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ARTICLE

Adult Sockeye Salmon Gastrically Tagged Near Spawning Grounds Exhibit Lower Survival Rates throughout the Spawning Period than Externally Tagged Conspecifics

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Abstract
Telemetry is a common tool for studying the behavior and fate of migrating adult Pacific salmon *Oncorhynchus* spp., yet few field studies have compared behavior and fate associated with different tagging techniques. In this study, adult Harrison River (British Columbia) Sockeye Salmon *O. nerka* were captured in their natal river near spawning areas, radio-tagged by gastric insertion or external attachment in the dorsum, and released. Tagging occurred on 5 d spread over 3–8 weeks prior to spawning, thus encompassing fish in varying stages of maturity and freshwater residency. Tagged individuals were monitored over the spawning season by using fixed receiver stations and mobile tracking. The probability of fish moving upstream or downstream of the tagging site within 35 h of tagging was a function of tagging date but not tag type. Tag type significantly influenced fate, with almost twice as many externally tagged fish (41.6%; 42 of 101) surviving to reach spawning areas compared to gastrically tagged fish (22.4%; 21 of 94). The number of active externally tagged fish in the Harrison River system was consistently greater than the number of active gastrically tagged fish that received tags on the same date for four of the five tagging dates. External tag attachment may be a better approach than gastric insertion for studies that tag adult salmon near or on spawning areas.

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Telemetry is an important tool for studying wild fish in their natural environment (Cooke et al. 2013; Hussey et al. 2015). Therefore, it is imperative to select a tagging technique that will minimize any potential effects on behavior and survival so as to obtain a more representative sample of the broader untagged population (Brown et al. 2011). Deciding on the type of tag and attachment technique to use is dependent on a number of factors, including the morphology and life stage of the study species, the environment in which the study will take place, and the duration of the study (Cooke et al. 2012). Additionally, understanding the limitations associated with various tagging methods is necessary for interpreting results from previous telemetry studies (Brownscombe et al. 2019). All tagging and handling techniques will cause a stress response (e.g., Dick et al. 2018; Sethi et al. 2018) and have the potential to cause injury, so understanding and selecting among tag options to mitigate these problems are imperative to maximize the utility of telemetry information.

Studies that assess the effects of tagging are performed primarily in laboratory settings, with few occurring under field conditions (reviewed by Cooke et al. 2011; Drenner et al. 2012). In a laboratory setting, there is an inability to accurately simulate predation, variable water velocities, dynamic water temperatures, and other environmental stressors. In a field setting, it is difficult to assess tagging effects in behavioral assessments due to the lack of appropriate controls for comparison (Wilson et al. 2016). To address this challenge, studies have compared different tag types (e.g., PIT tags versus gastrically implanted radio tags: Rivinoja et al. 2006; pop-up satellite archival tags versus data storage tags: Hedger et al. 2017), tag sizes (Matter and Sandford 2003), or tag attachment methods (Gray and Haynes 1979).

The main techniques for attaching electronic tags to adult Pacific salmon *Oncorhynchus* spp. are gastric insertion (Caudill et al. 2007) and external attachment (Raby et al. 2015). Electronic tags are applied to adult Pacific salmon during their coastal approach, in estuaries, and in rivers or lakes partway along their return spawning migration. Adult Pacific salmon die after spawning; therefore, tagging studies conducted during the spawning migration are typically short in duration (2–12 weeks) and require expedited procedures to minimize delay in the spawning journey. Gastric insertion is commonly used to tag migrating adult Pacific salmon, as they typically have ceased feeding just prior to leaving the marine environment. This quick and minimally invasive method requires little training on the part of the tagger (Ramstad and Woody 2003; Thorstad et al. 2013). External attachment of electronic tags is less common for adult Pacific salmon but is a good alternative to gastric tagging given that it can be done rapidly and has been widely used on Atlantic Salmon *Salmo salar* (Thorstad 2000; Jepsen et al. 2015) and more recently on Pacific salmon that are still potentially feeding during coastal migration (e.g., Raby et al. 2015). Intracoelomic surgical implantation is another tagging technique that is regarded as an approach used for long-term deployments (e.g., months to years); due to its additional logistic requirements, such as the need for anesthetic and the more involved laparotomy procedure, intracoelomic implantation is considered less favorable for telemetry studies on adult Pacific salmon that are en route to spawning grounds (Wagner et al. 2011). It is known that the short-term (<4 h) physiological response of adult Pacific salmon tagged via gastric insertion or external tagging does not appear to vary between tag types or control treatments (Dick et al. 2018); however, the impacts of these different tagging techniques on the short-term behavior and survival of salmon in the wild are unknown.

The lack of studies to compare the long-term behavioral and survival consequences of gastric and external tags in the wild is surprising given the large amount of effort focused on studying Pacific salmon in the northeast Pacific with telemetry (see review by Drenner et al. 2012). Differences in survival between gastrically and externally tagged Pacific salmon have been reported under laboratory conditions. Corbett et al. (2012) observed low survival of gastrically tagged adult Chinook Salmon *O. tshawytscha* compared to externally tagged and control fish. Corbett et al. (2012) posited that latent effects associated with stomach perforation of gastrically tagged Chinook Salmon may have resulted in mortality, but those authors were unable to specifically determine why survival for this group was much lower than that for externally tagged and control conspecifics. Similar concerns regarding stomach perforation with gastric tags and the potential physiological impact have also been addressed in Sockeye Salmon *O. nerka* (Dick et al. 2018). Major issues with external tags would include entanglement in fishing gear or flora (Adams et al. 1998), biofouling, and additional drag on the fish when swimming (Thorstad et al. 2001). Tag loss is a potential problem that would affect survival estimates for both methods—either through regurgitation of gastric tags or shedding of external tags (Arnason and Mills 1981; Bridger and Booth 2003).

Abnormal behavior of tagged adult Pacific salmon has been reported in previous telemetry studies, particularly for the period immediately after release. For example, tagged adult Chinook Salmon demonstrated a tendency to pause or move downstream after release (gastric tags: Burger et al. 1985, Pahlke and Bernard 1996; gastric and external tags: Gray and Haynes 1979; external tags: Bernard et al. 1999). However, over time abnormal behavior appeared to cease in most cases. Other adverse behavior reported in holding studies of other fish species affixed with tags include rotational swimming or "scouring" by

externally tagged Atlantic Cod *Gadus morhua* held in a large mesocosm (Broell et al. 2016) and substrate scraping by externally tagged Rainbow Trout *O. mykiss* (Mellas and Haynes 1985) and White Sturgeon *Acipenser transmontanus* (Haynes et al. 1978), perhaps in an effort to dislodge the external tag. It is common for studies to disregard data from the first day or week posttagging under the assumption that behavior was altered due to capture, handling, and tagging (Wilson et al. 2016); however, there is little evidence to quantify this effect (Murray and Fuller 2000). Behavior over this timeframe, even if it is considered "abnormal," may be important to consider, as it may reveal important tagging effects and could even influence the endpoints of a study, such as delay in migration or change in migration rate (Bernard et al. 1999; Donaldson et al. 2012; Sethi et al. 2018). Differences in postrelease behavior between tagging methods could also influence survival outcomes. For example, Mathes et al. (2010) found that the staging location used by Sockeye Salmon prior to spawning was related to survival to spawning areas in the Harrison River system, British Columbia. There is a need to identify optimal tagging methods to validate past results and to inform future research studies that are focused on the behavior and survival of adult salmon (e.g., Naughton et al. 2006; Caudill et al. 2007; Drenner et al. 2012; Hinch et al. 2012; Johnson et al. 2012; Brownscombe et al. 2019).

The objective of this study was to compare the behavior and fate of Sockeye Salmon that were affixed with either a gastric or external radio transmitter in the wild. We focused our study on fish that had arrived into their natal spawning stream and were tagged during their staging period, 2–8 weeks prior to the commencement of spawning. Adult Sockeye Salmon were tagged and then tracked in the Harrison River system throughout the staging and spawning period to quantify short-term behavior (~35 h postrelease) and fate (survival to the spawning area and spawning period). Equal numbers of male and female fish were tagged at a staging area within the spawning grounds. This allowed for testing the impacts of tag type on survival and behavior as well as accounting for the potential influences of tagging date (a surrogate for both maturation and freshwater residence) and sex. We predicted that gastrically tagged fish would have lower survival to the spawning period based on a previous laboratory holding study (Corbett et al. 2012). We also predicted that the short-term behavior of fish receiving the two tag types would be similar based on the common acute physiological stress response observed between the two methods (Dick et al. 2018).

METHODS

All protocols in this study were conducted in accordance with Canadian Council on Animal Care guidelines. Animal care protocols were approved by Carleton University (S. J. Cooke protocols from 2014-B14). A scientific collection permit (License XR-250-2014) was also obtained from the Department of Fisheries and Oceans (DFO) Canada.

Study area and species.— The study area was located on the Harrison River (~16.5 km in length), which flows southwest from Harrison Lake to join the Fraser River, about 100 km upriver from where the Fraser River flows into the Strait of Georgia (Figure 1). The Harrison River is the natal stream of the Harrison River Sockeye Salmon population, the focus of this study (Grant et al. 2011). Both First Nations and recreational fisheries occur within the Harrison River. The prolonged residency, or staging, of Harrison River Sockeye Salmon in the river environment prior to the spawning period means that the movement of tagged fish does not adhere to a linear trajectory as is commonly seen in tagged fish from other Pacific salmon populations migrating to an upstream spawning site. Over the past 15 years, this population has been the focus of a number of telemetry studies using different tagging techniques (English et al. 2005; Mathes et al. 2010; Donaldson et al. 2012; Robinson et al. 2015). Tag application for this study was planned to coincide with the appearance of migrating adult Harrison River Sockeye Salmon and to encompass early entrants arriving in mid-August and early September through to fish arriving near peak spawning in mid-November.

Transmitter attachment.— Sockeye Salmon were captured in a narrow, fast-flowing section of the river located approximately 9 km upstream of the Harrison–Fraser River confluence (Figure 1). This location is a staging area where Sockeye Salmon hold prior to spawning within the known spawning areas for the Harrison River population (Schaeffer 1951; de Mestral Bezanson et al. 2012). Capture and tagging methods were described in detail by Dick et al. (2018). In short, a beach seine was deployed from a jet boat, encircling fish within the staging area, and then was pulled in by hand to collect the catch riverside. At this time, fish were contained in the beach seine with sufficient water depth to allow for swimming in the bagged net. Fish for this study were held in the bagged seine net for 11–86 min (average = 50 min) prior to transfer to the tagging trough; this timing is consistent with other research tagging studies conducted on adult Fraser River Sockeye Salmon (e.g). Study fish were transferred into a V-shaped trough equipped with a continual flow of fresh river water over the mouth, gills, and body of the fish. Either a gastric or external radiotelemetry tag was affixed in an alternating fashion, aiming for equal numbers of either sex tagged using both methods on each tagging day (Table 1; tag models and tagging procedures were outlined in detail by Cooke et al. 2012; Dick et al. 2018), using established protocols for tagging adult salmon without

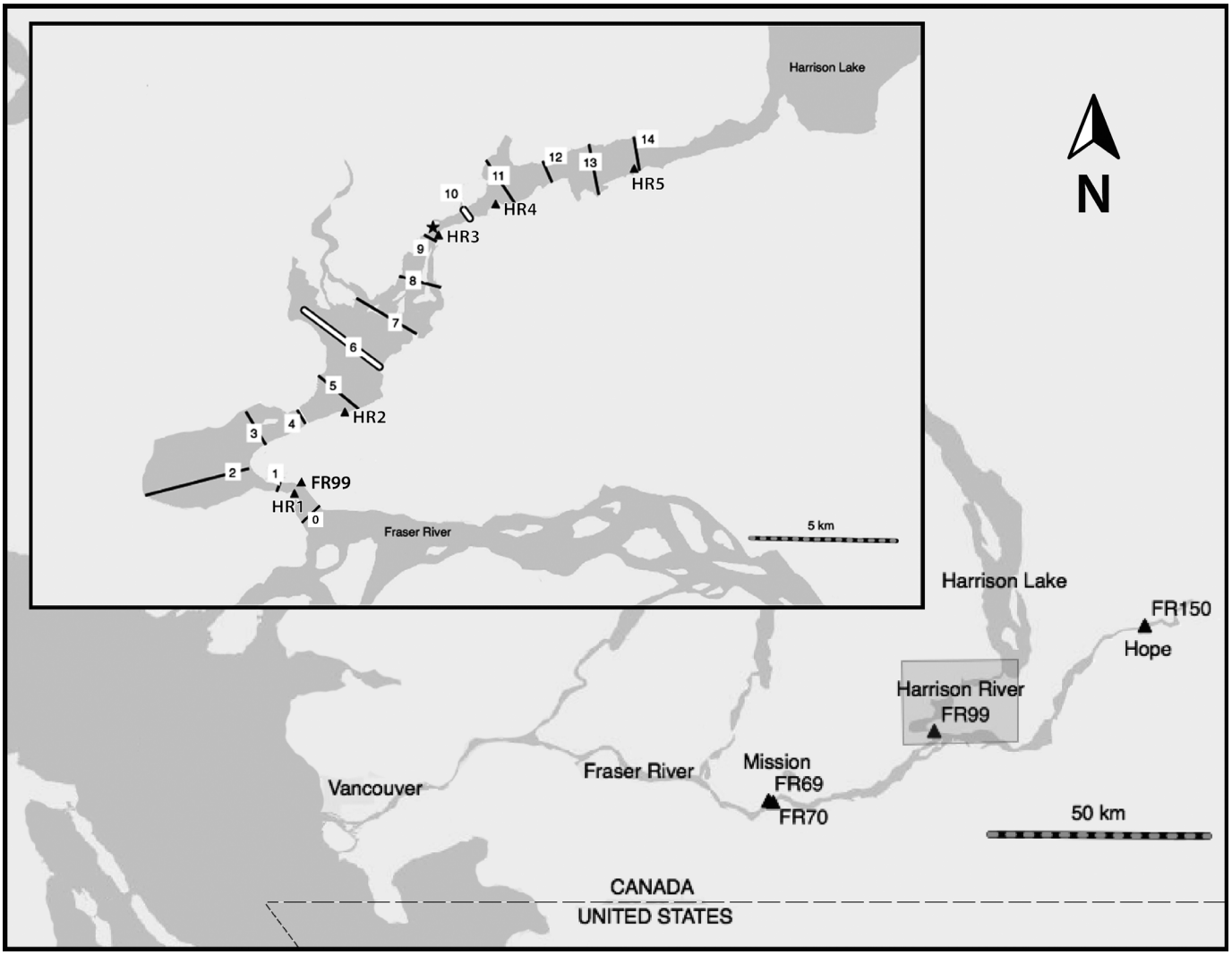

FIGURE 1. Map of the lower Fraser River, British Columbia, Canada, with inset depicting the Harrison River. The triangles represent the locations of fixed radio receiver stations. The star indicates the study capture/tagging/release site. One-kilometer segments of the Harrison River are delineated by numbered lines (0–14) perpendicular to the river thalweg. The upstream and downstream boundaries of the spawning area are delineated by river kilometers 10 and 6, respectively.

anesthetic (Cooke et al. 2005). The same individuals handled the fish in the application of both tagging methods to avoid potential survival and behavior bias that can be induced by the use of different taggers and tagging assistants (Hoyle et al. 2015). In brief, gastric tags (Model TX-PSC-I-1200-M, Sigma Eight, Newmarket, Ontario; 43 mm long, 16 mm wide, 16 mm high, and 15.2-g weight in air) were inserted through the mouth into the stomach by using a smooth plunger. External tags (Model TX-PSC-E-45-M, Sigma Eight; 32 mm long, 10 mm wide, 9.8 mm high, and 3.7-g weight in air) were attached by inserting two metal pins through the dorsal musculature at the base of the dorsal fin and then securing the tag by twisting the pin ends onto themselves to create a knot. Water temperature at the tagging site was 17.5°C on September 11, 18.4°C on September 18, 17.3°C on September 25, 13.0°C on October 18, and 12.8°C on October 23. During the tagging procedure, FL (cm), sex (based on secondary sexual characters), capture and release vigor (3-point scale), maturity/freshwater residency time (4-point scale, based on color and scale absorption), and duration in the tagging trough (nearest second) were recorded. A scale was collected to identify population origin as Harrison River, and an adipose fin clip was obtained to confirm origin if scales were unreadable (see Gable and Cox-Rogers 1993; Beacham et al. 2005).

The electronic transmitters used in this study transmitted on the 150-MHz band and were set to one of eight

radio frequencies: 600, 620, 640, 660, 680, 700, 720, and 740 kHz. Combining one of these frequencies with a unique transmission code allowed for each tag to be individually programmed. Transmitters were equipped with a motion sensor that was programmed to transmit at a different burst interval when a set movement threshold was attained to indicate a dead fish. When the number of movement events fell below 180 events/s for a consecutive 24-h period, the coded transmission signal reversibly switched from the default 5-s burst rate to a 7-s burst rate. A pilot assessment was conducted in a controlled environment to confirm this threshold. The application of this information was only used in assessing the status of the fish at the end of its detection pattern. A fish was assumed to be alive up until the final 5-s burst interval. A fish was only deemed "dead" if its final detections comprised consistent 7-s burst intervals. Each tag was labeled with researcher contact information in case a radio tag was found or removed from a study fish (e.g., if a fish was harvested by a fisher). An ongoing tag return reward program was in place to encourage the reporting of harvested individuals.

Tracking systems.— Radio-tagged Sockeye Salmon were monitored using fixed stations and mobile tracking. Five fixed receiver stations were installed on the Harrison River to track the activity of tagged fish (HR1–HR5 in Figure 1). An additional four fixed receiver stations were located in the Fraser River (FR69, FR70, FR99, and FR150 in Figure 1) and were maintained in collaboration with a concurrent radiotelemetry study (Bass et al. 2018) to provide tracking information on tagged individuals that left the Harrison River system downstream (Figure 1). Each station was equipped with either an Orion radio receiver (manufactured by Sigma Eight) or an SRX400A receiver (manufactured by Lotek Wireless, Newmarket, Ontario). One fixed receiver station was located across the river from the tagging site in the Harrison River (Figure 1), allowing for tracking to commence immediately upon release of tagged individuals. Each fixed receiver station was equipped with at least one Yagi antenna having three, four, or five elements. Mobile tracking supplemented the data collected by the fixed receiver stations in the Harrison River system by providing higher-resolution information and allowing for monitoring of river sections that were not included in the detection range of the fixed stations (Dionne 2018). Mobile tracking covered the extent of the spawning grounds, but due to limited accessibility by boat, mobile tracking did not cover all of the areas that Sockeye Salmon could go within the Harrison River system. The general location of each tag detected by mobile tracking was determined using a mobile receiver and Yagi antenna. When coupled with GPS coordinates,

TABLE 1. Comparison of how significantly more externally tagged Sockeye Salmon than gastrically tagged fish survived to be active in the Harrison River spawning area on or after November 7, 2014 ($P < 0.002$), termed "successful arrivals," and how the numbers varied by tagging date. Sample size is the number of Harrison River Sockeye Salmon tagged by date and tag type. Sex ratio represents the estimated proportion of females for all fish tagged by tagging date and tag type and indicates that survival is independent of sex ($P > 0.05$). The "35 h stayed" column indicates the proportion of all fish that were still detected within 1 km of the tagging site 35 h after the tagging event for each tag group.

Tagging date, tag type	Sample size	Sex ratio (♀)	35 h stayed (proportion)	Successful arrivals
September 11[a]				
Gastric	27	0.42	0.44	5
External	27	0.52	0.37	12
September 18				
Gastric	26	0.50	0.69	4
External	30	0.43	0.63	9
September 25				
Gastric	21	0.48	0.19	9
External	24	0.46	0.04	10
October 16				
Gastric	10	0.50	0.90	1
External	10	0.50	0.80	5
October 23				
Gastric	10	0.50	1.00	2
External	10	0.50	1.00	6
Total				
Gastric	94	0.47	0.56	21 (22.3%)
External	101	0.48	0.48	42 (41.6%)

[a]One gastric-tagged fish was "unrecorded" for sex on September 11.

we were able to generate visual assessments of the distribution patterns over time. A mobile tracking event occurred within about 35 h after a tagging event to determine short-term behavior and to inform postrelease survival; mobile tracking was also repeated on a weekly basis until the end of the spawning period.

All Harrison River fixed receiver sites were actively scanning for detections 85–100% of the time except for site HR4, which experienced some technical difficulties and was functional for 71% of its operation period (Figure 1). The four fixed receiver sites in the Fraser River performed 95–100% of the time during their respective operation periods (Figure 1). Detection efficiency of fixed receivers was estimated in this study by comparing the number of times a subset of tagged fish (those that exhibited intrasystem movement) with both gastric and external transmitters passed a fixed receiver and the number of times the fish were detected by that receiver (Melnychuk 2012). Detection efficiencies were 89% for HR1, 77% for HR2, 83% for HR3, 92% for HR4, and 100% for HR5 (see Figure 1).

Data processing and analysis.— Analyses of the tagging data were conducted using custom functions created in R version 3.1.2 with user-defined criteria. Filtering of the raw data was necessary to identify duplicates, flag unusual data, and remove potential false detections caused by electronic noise. A false detection was identified by evaluating the surrounding detection patterns of a tag at a given site; a detection was considered "true" when it was a part of at least two other detections that occurred within a site-specific period (defined by the receiver type and scan settings) and when the time that elapsed between those detections was a multiple of the two burst rates (5 or 7 s; ±1 s). The detections that met these criteria were then used to calculate the residency duration of individual tags at a site when at least three "true" detections occurred within a user-defined period of 30 min. These residency events—in combination with the mobile track detections—were used to depict individual fish movements. The detections from the weekly mobile tracks did not undergo the false-positive filtering criteria; false positives from the mobile data were removed manually from the mobile tracks. The raw mobile detections were used to supplement the fixed receiver data. Once potential false positives were removed, a database of sequential detections for each fish was generated with both fixed and mobile detections. Each record included the fish identification code, the fixed receiver station, the river kilometer (rkm) in which it was detected, and detection power. The filtered database was used to generate spatiotemporal figures describing residence times at each station, detections between fixed sites from mobile tracking, and sites of last detection. Raw detections were analyzed to calculate the frequency of 5- and 7-s burst rate intervals in each fish's tracking history and to determine the burst rate interval of the final detections. Detections collected by mobile tracking were assigned positional data by matching the corresponding GPS information.

Behavior and survival.— To assess postrelease behavior for fish with each tag type, we first determined whether a fish was still in the vicinity of the release location receiver at HR3 after 35 h. For fish that had moved, we then evaluated the remaining fixed stations to see where they were last detected within the first 35 h. For survival evaluation, by using a combination of the fixed station data and mobile tracking data, each radio-tagged fish was classified into one of two fate categories: (1) successful or (2) unsuccessful. Successful fish were those that were detected in the spawning area (see Figure 1) on or after November 7, 2014. This date was the beginning of spawning activity (peak spawning = November 10–20, 2014; DFO, personal communication) and coincided with a mobile tracking event by boat that spanned the length of the Harrison River. The rest of the fish were deemed unsuccessful. Unsuccessful fish were further classified into one of four categories: (1) premature mortality, (2) left the system, (3) fisheries removal, and (4) unknown. Premature mortalities were fish that were detected as being in the Harrison River and emitting 7-s burst frequencies consistently before November 7. Fish that were categorized as having left the system were last detected at either the Harrison–Fraser River confluence (rkm 0 or rkm 1 in Figure 1) or the upper end of the Harrison River toward Harrison Lake (rkm 14 in Figure 1), emitting 5-s burst frequencies, and were not subsequently detected in the Harrison River system. Fisheries removals were tagged individuals reported to us as having been captured by fishers. Unknown fish were those in the Harrison River emitting 5-s burst frequencies, but their final detections occurred prior to November 7 or they resided somewhere other than the spawning area for the remainder of their detections. The reasoning behind including the "unknown" category was to avoid overestimating premature mortalities. One single external tag was not recorded in any fishery, tag recovery, mobile tracking event, or fixed tracking; thus, it was considered a tag malfunction and removed from further analysis.

Statistical analysis.— Significance levels were set at 0.05. Statistical analyses were conducted using JMP version 12.0. Pearson's independent chi-square analysis was used to test for differences in behavior within the first 35 h posttagging and differences in fate (successful versus unsuccessful) between tag types, sexes, and tagging dates. Three-way ANOVA was used to assess the effects of tag type, sex, and tagging date on minimum estimates of the number of hours the fish were alive. All potential

interactions between the three predictor variables were included; this was done to account for the potential interaction of tag type with the large changes in body morphology associated with senescence (i.e., tagging date) and/or sex. When statistical differences were detected, Tukey honestly significant difference post hoc tests or *t*-tests were performed to determine the nature of those differences. The response variable (minimum estimated time for which the fish was detected alive) was transformed using order quantile normalization to address heteroscedasticity before the ANOVA was applied.

RESULTS

Overall, 195 Harrison River Sockeye Salmon (mean ± SE = 61.5 ± 3.5 cm FL) were tagged and released in the study over five sampling days in 2014 (101 external tags, 94 gastric tags; September 11, 18, and 25, and October 18 and 23; Table 1). Tagging took an average of 39 s (range = 22–76 s) for the gastric procedure, which was significantly faster ($t = -9.6$, df = 182.9, $P < 0.001$) than the 64 s (range = 39–149 s) required for external tagging. The power output of the gastric tag was stronger than that of the external tag (Cam Grant, Sigma Eight, personal communication). This resulted in a slightly higher probability of detection for gastric tags over external tags at all Harrison River receiver stations based on a related study on detection probability (Dionne 2018).

We estimated that twice as many externally tagged fish (41.6%; 42 of 101) survived to be detected within spawning areas during the known spawning period (on or after November 7) compared to gastrically tagged fish (22.3%; 21 of 94; Table 1). The fate of Harrison River Sockeye Salmon was significantly influenced by tag type ($\chi^2 = 8.244$, df = 1, $P = 0.004$) but not by sex ($\chi^2 = 2.292$, df = 2, $P = 0.318$) or tagging date ($\chi^2 = 4.747$, df = 4, $P = 0.314$).

Tag type did not have an effect on the short-term directional movement from the release site ($\chi^2 = 0.033$, df = 2, $P = 0.856$) or on the likelihood of movement away from the release site within 35 h posttagging ($\chi^2 = 0.385$, df = 1, $P = 0.535$). The likelihood of short-term movement away from the tagging site did vary by tagging date ($\chi^2 = 81.263$, df = 4, $P < 0.001$), but the ratio of gastrically to externally tagged fish that stayed within the vicinity of the release site was similar for a given sampling date (Table 1). The magnitude and direction of movement away from the release site both upstream and downstream within 35 h posttagging for fish with each tag type are represented in Figure 2.

Tag type was the only variable that had a significant influence on the minimum estimated time alive for fish within the Harrison River system (Table 2). Tag type had a small to medium effect on the minimum estimated time detected alive (effect size [Cohen's *d*] = 0.41; Cohen 1992). Tagged fish with a higher minimum estimated time alive were 36% (95% CI = 34–46%) more likely to be externally versus gastrically tagged. More specifically, the number of fish that were active on a given day was consistently less for gastric-tagged fish than for externally tagged fish from four of the five tagging dates (Figure 3). Sex, tagging date, and the interactions of sex, tag type, and tagging date did not have significant impacts on the duration of activity ($P > 0.05$).

For the fish that were not considered to be successful arrivals, there were similarities and differences in the final assignment based on tag type. Tagged Sockeye Salmon that were classified as premature mortalities ($n = 10$) based on the movement sensor consisted of equal numbers of gastrically and externally tagged fish. The percentage of individuals that were last detected as leaving the system was 27% ($n = 27$) for externally tagged fish and 36% ($n = 34$) for gastrically tagged fish. The percentage of Sockeye Salmon with an unknown assignment was 35% ($n = 33$) for gastrically tagged fish and 22% ($n = 22$) for externally tagged fish. Six tagged individuals were reported as captured by fishers; five had external tags and one had a gastric tag (Table 1).

DISCUSSION

Externally tagged Sockeye Salmon were twice as likely as gastrically tagged conspecifics to survive to reach their spawning grounds within the known spawning period, consistent with our prediction and previous laboratory work on Chinook Salmon (Corbett et al. 2012). The short-term behavior of the fish after release did not differ based on tag type, which complements the concurrent physiological study on comparable stress responses between fish receiving the two tag types (Dick et al. 2018). Collectively, these results suggest that the factors driving the differences in survival are delayed beyond the commonly assessed 24-h tag impact period (e.g., Jepsen et al. 2015); this tag effect has implications for the analysis, design, and implementation of tagging studies. The possible reasons for the observed difference in survival to spawning between groups receiving the two tag types are discussed below, focusing on the potential biases that could be associated with technology and handling as well as the environmental and biological factors that could interact with tag type to affect delayed mortality.

The differences in technology and attachment methods between tag types could bias the interpretation of telemetry results. For example, the gastric tags had a higher power output and longer battery life than the external tags in our study and this would create a potential bias toward an increased detection of gastric tags over external tags (Heim et al. 2018). This detection bias was confirmed under a control study in which both tag types were used to

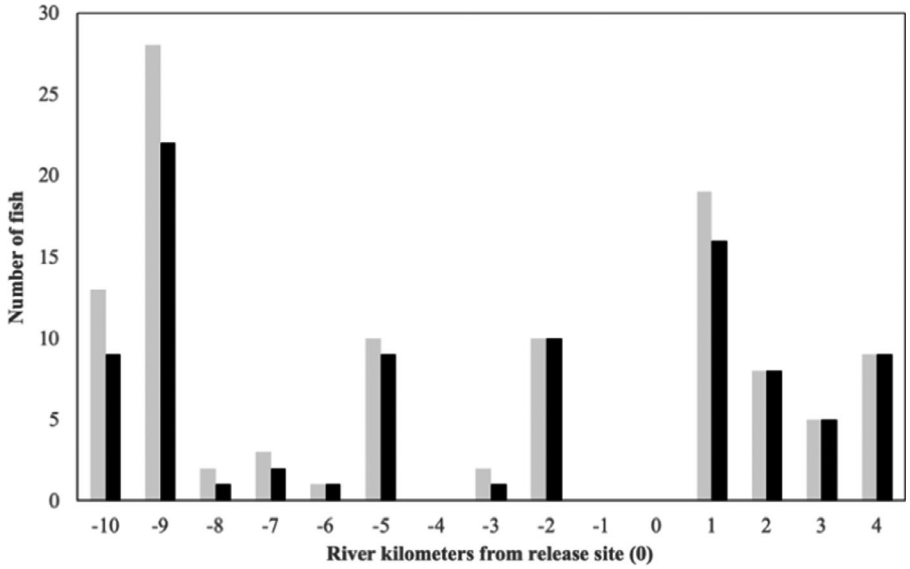

FIGURE 2. Magnitude of movement by Sockeye Salmon within 35 h postrelease. The release site is represented by river kilometer 0 on the *x*-axis, with positive values representing numbers of kilometers upstream and negative values representing kilometers downstream from the release site. Gray bars show the number of tagged fish that moved upstream or downstream to that section of the river within 35 h posttagging, and black bars show the number of those tagged fish that returned toward the release site at some point during their entire detection pattern.

TABLE 2. Results of three-way ANOVA examining the response variable (minimum estimated time alive [MTA] for Harrison River Sockeye Salmon), with tag type, sex, capture (tagging) date, and their interactions as effects. The MTA was calculated as the proportion of the number of days between an individual's first and last detections and the number of days over the period of time during which the individual may have been detected. The MTA was transformed using order quantile normalization before the ANOVA was applied. Significant values ($P \leq 0.05$) are shown in bold italics.

Effect	*F*	df	*P*
Tag type	8.05	1	***0.005***
Sex	0.31	1	0.577
Capture date	1.85	4	0.121
Tag type × Sex	0.62	1	0.432
Tag type × Capture date	0.95	4	0.435
Sex × Capture date	0.90	4	0.464
Tag type × Sex × Capture date	1.45	4	0.221

calculate the detection probability of different tags at set distances from the receivers in the Harrison River (Dionne 2018). The gastric transmitters were four times heavier than the external tags but still represented a tag mass : body mass ratio less than 1% (Dick et al. 2018), which is well below the recommended threshold for tag burden (2% of fish body mass; Winter 1983). The tag size selected for gastric placement was based on previous experiments that found zero tag expulsion over a 24-h holding period (Cooke et al. 2005). Regurgitation rates for other salmonids in field telemetry projects have ranged from 0% to 10% (Keefer et al. 2004; Dick et al. 2018). Comparable tag loss evaluations for external tag attachments in Chinook Salmon have found estimates of loss well above 10% in both laboratory studies (90%; Corbett et al. 2012) and field studies (up to 25%; Keefer et al. 2010). Reasons for external tag loss are associated with higher entanglement rates in fishing gear and vegetation, of which the former is a distinct possibility within this study system. Therefore, it is plausible that tag loss may be higher for externally tagged fish. We submit that the observed difference in survival was unlikely to have been a direct effect of technological issues associated with tag type given that most of the potential biases (i.e., output power, detection probability, and tag loss) would have favored higher survival estimates for gastrically tagged Sockeye Salmon.

There are several environmental and biological factors that could have influenced the latent or delayed effect of tag type on survival in this study. Predation by seals or fishing vulnerability is likely higher for externally tagged individuals given the visual cue and the increased likelihood of snagging on nets, respectively (Ross and McCormick 1981). There were no data on seal predation, but recovery of tags from fishing crews was higher for external tags; this is still in the opposite direction of the overall tag type effect on survival. We had also expected higher mortality for female Sockeye Salmon based on previous research in the system (e.g., Robinson et al. 2015), but we did not find any sex effect or an interaction with tag type that would explain the survival pattern described for tag type. Previous studies that used only gastric tags on

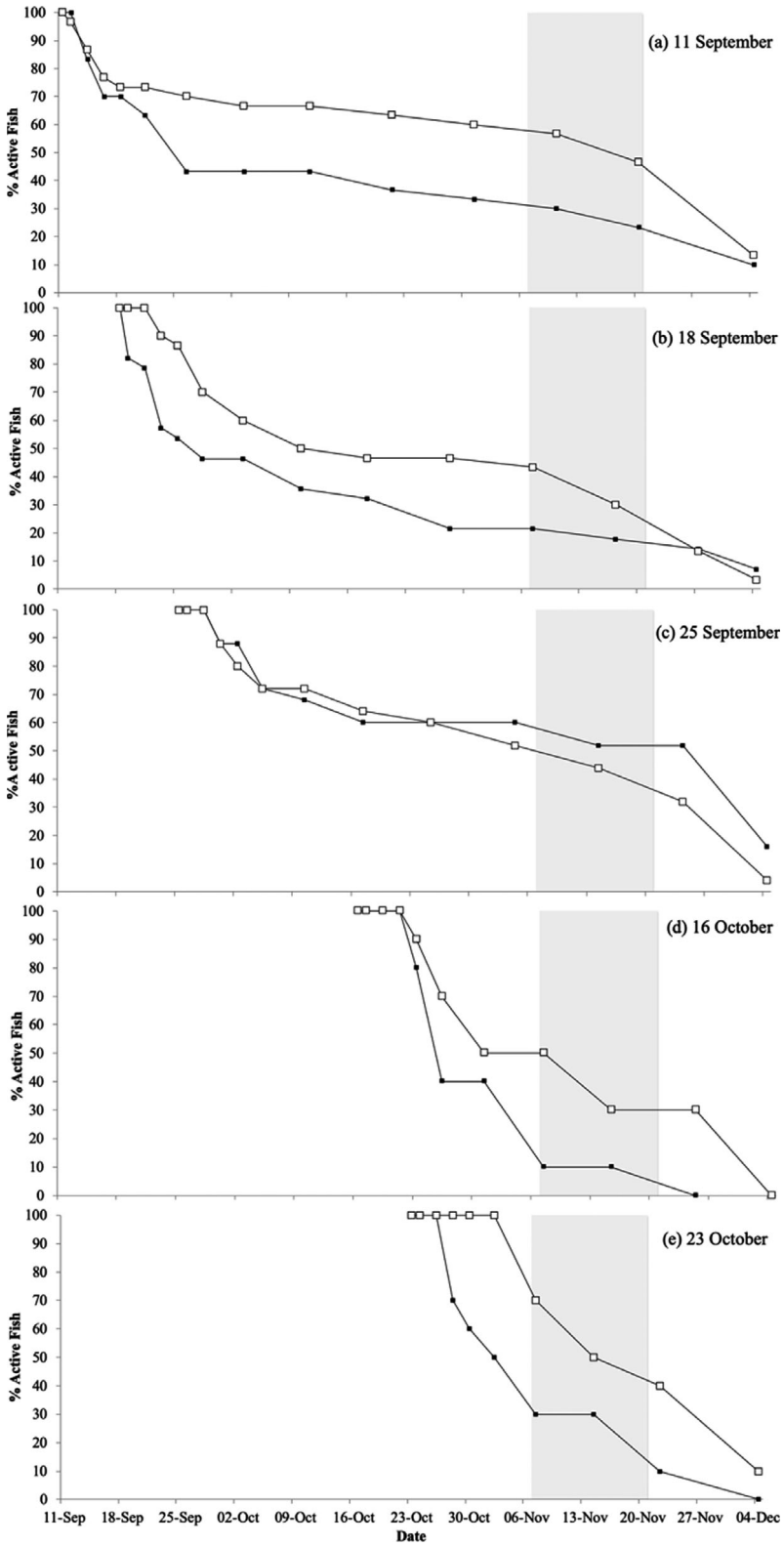

FIGURE 3. Percentage of active study fish over time for Sockeye Salmon that were tagged on the five tagging dates. A study fish was considered active if its detections suggested movement in the Harrison River system or if it was outside of the system but returned at a later date. Black filled squares represent gastrically tagged fish; open squares represent externally tagged fish. The gray shaded area represents the peak spawning time (November 10–20) in 2014.

Harrison River Sockeye Salmon found that short-term behavior after release influenced long-term survival (Mathes et al. 2010; Robinson et al. 2015). Thus, if tag type had an influence on short-term behavior, this could provide some insight into the observed differences in survival herein. Differences in short-term behavior across sample dates occurred, but they were not related to tag type. Tagging date accounted for some variability in the model, similar to what was reported by Caudill et al. (2007), but again there was no tagging date × tag type interaction to suggest that this influenced the tag type effect on overall survival. Although the mechanism behind this effect is unclear, it is still plausible that the tag type effect is linked to a delayed response to the physical placement of the gastric tag in the stomach.

Prolonged handling times are known to have a negative impact on postrelease survival in adult Pacific salmon (see review by Patterson et al. 2017). The application of gastric tags took on average 39 s versus 64 s for external tags, similar to the net difference in tag time reported by Dick et al. (2018). However, tag type did not have an effect on short-term physiological stress response after tagging—most likely due to the overall stress of capture and handling masking any incremental stress response caused by the minimal differences in tagging duration (Dick et al. 2018). There are clear differences in the potential for immediate physical damage caused by the different tag attachment methods, but it is difficult to predict which physical injury type is more likely to negatively influence survival under different environmental conditions. External tagging creates a conspicuous dorsal puncture wound with the potential to worsen based on tag movement through water, changes in body shape associated with senescence and sexual maturation, and infection (Roberts et al. 1973). Gastric tagging has the less conspicuous but possibly more damaging injury potential due to immediate stomach perforation (Corbett et al. 2012; Dick et al. 2018). In the related study by Dick et al. (2018), postmortem examination of externally and gastrically tagged fish at 4 h after tag application did not find major wounds or bleeding for either tag type. Rates of stomach perforation for fish with gastric tags were low in September (1 of 39 fish) but were markedly higher in October (70% of fish) (Dick et al. 2018). In the present study, all gastric-tagged fish from October were still assessed as being alive within the first 6 d postrelease (Figure 3). This suggests that the immediate injuries from tagging or handling time differences are unlikely to bias the tag type survival reported herein. We speculate, along with others (i.e., Gray and Haynes 1979; Corbett et al. 2012), that damage to the stomach could develop physiological imbalances and adverse whole-animal changes in performance over multiple days. As mentioned earlier, it is unlikely that fish tagged via gastric insertion early in the migration period experienced stomach damage during or shortly after the tagging event, yet the activity curves for those dates clearly showed lower success relative to fish that were tagged externally on the same date (Figure 3). It is unclear whether the stomach of a gastrically tagged fish is weakened by the tag presence and ruptures days or weeks later or if the stomach remains intact (Schubert and Scarborough 1996). Semple et al. (2018) reported evidence of chronic inflammation caused by intracoelomic tag implants, which may manifest similarly in the stomach due to the presence of a gastric tag. Gray and Haynes (1979) postulated that the precise location of gastric tags in the stomach and the type of antenna may elicit adverse effects on the gut lining. The presence of the antenna may cause leaking of water into the gut, thus impairing water balance and osmoregulation. However, it is unlikely to be the sole cause given that gastric tags without antennas can also result in delayed mortality (~18 d posttagging) in salmonids (Kennedy et al. 2018). Assessing the physical limitations of the stomach over time as well as potential physiological and immunological disturbances when a gastric tag is present would elucidate the adverse effects that are potentially associated with this tagging method.

We recommend that researchers consider the use of external attachment methods when conducting freshwater telemetry studies on adult Pacific salmon that are staging at or near spawning areas. Instances in which the use of external tags may not be more desirable near spawning grounds include times of high fishing pressure when entanglement in gear may be biased to externally tagged individuals (Rikardsen and Thorstad 2006) or studies requiring only short (<2 week) monitoring periods (Jepsen et al. 2015). Gastric tagging is associated with high migration survival in adult salmon that have been tagged long distances away from spawning areas. English et al. (2005) estimated 92% survival for Sockeye Salmon that were tagged in the ocean and then tracked for several hundred kilometers to freshwater spawning areas. Salmon that recently have entered freshwater may have more robust stomachs than the Harrison River Sockeye Salmon that were used in this study, some of which had already been in freshwater for several weeks prior to tagging. Another reasons why gastric tagging could be preferable when implemented at long distances from spawning areas is that extra drag associated with external attachment could limit migration ability for the more energetically demanding upstream migrations. Furthermore, external attachments might not be ideal when water temperatures are extremely warm, as pathogen development can be exacerbated with small surficial wounds, such as those caused by external tags and their application (e.g., *Saprolegnia* infections; Pickering and Willoughby 1982). Martins et al. (2012) found that in years of high river temperatures, survival of gastrically tagged fish, particularly females, declined in

locales approaching spawning areas. Understanding the interactions between tagging approaches and high temperatures is clearly an area for future research. In general, more comparable studies of tag attachment methods are warranted, as this will be a crucial factor in determining whether there is a need to re-evaluate previously published survival estimates.

Deploying similar numbers of gastrically inserted and externally attached radio transmitters demonstrated comparable short-term posttagging behavior as well as differential survival in wild adult Harrison River Sockeye Salmon that were subjected to the two tag attachment techniques, which are commonly used in telemetry studies of Pacific salmon. This highlights the importance of selecting the appropriate tag attachment method in study design, especially if there are concerns regarding stomach perforation and/or if fish are to be monitored for multiple weeks in freshwater.

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