192)	0.667 (±0.192)	0.800 (±0.179)	0.667 (±0.192)	0.669 (±0.193)	0.671 (±0.194)
13	Estuary	21.328	1.000 (±7.5E-9)	1.000 (±4.5E-8)	1.000 (±7.5E-9)	1.000 (±0.000)	0.983 (±0.006)	0.971 (±0.014)
14	Estuary	15.646	1.000 (±1.3E-7)	1.000 (±3.4E-8)	1.000 (±5.7E-8)	1.000 (±0.000)	1.019 (±0.007)	1.035 (±0.015)
15	Ocean Entry	13.918	0.866 (±0.000)	0.866 (±0.000)	0.866 (±901.4)	Na	Na	Na

Discussion

Tag retention

In estimating tag retention rates, it is important to take into account both number and time period over which tags are shed. Our results indicated no statistical difference in the rate at which steelhead trout shed V9 and V7 tags. This could be explained by the size of the steelhead trout used in this study. While a similar number of V9 tags (10) were expelled during the study, the majority of them were shed earlier in the study. Smolts expelled six V7 tags over a longer time interval. In our study, the first V9 tag was expelled on day 18 of the study and the last V9 tag was shed on day 66. Smolts implanted with the smaller tag were not observed to have lost a tag until 21 d post surgery, and the last tag was shed on day 143. The V9 tag loss also occurred more uniformly over time, with one tag loss every day or so at first and less frequent loss toward the end of the time period (Fig. 3). The date of tag shedding is similar to that observed in Welch et al. (2007) with smaller steelhead trout. We saw tag shedding begin around 3 weeks post surgery and then peak shortly after with two individuals shedding their tags at much later dates. The lack of an effect of smolt size (within the limited size range used in this study) on the retention rate or date of tag shedding was contradictory to what Welch et al. (2007) observed, but was likely due to the larger size of smolts we utilized in this study. Welch et al. (2007) tagged fish from 110 mm to 170 mm FL and found that tag loss and mortality were related to size. They also found smaller impacts on smolt growth when individuals were >140 mm FL. The smallest individual tagged with a V7 tag was 190 mm and the smallest V9 smolt was 183 mm, and we observed no significant difference in the growth rates of any group (Table 6). Several studies in the Sacramento River watershed implant similar sized steelhead smolts with V7 and V9 tags (Del Real et al. 2011; Singer et al. 2012).

Multiple studies have documented tag shedding. Jepsen (2002) listed the three primary ways tag shedding occurs 1) expulsion of the tag through the incision (Knight and Lasee 1996), 2) expulsion of the tag through the body wall, (Welch et al. 2007) and 3) loss through the intestine (Chisholm and Hubert 1985). In our study, none of the tags appear to have been expelled through the intestine. We base this conclusion on the visual inspection of smolts on a monthly basis. The tag shedding process has been related to granulation tissue that develops contractile tissue characteristics (Gabbiani et al. 1972; Welch et al. 2007). The

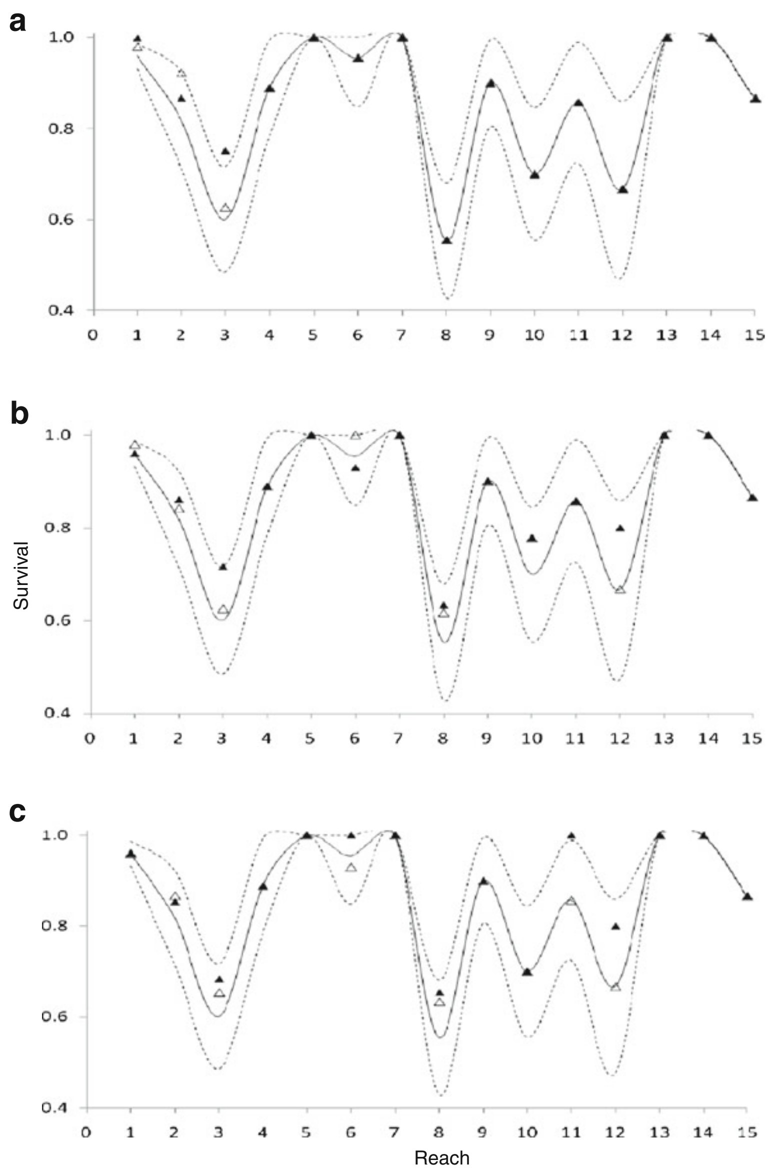


Fig. 6 The three graphs show the impact on survival estimates for each of the 15 reaches under three different scenarios. The solid line represents the unadjusted survival estimate and the dashed line is±SE. The solid triangles represent the adjusted estimates for the V9 treatment and the open triangles represent the adjusted estimates for the V7 treatment. Location and length of each reach can be found in Table 7. Only smolts near the release site (<55 RKM) were removed **a**, smolts were selected for removal at random **b**, and an equal proportion of shed tags was applied to smolts that were only detected at the first three sampling locations, the lower river, and the estuary **c**

tag shedding observed in our study is believed to have occurred by tags exiting through incision and being passed through the body wall. If a tag was lost early in the study, before the first examination at 31 d, it was likely expelled at the incision site. If the tag was expelled later in the study we suspected that it was passed through the body wall based on tag bulge and inflammation. Tag shedding appeared to occur similar to that observed by Frost and McComas (2010) with sub-yearling Chinook salmon, and Welch et al. (2007) with steelhead trout (Fig. 4). While Welch et al. (2007) observed mortality during the retention study we did not document any mortality associated with tag shedding, although larger fish were utilized in our study. While most of our smolts encapsulated tags, it is unclear if encapsulation means the fish will expel the tag. Many smolts retained their tag for the duration of the study and were observed to have encapsulated the tag, but showed no signs that the tag might be expelled.

Many surveyed researchers, 62 %, viewed surgeon performance as a variable that should be included as a covariate in analyses (Wagner and Cooke 2005). Our results supported the concept of an effect of surgeon on tag retention based on treatment. Both surgeons tagging fish for this study had multiple years of

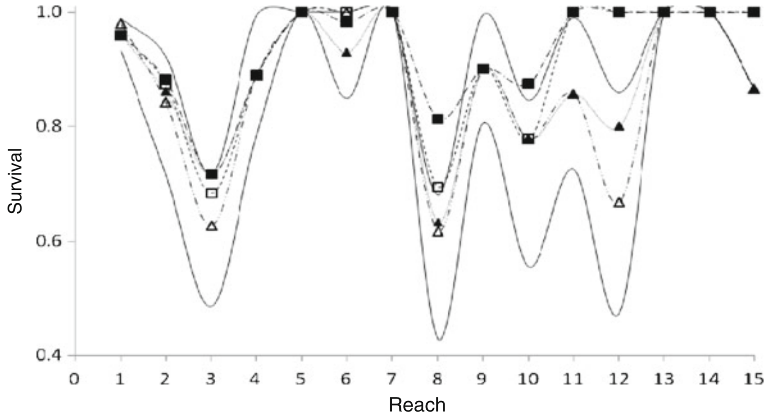


Fig. 7 Adjusted survival estimates for each of the 15 reaches under 4 different tag shed rates (15 %, 25 %, 35 %, and 45 %) proportionally applied to the unadjusted estimates. The solid lines show the unadjusted survival estimates±SE. The open triangle and dashed line represents the V7 treatment (15 %), the solid triangle with the dotted line represents the V9 treatment (25 %), while the open and solid squares represent the 35 % and 45 % tag shed rates respectively

experience tagging juvenile salmonids with both sized transmitters and received the same initial training. While surgeon 2 only tagged eight V9 treatment and nine V7 treatment smolts, it was interesting that there was a significant difference in retention rate by surgeon given that both surgeons received the same training and had similar surgical experience. It has been suggested that surgical training and ability may be more important than simply experience/number of fish tagged (Deters et al. 2010).

Impact of the surgical procedure

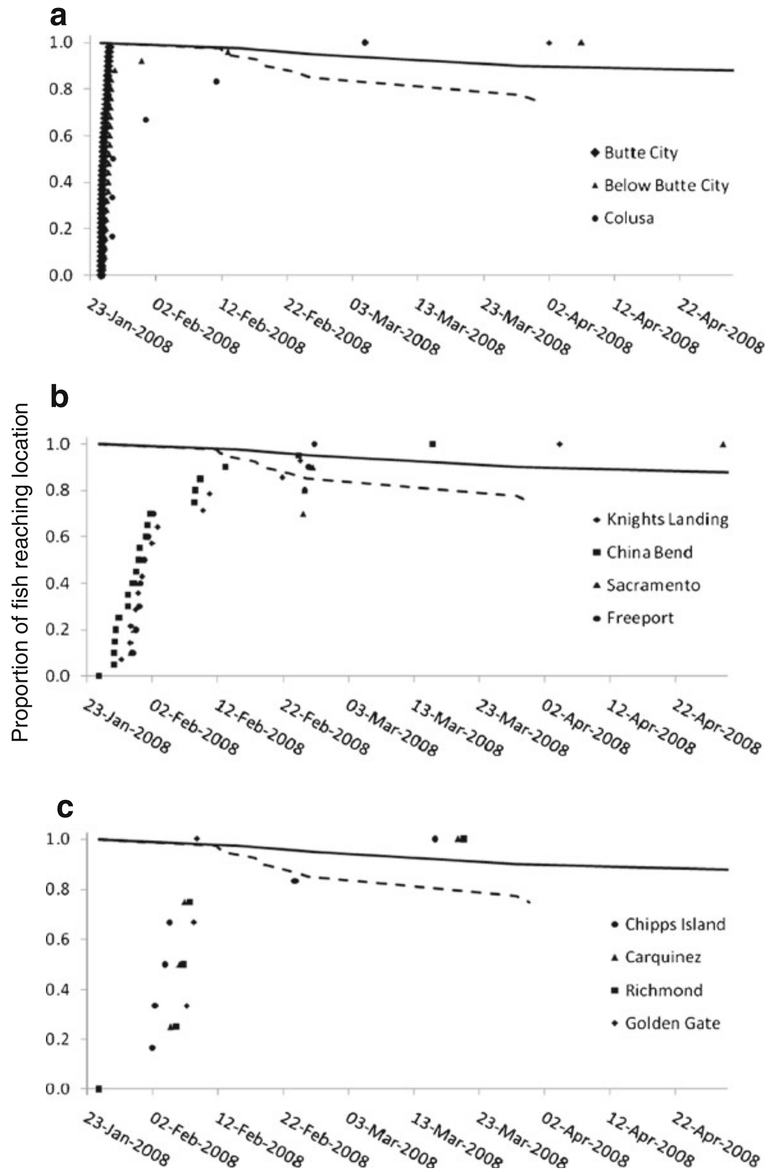
Individuals appeared to heal from surgery relatively quickly. Similar growth rates of all three treatment groups over the course of the study suggest that the impact of the surgical procedure is minimal over the life of the acoustic tag. In the short term, there could be some growth or behavioral impacts to the individual of interest in the days following the surgical procedure but that is beyond the scope of this project. However, our study would suggest that larger juvenile steelhead can easily accommodate tags that are as much as 5 % of the body weight since there were no differences in the growth rate (FL and weight) observed among the three treatment groups during the study.

Most smolts lost their sutures within 64 days regardless of whether the material was absorbable or non-absorbable; two individuals retained one of their sutures through the end of the experiment. The loss of non-absorbable suture material was slower than that observed by Deters et al. (2010) with juvenile Chinook salmon, but comparable with the absorbable material. We regarded the loss of suture material as a positive result since inflammation has been documented in smolts that retain sutures over the long term (Cupauto et al. 2009; Rechisky and Welch 2009). Our smolts tagged with non-absorbable sutures retained the suture for a longer period of time, but this retention was often associated with inflammation near the sutures along the incision.

Survival estimates and adjustments

It is crucial to consider how tag retention and surgical procedures affect migration/survival study results. *O. mykiss* presents a particularly difficult scenario. First, the smolts may hold for a considerable period of time prior to emigrating from the river. This behavior not only leaves them susceptible to predation in the river for a longer period of time, but it also increases the likelihood that an individual will shed a tag prior to their migration. Steelhead trout may also residualize in the river rather than migrating to sea. A number of smolts have been documented as residualizing, including the Central Valley Mokelumne River (Del Real et al. 2011). A Sacramento River CNFH kelt residualized in the upper Sacramento River for the entire year before returning to the hatchery to spawn (Teo et al. 2011), and telemetry studies of reconditioned kelts have also documented fish residualizing in the river (Null 2012). In addition to residualization, many steelhead smolts in the Sacramento River have remained in

Fig. 8 The proportion of fish reaching a location by a given date with V7 tags (solid line) retaining their tag to a given date based on our tag retention data. The dashed line is the proportion of smolts tagged with V9 tags that retain their tag to a given date based on our tag retention data. Sites in the legend are arranged top to bottom, from closest to furthest from the release site. The sites are separated onto three graphs according to location. From top to bottom contains the initial sites of potential detection following release **a**, shows sites in the lower river **b**, and includes the estuary sites in the study region **c**



the river for extended periods of time before migrating from the system. Two individuals in the acoustic data sample to which the tag retention rate was applied did not begin to migrate until more than 70 days post release (Sandstrom unpubl. data).

Townsend et al. (2006) state the importance of understanding tag failure by pointing out that sample sizes are generally smaller because of the acoustic tag costs and the more detailed gained on the movement and survival of individuals. This smaller sample size leads to a larger error if a tag prematurely fails. In this case, the individual has retained the tag, but there is no detection at monitoring sites (Townsend et al. 2006). For research purposes tag expulsion is essentially the same outcome as tag failure; that is, a smolt appears to be a mortality when it isn't tracked by the monitors after a certain date, even though the smolt may still be alive.

A significant issue for applying a tag retention rate to any set of reach-specific survival estimates is the accuracy in its application to the population. This issue is particularly salient when studying steelhead trout since tag expulsion, tag failure, mortality, and residualization cannot be accurately resolved. Ideally, investigators would be able to account for all individuals that retained tags past the period over which tags are shed, as well as any individuals who may have residualized or died and retained tags. However, since all individuals cannot realistically be accounted for within the period over which tags are shed, we must make two key assumptions when projecting survival rates. We assume all smolts shed their tags in a specified time window. This first assumption allows us to ignore the issue of tag shedding outside of the specified time period, as it is likely to be minimal or of decreased importance as smolts will have exited the area of interest. Our results suggest the majority of tag shedding occurs between 18–66 days after the surgical procedure for both V7 and V9 tags. V7 tags continued to be expelled at a reduced rate, however, throughout the remainder of the 143-d study. We will assume the above time periods to be representative for each treatment for this example.

If an individual exits the system before tag shedding is expected to occur, then the issue does not need to be accounted for in that particular instance. For example, some tagged wild steelhead smolts exited the Sacramento River watershed in less than 10 days (Sandstrom et al. unpubl. data). Thus, applying a tag retention rate should not be a factor when making survival estimates. Another scenario could arise where the individual does not begin to emigrate until 2 to 3 months after it is released and is not detected until 90 d post-release. Acoustically-tagged steelhead from CNFH have been documented to hold in the upper river for long periods of time prior to the first detection while emigrating from the system (Sandstrom et al. unpubl. data). At this point, we can make the assumption that the individual will not shed its tag for the purposes of the study.

The second assumption that individuals who shed their tag behave similarly to those who do not shed their tag is crucial, especially when the study species exhibits several forms of behavior. For instance, steelhead trout may begin to emigrate after release, hold near the release site, and wait until a later time period to migrate out of the system, or residualize within the river. If smolts that shed their tag exhibit one of these three behaviors at a greater rate than another, then the survival estimates could be biased. This, of course, would lead to the possibility of bias. However, at this point we are unable to determine the final fate of smolts that shed their tags.

The methodology of applying a tag retention rate to a study population impacts the outcome of the survival estimate adjustments as we see from the examples shown in this manuscript (Fig. 6). Applying the tag retention rate to smolts that were only detected near the release site did not have a large impact on the survival estimate outside of the initial sites as expected. A tag retention rate may be applied to a population in such a manner if researchers believed that the surgical procedure affected the initial behavior of smolts, leading them to hold in a location until they expelled their tag and healed from the process. This tag retention application methodology may also be considered if the researcher considers smolts that shed their tag more susceptible to predation than smolts that retain their tags.

When random individuals were selected from the pool of potential tag shedding smolts, the shape of the survival curve changed in several locations. Reaches lower in the system that had smaller numbers of individuals successfully reaching and migrating through were impacted more heavily by censorship of smolts at random. The application of the V9 tag retention rate dampened the decrease in survival in the estuary on the un-adjusted survival curve suggesting a more uniform lower survival three stretches rather than two reaches with lower survival separated by a reach with higher survival.

The proportional application of the tag retention rate to the population seems to be the most valid of the three methods of removing individuals in Program MARK to adjust survival rates. We do not have reason to believe that smolts that shed their tag behave differently than those that retain their tags. Applying the tag retention rate proportionally also spreads out the impact of tag loss and does not isolate the effect to a single area. It seems unlikely that all tag shedding would happen in a specific region as smolts do not all begin to emigrate at the same time and were observed to shed their tags as late as 101 and 143 days after the surgical procedure, although the bulk of the shedding occurred between day 20 and 65.

The results from the V7 (15 %) and V9 (25 %) adjustments observed in ATLAS were similar to the Program MARK in that they were relatively small and the unadjusted and adjusted estimates had SE that overlapped. There were two survival estimates where the adjusted survival rate was actually smaller than the unadjusted rate. There are four assumptions for the ATLAS software. Violations of the second and third assumptions that the observed fish travel time distribution is not affected by nor does it reflect tag loss, and the distributions of the lab study and field study tag failure times are the same, can lead to a negative bias (Townsend et al. 2006). Both locations where the estimates are biased downward are in the estuary where data is sparse and perhaps the travel time distribution was affected by tag loss in these two lower reaches.

While both methods of adjusting survival estimates for tag loss require assumptions, the ATLAS software is a more robust method correcting for tag loss and spreads the tag correction out over the reach survival estimates without changing the behavior of the curve. The results from the survival estimates in ATLAS were similar to those observed in Program MARK except in the estuary, when the tag retention rate was applied proportionally to the different groups of smolts based on their final detection point and date. The results in ATLAS are likely more statistically sound than the censorship methodology utilized in Program MARK due to the uncertainty associated with the censorship of individual smolts. The adjustments to the survival estimates made in Program MARK were based on the timing of the first and last tag expulsions as well as two assumptions which deal with the detection histories typically encountered with steelhead trout in the Sacramento River. Adjusting the reach specific survival estimates by removing individuals is interesting and has the potential to significantly change the estimates or the shape of the survival curve. However, there are concerns with the accuracy of this methodology.

The lack of a difference in reach specific survival estimates was likely due to low survival rates and detection probabilities. For our study, estimates were not considered to be different if the SE of the unadjusted and adjusted estimate overlapped. The standard errors were high for our reach specific survival estimates, especially in the lower reaches of the system when our sample size became decreased (Fig. 6). The small changes in survival estimates were less than a SE from the original estimate in most cases which is similar to Rechisky and Welch (2009) who observed the adjusted estimates to fall within the 95 % confidence intervals of the unadjusted estimates, and Townsend et al. (2006) who also observed changes smaller than the SE. The only adjustments that were outside of the SE of the unadjusted survival estimates resulted from adjusted estimates based on tag shed rates of 35 % and 45 %.

Adjusting the survival estimates by applying a tag retention rate did not create a significant difference under any of the described methods. These results may be due in part to the overall low survivorship of the juvenile steelhead trout. We did see significant differences when we lowered the tag retention even further than what was observed in our laboratory experiment. The application of the tag retention rate to a small group of acoustically tagged steelhead trout released in 2008 suggested that it may be more important to develop better surgical techniques to reduce tag expulsion rather than trying to correct for tag expulsion with a tag retention rate. It is worth noting that researchers or management interests may consider small changes in survival estimates to be a significant factor in the outcome of a study (Townsend et al. 2006).

Conclusions

Tagging smolts with tags that weigh as much as 5 % of the body weight appears to have a negligible effect on survival and growth. However, individuals may still expel implanted tags. If size is not a constraint, and researchers are working with captive fish, it may be worthwhile to implant smolts 2 or 3 months prior to release. This practice would allow individuals to recover from the surgical procedure. It would also allow the researcher to document the total number of individual smolts that have expelled tags, thereby reducing the need to apply a tag retention rate while reaffirming the shape of a potential curve that might be applied to the population.

Tag shedding has the potential to bias the results of survival estimates regardless of the size of tag used. While smaller tags shed at a lower rate, although not statistically significant, during the course of the study, they did so over a greater period of time relative to the larger V9 tag used in the study. The outcome of an application of a tag retention rate to a study population is affected by several factors, such as sample size of the population, the success of the population, the behavior of the study animal, and timing/amount of tag shedding. Changing anyone of these factors could greatly impact a study. If all individuals leave the study area before tag shedding begins, then there is no need to apply a shed rate. Perhaps tag shedding is constant over time and thus needs to be applied to the entire population rather than a sub-sample of individuals that fall within a tag shed window. Variation of factors affecting survival rates should be understood on a species if not at a local population level in order to accurately understand the potential of tag shedding to bias study results and whether survival estimates should be adjusted accordingly.

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