Estimating detection probability and detection range of radiotelemetry tags for migrating sockeye salmon (*Oncorhynchus nerka*) in the Harrison River, British Columbia

by

Kaitlyn Dionne

B.Sc. (Hons), Dalhousie University, 2014

Project Submitted in Partial Fulfillment of the
Requirements for the Degree of
Master of Resource Management

in the
School of Resource and Environmental Management
Faculty of Environment

Report No. 693

SIMON FRASER UNIVERSITY
Spring 2018

Approval

Name:	**Kaitlyn Dionne**
Degree:	**Master of Resource Management**
Report No:	**693**
Title:	**Estimating detection probability and detection range of radiotelemetry tags for migrating sockeye salmon (*Oncorhynchus nerka*) in the Harrison River, British Columbia**
Examining Committee:	**Chair:** Jessica Gill, Master of Resource Management Candidate

Sean Cox
Senior Supervisor
Professor

David Patterson
Supervisor
Adjunct Professor

Date Defended/Approved:	1 March, 2018

Abstract

Radiotelemetry is a commonly used tool for tracking migration rates, estimating mortality, and revealing fish behaviour. However, researchers risk misinterpreting tag detection data by not appropriately accounting for signal detection probability or detection range of fixed antennas. In this study, I use generalized linear mixed effects models to estimate signal detection probability and detection range of six radiotelemetry tags at four fixed antenna sites. Detection probability differed among the four telemetry fixed sites despite identical techniques and similar receiver site equipment in a relatively small geographic area. The interaction of depth and distance demonstrated the greatest impact on detections at all sites. I conclude that rigorous testing of detection probabilities and detection range of test tags at individual receiver sites should be standard protocol for telemetry studies to optimize study designs and to ensure that appropriate inferences are drawn when telemetry data are used to support management decisions.

Keywords: radiotelemetry; detection probability; Fraser River sockeye

Acknowledgements

I'd like to thank my supervisors, Sean Cox and David Patterson, for their support throughout the course of this project. Additionally, I'd like to extend my gratitude for the support and internship experience to Doug Braun and Instream Fisheries Research Incorporated.

To the DFO E-Watch team, especially Kendra Robinson, Melissa Dick and Vanessa Minke-Martin, thank you for providing field support, listening to presentations and providing feedback.

Thanks to those currently and formerly involved with the Quantitative Fisheries Research Group, especially Michelle Jones, Sam Johnson, Steve Rossi, Lindsay Gardner, and Lauren Weir for your comradery, support and feedback during this program.

This project was supported financially through the Mitacs Accelerate program, the Southern Endowment Fund and the DFO Environmental Watch Program.

Table of Contents

List of Tables

List of Figures

Glossary

Burst Interval	The time between two sequential radio signals programmed into a radio-tag; commonly referred to as a burst rate.
Migration Detection efficiency	The likelihood of detecting a telemetry-tagged fish while it passes through the detection space; it is function of swim speed, burst interval, and detection probability
Detection efficiency	The likelihood of detecting a fish while it is within the detection space
Tag Detection probability (single)	The probability of detecting 1 tag signal at a specific space and time; it is synonymous with probability of detection.
Mean Detection probability (mean)	The mean probability (calculated from all tags) of detecting a tag at a specific space and time
Detection range	The relationship between detection probability and the distance between tag and receiver
Detection space	The zone in which there is an above 0 probability of detecting a tag signal
False alarm	An erroneous signal that is detected by the receiver due to ambient noise or interference that can be mistaken for accurate tag signal
Filtering criteria	The number of tag signals over an observation period, or specified time, that a researcher uses to filter out potential false alarms from the telemetry dataset
Missed signal	A signal that was emitted by the tag but not detected by the telemetry receiver
Radiotelemetry	The process of measuring a number of transmitted radio signals to a distant station, recording and interpreting the results

1. Introduction

Monitoring the movements of wild animals is challenging, particularly for fish populations that we cannot observe directly. Tagging fish provides the opportunity to observe movement when used in conjunction with mark-recapture techniques. Passive tagging studies, where tags do not emit a signal, provide scientists with a tool to monitor fish as they move throughout their range. However, these tools rely on physically recapturing fish multiple times causing stress to the tagged fish (Turchin, 1998; Williams et al., 2002; Pine et al., 2012). Radio and acoustic telemetry, a form of active tagging, solves this problem by replacing physical recapture with tag signal detection by a receiver (Powell et al., 2000; Cooke et al., 2004a; Pollock et al., 2004). Another advantage is that fixed telemetry receivers will detect signals without a researcher present. This is particularly useful for determining movement and behaviour on a fine scale (Turchin, 1998). However, telemetry data analysis poses a major challenge for researchers when environmental interference interrupts the receiver's ability to detect a tag signal. Failure to account for these imperfect detections can limit the ability to draw meaningful conclusions regarding fish movements and survival.

Telemetry relies on sending and receiving acoustic or radio signals from the tagged animal to a fixed or mobile receiver. These signals interact with the physical environment around the receiver and can be interrupted through tag code collisions, ambient noise, rain, and wind resulting in a missed signal or a false signal detection (Heupel et al., 2008; Gjelland and Hedger, 2013; Huveneers et al., 2016); both of which can influence the probability of detecting a tag burst. It is critical for telemetry studies to account for imperfect detections (i.e. missed signals and false alarms) and to understand the detection range of a study system as failing to do so can lead to misinterpretations of the data and thus erroneous conclusions (Freund and Hartman, 2002; Drenner et al., 2013; Payne et al., 2010). Unfortunately, many telemetry studies typically neglect to outline their methodology and criteria for determining detection range and detection probability at their receiver sites (Kessel et al., 2014). Detection range, commonly defined as the maximum distance at which a tag signal can be detected, is more accurately defined as the distribution of tag detection probability within the detection space around the receiver (Kessel et al., 2014). Developing an understanding of how tag signal detections vary in the physical detection space around a receiver provides critical insight for making inferences from telemetry data.

Telemetry is increasingly used to study fish movement (Cooke et al., 2004a; Drenner et al., 2012; Kessel et al., 2014), however estimating detection range and probability of detection are rarely reported, suggesting that some researchers opt out of testing completely. Additionally, those claiming to have tested detection range often neglect to report their methods (See Review Drenner et al., 2012; Melnychuck, 2012; Kessel et al., 2014). A review by Kessel et al. (2014) determined that of 378 fisheries telemetry studies, 15% did not acknowledge detection range in their analysis and nearly 50% of all studies did not report some form of detection range testing. Of the studies that conducted detection range testing, more than half of the studies presented their detection range as fixed while the others allowed it to vary through time and over different weather patterns (Kessel et al., 2014). Numerous studies have determined that environmental heterogeneity affects radio and acoustic telemetry detections (Heupel et al., 2008; Payne et al., 2010; Gjelland and Hedger, 2013). Opting to use a fixed detection range does not account for potential changes in the environment and can lead to over- or under-estimating survival if not appropriately addressed (Drenner et al., 2012). The impacts of environmental factors on tag signal detections in acoustic telemetry is exemplified by Payne et al. (2010) where they examine patterns of offshore migration in cuttlefish. The analysis of the raw acoustic telemetry data demonstrates increased offshore migratory activity during the day compared to the night. However, after applying several correction factors related to changes in detection probability, the results show that offshore migration increased at night and decreased in the day corroborating with previous research on this species. Payne et al. (2010) demonstrates the risk in drawing conclusions from telemetry data if environmental effects on tag burst detections are not considered.

In addition to the possibility of misinterpreting data, inconsistent methods used to estimate detection probability are particularly problematic for comparing the results of similar studies. Gjelland and Hedger (2013) modeled detection probability for an acoustic telemetry array in saltwater using a model for sound propagation in water. While this method shows promise for adaptability to other systems, Huveneers et al. (2016) found that the results of their study conflict with the findings of Gjelland and Hedger. Gjelland and Hedger (2013) determine that acoustic tag detections decline exponentially at distances less than 500 meters while Huveneers (2016) asserts that acoustic tag detections remained stable until distances exceeded 500 meters despite using the same attenuation model. Additionally, sound attenuation models are not tested or reported for the effect of distance on detections and the relationship is instead assumed (Melnychuk and Walters, 2010; Gjelland and Hedger, 2013; Huveneers et al., 2016; see Dance et al., 2016 for exception). These findings suggest that modelling approaches alone are not sufficiently rigorous and that field calibration remains critical to understanding the impact of environmental characteristics from individual studies.

Traditional telemetry mark-recapture analysis methodology for unidirectional fish migration infers detection probability at a specific receiver from recaptures obtained at receiver sites up or downstream (Melnychuk and Walters, 2010). As a consequence, the final receiver is usually omitted from analysis because survival and movement to that final receiver are confounded. A fixed value can be assumed for this receiver (Welch et al., 2009) to ensure its inclusion in analysis but this could result in a biased estimate of survival. Melnychuck and Walters (2010) attempt to mitigate this issue by estimating the proportion of fish not detected while crossing a fixed station based on the detection patterns of fish that were detected using a logistic attenuation model by assuming that more signals will be detected as the fish swims in-line with the antenna and less as it swims away. While they were able to successfully correlate these estimates of detection probability with the mark-recapture estimates of detection probability, they found that their estimates tend to be biased depending on the exclusion parameters used for false detections. In using fish detections to infer detection probability, Melnychuk and Walters (2010) are unable to quantify an effect of distance on detections resulting in an assumed relationship. Several studies use complex Bayesian methods to estimate the relationship between distance and detections relative to the receiver (e.g. Martins et al., 2014; Harrison et al., 2014) but are less accessible to many researchers who aim to perform these types of analysis. As telemetry continues to be increasingly used for tracking fish behaviour and mortality, it is important that statistical tools available to a wide range of researchers are developed to quantify relationships between detections and environmental variables.

Variables that influence radiotelemetry detection probabilities can be categorized several ways. There are factors that the researcher can control such as gain on the receiver, frequency code, power, and tag burst interval, and there are environmental factors that the researcher cannot control such as wind, rain, bathymetry, water chemistry, and noise from the surrounding environment. These can be further divided by whether or not the factors influence the missed signal and/or false alarm rates. For example, telemetry researchers often apply filtering criteria (i.e. true movement event is defined as X number of tags signals over a specified time) to their data in order to limit false detections in their analysis (e.g Melnychuk and Walters, 2010). However, this will affect the likelihood of detecting a true movement event, the same way that altering the gain settings on receivers will influence likelihood of recording either a false detection or a missed signal. All of these settings and filters ultimately play a key role in tag detection probability, detection range and ultimately receiver detection efficiency.

Species life history is important for determining the best methodology to address the question of each study. For example, a sessile fish is likely to spend a longer period of time within the detection space compared to a migrating fish that will likely move quickly through the detection range (Harrison et al., 2014). Telemetry site testing should aim to mimic these behaviours so that data can be best interpreted for the likely behaviour of the fish of interest. Testing telemetry antennas and receivers with tags in a fixed location over time allows researchers to understand how detection probabilities may vary throughout the detection space in a situation where an animal is likely to be relatively stationary. However, a migrating fish is likely to pass through this detection range much quicker so performing test tag drifts to examine how tag detections change as they pass the receiver will result in a better description of the expected tag detections we should observe for tags attached to fish.

The ability to understand and predict the movement of adult Pacific salmon (*Oncorhynchus spp.*) can help to improve the management of fisheries for First Nations, recreational, and commercial groups (Hinch et al., 2012) and conserve what is an integral part of the socioeconomic and ecological landscape in British Columbia, Canada. For example, research over the past decade has demonstrated the increase in mortality associated with early marine exit timing for some Fraser River sockeye populations (*O. nerka)* (Cooke et al., 2004; Hinch et al., 2012). The resulting increased mortality rates prior to spawning have restricted fisheries and created large uncertainty in predicting spawning abundance estimates (Cooke et al., 2004; English et al., 2005; Hinch et al., 2012). Understanding how migration timing changes impact mortality has helped sockeye salmon management (Patterson et al. 2016), however further improvements to effectively manage Fraser sockeye salmon require more precise information on movement and survival (Macdonald 2010; Hague et al., 2011).

Annual sockeye salmon fisheries within the Harrison River, a major tributary to the Fraser River, exemplify how changes in migration timing have impacted local fisheries and how better information could improve management outcomes. Three major sockeye salmon populations, Harrison Rapids, Weaver Creek, and Birkenhead River, migrate and hold within the Harrison River as maturing adults (Mathes et al., 2010; Donaldson et al., 2010; Robinson et al., 2015). Changes in the start of migration and residence time for Harrison Rapids and Weaver sockeye (JO Thomas, 2008-2011) has increased the overlap among all three populations during their migration period. This creates a challenge for terminal fisheries on the more abundant Harrison Rapids sockeye without threatening the less productive Weaver and Birkenhead stocks. However, this system is challenging to assess using telemetry and mark-recapture methods because of variation in fish behaviour through the fishing area (Mathes et al., 2010; Donaldson et al., 2010; Robinson et al., 2015; JO Thomas, 2008 - 2011). For example, Birkenhead sockeye are assumed to migrate straight through the fishing area to their spawning grounds in late August and September, while Harrison Rapids and Weaver sockeye enter the Harrison River from August to October, and either stay within the fishing area (i.e. sessile fish) or else make migrate (i.e. migrating fish) upstream in Harrison Lake or downstream into the mainstem Fraser River before returning back to spawn (Mathes et al., 2010; Donaldson et al., 2010; Robinson et al., 2015; JO Thomas, 2008 – 2011).

The complexity of managing the three stocks that inhabit the Harrison River provides context for improving estimates of migration behaviour and mortality through use of telemetry. However, to ensure that estimates of migration and mortality are unbiased, we need effective estimates of detection probability for both sessile and migratory fish to generate estimates of detection range around radio telemetry receiver sites. Previous research on acoustic telemetry has demonstrated that attenuation models can effectively estimate detection probability (Melnychuck and Walters, 2010; Gjelland and Hedger, 2013; Huveneers et al., 2016) but there has been little research in this area on radiotelemetry. Additionally, the attenuation models used in acoustic telemetry appear to yield different results under different conditions (Huveneers et al., 2016) suggesting a more flexible modeling approach may be more effective. This leads to the question of whether generalized linear mixed effects models (GLMM) can provide accurate estimates of tag detection probability, detection range and detection efficiency of receivers. Generalized linear mixed models (GLMM) are tools that have been in use for approximately a decade in fisheries research but allow for greater flexibility when it comes to correlated observations and nested data structures that often occur with ecological data (Bolker et al., 2008; Zuur et al., 2009; Johnson et al. 2012). Commonly used statistical methods for ecological data such as analysis of variance (ANOVA) or regression analysis require strict assumptions about normality and heteroscedasticity of the data that are often difficult to adhere to for the questions often asked in ecology. GLMM allows for the analysis of the effect of both fixed and random effects while allowing for different distributions to describe the error.

In this study, I used site-specific generalized linear mixed effects models to estimate tag signal detection probability, which I will refer to as $P.Det_S$, in the detection space of each site and use this to estimate the detection probability of fixed radiotelemetry receivers on the Harrison River in British Columbia, Canada. The models were generated using test tags at nine fixed grid point locations around the four telemetry antenna sites and the models generated from this data were used to estimate the detection probability of a mobile drifting tag to mimic a migrating salmon. This study is novel as it is the first to use test tags at a known location in time and space for analyzing the impacts of environmental variables and site-specific characteristics for radiotelemetry in freshwater and how they relate to the probability of detection of tags and detection range of radiotelemetry receivers.

2. Methods

In the summer of 2014, a telemetry study was performed to examine the impacts of different types of tagging on adult migrating sockeye salmon in the Harrison River (Dick et al., 2016). The Harrison River, located 100 km upstream from the mouth of the Fraser River, is the spawning grounds and/or migratory corridor for seven species of Pacific salmon including sockeye (*Oncorhynchus nerka*), Chinook (*O. tsawytscha,* chum (*O. keta*), pink (*O. gorbuscha*), coho (*O. kisutch*), cutthroat trout (*O. clarkii*) and rainbow trout (*O. mykiss)*. Physically, the river is relatively short (16.5 km in length), shallow, and wide (up to 3 km in some locations) (Mathes et al., 2010). Seven fixed-site radiotelemetry receivers were placed throughout the Harrison River (Figure 1) to monitor fish behaviour throughout the spawning season. This provided an opportunity to determine how detections of radiotelemetry tags vary based on depth, distance, and tag type.

I used two methods for testing tag detections around fixed telemetry sites: a stationary grid method and a mobile drift method. The stationary grid method allowed me to determine how physical characteristics of the site, such as depth and distance, influence detection probability of test tags around fixed receiver sites while the mobile drift provided me with the opportunity to test model performance for estimating detection probability of a moving target (i.e., a migrating fish). Furthermore, I analyzed how different filtering criteria influence probability of detection over a range of distances.

2.1 Study Design

Detections of test tags were examined systematically around four of these seven sites (see Table 1 for site descriptions). Each of the chosen test sites was equipped with an Orion receiver (manufactured by Sigma Eight Inc.). Receivers were powered by two 12V marine batteries attached to solar panels and Yagi antennas with 3 elements (HR4 and HR6), 4 elements (HR1) and 5 elements (HR8) were used. External tags (TX-PSC-E-45 from Sigma Eight, 32 mm long, 10 mm wide, 9.7 mm high, 3.7 g, and estimated lifespan of 197 days) and gastric tags (TX-PSC-I-1200 from Sigma Eight, 43 mm in length, 16 mm in width, 16 mm in height,15.2 g, and estimated lifespan of 6669 days) were used for testing as another study performed on this same system was testing the effect of gastric and external tags on the survival of spawning sockeye salmon (Dick et al., 2018). The burst interval for each tag was programmed to emit a signal once every five seconds, similar to other sockeye tagging studies in the system (e.g. Robinson et al. 2015). The tags frequencies used were, 150.600, 150.660, and 150.700, split evenly between gastric and external tags.

2.2 Tag Testing and Analyses

A Garmin © GPS was used to track the position of these tags relative to the antenna during the grid testing phase. Tags were taped to a horizontal block of wood (Figure 2) and fixed behind a boat for the mobile drifts so that the tag antennas would be oriented similarly to how they would be if they were on an externally tagged fish.

For the stationary grid method, tag detections were recorded by depth, distance, and tag type on a grid of nine stationary points at known distances within the detection range of each receiver over a three-minute interval above the surface of the water, one meter below the surface, and approximately 10 cm from the bottom (Figure 3). The resulting observed proportion of signals detected, or detection probability (p in Equation 1), was calculated as

(1)

$$p_{ij} = \frac{d_{ij}}{n_{ij}}$$

where d is the number of successful detections of tag i at observation j and *n* is the number of possible detections of tag i at observation j based on the five second burst interval and three- minute observation period.

A series of mobile drifts were performed to mimic fish migration past receiver sites. Drifts were performed in a boat moving the tags past the antenna. Drifts were performed along the furthest transect of the grid (see Figure 3), through the middle transect of the grid and from the nearest transect of the grid for sites HR4 and HR6 while channel width, depth and current speed resulted in only two drifts being logistically possible for HR1 and one drift possible for HR8. Observed drift detection probability was calculated as the number of observed detections divided by the number of possible detections n over the observation period (range of time from 135 to 680 secs) for an average distance and fixed depth (1 m) away for the antenna for each drift using Equation 1.

I then estimated effects of depth, distance, orientation, and tag type on mean detection probability via the following (full) generalized linear mixed-effects model:

(2)

$$logit(p_{ij}) = \alpha + \beta_1 D_{ij} + \beta_2 X_{ij} + \beta_3 T_{ij} + e_i$$

where p_{ij} is the probability that tag i is detected at observation j, D_{ij} is the depth of tag i at observation j, X_{ij} is the distance from the receiver of tag i at observation j, T_{ij} is an indicator variable for the type (gastric or external) of tag i at observation j and e_i is the random error, which is assumed to be normally distributed with a mean of zero and variance σ^2_a. The top model for each site was used for estimating probability of detection of one tag signal ($P.Det_S$) for each fixed telemetry site. Additionally, the top model for each site was used to predict the detection probability of a drift transect for an average drift distance at one meter depth and compared to the observed drift detection probability calculated from Equation 1.

Preliminary analysis demonstrated that there was large variability between individual tags even after accounting for tag type. To account for this high variability among tags, I included tag as a random effect in the model. The effects of environmental factors on probability of detection were analyzed using the *glmer* function in the lme4 package (version 3.3.3; Bates et al., 2015) in R (R core Team 2018). Akaike's Information Criterion *(AICc)* for small sample sizes (Equation 3) was used to determine relative model fit:

(3)

$$AICc = \ln(SS) + \frac{2m}{n} + \frac{2m(m+1)}{(n-m-1)}$$

where SS is the residual sum of squares, m is the number of model parameters, and n is the number of observations.

The filtering criterion chosen for a true detection event in this study was set as capturing three detections in one minute as this is a common filter applied to telemetry data to remove false detections. The tag burst interval during this study is every five seconds so there is a total of twelve possible detections in one minute. This filtering criterion was used on the test tags in my study to determine if test tag detection probability is high enough to be recorded as a true detection. I used a binomial distribution to calculate the probability of achieving at least three out of twelve possible detections (Equation 4):

(4)

$$P(x) = {}_{n}C_{x} \cdot p^{x} \cdot (1-p)^{n-x}$$
$$x = 0, 1, 2, 3 \ldots .12$$

where $\mathrm{P(x)}$ is the probability of recording a true detection for each tag, n = 12 possible bursts, x = 3 minimum number observed, and p is either the model predicted probability of detection or the observed proportion detected. The cumulative probability of at least three detections was calculated by subtracting the probabilities of zero, one, and two detections from 1. This formula was also used to calculate the filtered detection probability of three detections in two minutes but used an n value of 24 possible tag bursts to account for the longer observation period.

3. Results

Strong effects of tag type, depth and an interaction between distance and depth (Table 2) for all sites ($p < 0.05$) were determined from the site-specific GLMM models. The top models for all sites included the interaction of depth and distance, and distance as being significant ($p < 0.05$) factors contributing to the probability of detection (Table 3). The interaction of depth and distance necessitated keeping the depth parameter in the model despite its lack of significance for all sites. Site HR1 was the exception where depth was significant without the interaction term. Tag-type was not a significant fixed effect for site HR1 but was significant for all other sites.

The effect of distance and depth on detection probability differs by tag type for all sites (Figure 4). Gastric tags (Figure 4a) were more likely to be detected particularly at shallower depths and closer distances than external tags (Figure 4b). For example, the model predicts a detection probability of 90% for gastric tags when depths are less than 2 m and distances are less than 100 m from the antenna. At this same depth and distance, external tags show a probability of detection ~70%.

In general, the top model for each site fit the data moderately well given R^2 values between 0.48 and 0.65 for the predicted and observed probability of detection (Figure 5). The weakest relationship between model fit and the data is for site HR6 ($r^2 = 0.48$; Table 2; Figure 5). The observed tag detections for HR6 tended to be high with very few low probabilities calculated within the grid tested.

The negative relationship between mean detection probability ($P.Det_m$) and distance varied by location (Figure 6). For example, Site HR1 exhibits a steep linear decline within the first 200m to a $P.Det_m$ of ~50%. In contrast, Sites HR4, HR6 and HR8 showed relatively stable estimates of $P.Det_m$ at distances less than 200m ($P.Det_m$ >75% at 200m all 3 sites), after which values tended to decrease.

Variation in the observation period can influence the probability of detecting a tag as the distance increases from fixed telemetry receivers. Figure 7 demonstrates how this relationship changes based on a data filter of three detections in one minute vs. three detections in two minutes. The longer two-minute observation period has higher detection probability and this difference increases at distances above 100m. For example, 80% detection probability occurred at 100m for 2min versus 150 m for 1min.

The site-specific GLMM models fit with the stationary grid data tend to be biased high compared to the observed detection probabilities of a mobile tag drifting through the grid (Figure 8). However, when the models are biased low relative to the drift data, the observed detections still fall within the 95% binomial proportion confidence intervals. In general, as distance from the antenna increases the model detection probabilities decrease. However, there were a few exceptions to this pattern. Site HR4 exhibited the lowest detection probability in the middle drift (DS2) while site HR6 exhibited the highest detection probability in the middle drift (DS2). The HR1 model estimates similar probability of detection values for both up and downstream drifts but the observed upstream drifts are up to 25% lower than the observed downstream drift detection probabilities.

4. Discussion

The results from this research demonstrate that detection probability varies by depth and distance around radiotelemetry receivers. However, detection probability patterns vary by receiver site even in a relatively small geographic area. This demonstrates the need to account for this variation between sites in telemetry studies to make inferences about movement and survival. I generated several site-specific models for calculating detection probability of a tag signal that varies by depth and distance from antennae, and by tag-type. These models were based on data collected from test tags placed at nine grid locations with known distance and depth from the receivers and can be applied to estimate detection probability for mobile and stationary fish. I discuss the importance of these findings in relation to critiquing existing telemetry studies and in planning future radio-telemetry projects.

I demonstrated that the relationship between distance and detection probability is significantly affected by receiver site choice. Many studies have demonstrated that increasing distance negatively impacts telemetry tag detections (Gjelland and Hedger, 2013; Dance et al., 2016; Huveneers et al., 2016) but this is the first study to demonstrate that this relationship differs between receiver sites in the same study system. Previous research has inferred the relationship from other tagged fish and assumes that probability of detection decreases with distance according to a sound attenuation coefficient (Melnychuck and Walters, 2010) rather than formally testing the relationship of distance and detection probability for their particular study. I used observed signal detections to known distances within the detection space to demonstrate that signal attenuation by distance cannot be assumed to be the same across fixed receiver sites. Differences among relationships between detection probability and distance suggests that environmental characteristics currently unaccounted for are likely influencing tag detections. Therefore, it appears that a universal model of detection probability throughout the detection range and applied across all locations in a telemetry study is not appropriate based on the large differences discovered for four sites within a ten km section of the same river. Only one site was tested per day resulting in a lack of replication necessary to fully examine the impacts of different wind, rain, and noise levels in this study.

The interaction between depth and distance was the most significant factor influencing detection probability across all sites. Contrary to previous telemetry research that found a significant effect of depth on detection probability, depth was not significant in this study. Huveneers et al. (2016) found a negative effect of depth on detection probability of acoustic tags in the marine environment. Previous work on radiotelemetry in the Ohio River suggested that increasing depth resulted in an exponential decay of the radiotelemetry signal (Freund and Hartman, 2002). Depth, independent of distance, was likely not a factor in our study due to the low range of depths that were able to be examined in the Harrison River. By understanding how depth and distance influence tag detection probability, researchers can use this approach to determine the best telemetry study design given their objectives.

My research also demonstrated that inferences from telemetry can also be sensitive to tag type. Different tags and tag types have variability in power outputs and battery life, which can both influence detection probability as exemplified. The relationship I observed between depth, distance, and detection probability in this study system confirms that gastric tags with higher power have a higher probability of detection particularly at shallow depths and distances closer to the receiver than external tags. This difference appears to decrease at greater depths and distances, which has implications for studies comparing mobile versus sessile fish movement patterns. For example, the difference in detection probability between tag types at close distances is likely more important for migration studies where fish are only within the detection space for short period of time. The lack of difference in detection probabilities at larger distances suggest that tag type is a less important consideration for sessile fish studies. On the other hand, there is a greater mortality risk associated with gastric tags relative to external tags (Dick 2016), suggesting that researchers should consider whether a weaker tag will achieve the objectives of their research to improve survival of tagged fish. The results of my study suggest future work would benefit from including tag type in modelling relationship between depth and distance on detection probability if different tag types are used.

When setting up a telemetry receiver to maximize detection probabilities, researchers employ common practices such as setting a specific tag burst interval, choosing a tag power and frequency that match the range requirement and environmental conditions, setting noise floor levels on receivers, choosing a certain number of receivers on a site, and simple range testing of tags. I argue that a simple grid tag-testing method focused on detection probability will improve estimates of detection probability of mobile fish (as defined by Kessel et al. 2014), as well as define the detection range for sessile fish. For migratory fish, determining how detection probability of telemetry tags is distributed around a receiver site can allow researchers the opportunity to simulate different paths of migration past the antenna using a known tag burst interval and an assumed swim speed. I found agreement between detection probability of the mobile drifts and model estimates based on a grid system, but there were some deviations. The model tended to overestimate detection probability relative to the drift detections which likely has to do with the constant changing of the position of the tag relative to the antenna for a moving tag. However, when the model underestimated drift detection probability, the observed data fell within the 95% binomial proportional confidence interval. This methodology would provide the best available information for telemetry researchers to determine detection efficiency of their receiver sites for migratory fish.

Researchers commonly assert that they have appropriately accounted for detection range around their receivers. However, they often neglect to outline how long they observed tag detections on the receiver in order to estimate their detection range. The differences in the relationship between filtered detection probability and distance at Site HR1 exemplifies this problem, as the observation period used in the filter can have a large influence on detection probability at certain distances from the receiver. This highlights the need for researchers to carefully consider the need to either remove false positives from the dataset or increase the likelihood of detecting a tag or a fish. However, this relationship can also be used to determine fine scale differences in fish movement and path choice if the relationship between detection probability and distance is known for an individual telemetry site. For example, if a researcher intends to examine fish movement at the edge of the detection space around the receiver, they would likely extend the observation period of the filter to increase the opportunities of observing fish that are less likely to be detected. I recommend that other researchers quantify the impact of using different observation periods in their filtering criteria.

Each individual GLMM was developed using the fixed grid system with tags being held stationary at different distances and depths for a known period of time. While this was possible in this particular study due to the relatively slow current and large width of the Harrison River, this would be extremely difficult to do in faster river systems. The grid method would most likely be appropriate for sessile species that spend a longer duration within the receiver detection space in similar study systems that are relatively calm. However, I successfully demonstrated that using the grid method to develop a model to estimate probability of detection for drift data can also be effective. A caveat of this analysis is that, although I estimated the detection probability for drifts at each site, this was generated using an average distance from the antenna for each drift. Drifting with a boat past the antenna receiver is also difficult in many other systems where depths are too shallow or currents are too swift. Mimicking a drift with a known tag is possible using a fishing line and rod and reel but determining accurate estimates of distance from the receiver may be difficult.

The variability in detection probability by depth and distance around each radiotelemetry receiver site demonstrated in this study is an important consideration for future telemetry research. Huveneers et al. (2016) cautions against using environmental models developed for different situations to estimate detection probability and I support this assertion based on the site-specific model results. Moreover, I argue that this GLMM model form, that includes key site-specific factors (i.e. depth, distance, tag type), adequately addresses the complex nature of estimating probability of detection while accounting for tag variability and can be applied to other telemetry systems. In the current form, this model adequately predicts detection probability for migratory species, but future research should attempt to develop models for migratory species using the drift methodology or to simulate fish moving through the detection range estimated from the grid data. I have provided some examples of how to incorporate mobile detections, as well as filtering criteria to estimate overall detection efficiency, the main goal for many migration telemetry projects. Future iterations of this research should correlate the probability of mark recapture estimates from traditional telemetry mark recapture analysis to the model estimated detection probabilities that our GLMM has estimated. Furthermore, this research is a step toward the further development of predictive models that allow researchers to optimize telemetry set ups by considering the swim speed of the fish and burst interval of the tag. In summary, I have demonstrated that rigorous testing of telemetry studies to understand detection range of receivers, to account for imperfect detection probabilities and relate them to the detection efficiency of their telemetry set ups are important tests in which researchers should invest time prior to study execution.

5. Tables

Table 1. **Description of each receiver site tested including bank orientation of the antenna, the date of data collection and the weather on that date**

Site	Approximate Channel Width	Site Characteristics	Antenna Location	Date Tested	Weather conditions
HR1	200 m	Rocky bank on river right, sandy beach on river left	River right	Oct. 15, 2014	light wind, light to moderate rain
HR4	1000 m	Campsite on river left, golf course and expansive shallow delta on river right	River left	Nov. 26, 2014	light wind, heavy rain
HR6	200 m	Fairly uniform channel with the Sts'ailes Nation fishing site on river right	River left	Nov. 27, 2014	heavy wind, light rain
HR8	500 m	Narrow channel in the middle with shallow gradual banks on either side	River left	Oct. 30, 2014	light wind, moderate rain

Table 2. **Evidence for the top model selection for the site specific models for estimating detection probability of four radiotelemetry sites on the Harrison River, British Columbia where D is depth, X is distance, and T is tag type. ΔAIC_c is the difference in AICc values from the top model and the other models examined, w are the model weights.**

	Site HR1		Site HR4		Site HR6		Site HR8	
Model	**ΔAIC_c**	**w**	**ΔAIC_c**	**w**	**ΔAIC_c**	**w**	**ΔAIC_c**	**w**
D + X + D* X + T	0.24	0.47	0	0.61	0	0.79	0	1
D + X + D*X	0	0.53	0.9	0.39	2.7	0.21	12	0
D + X + T	12.8	0	51	0	22	0	26	0
D + X	12.6	0	52	0	25	0	38	0
D + T	199	0	300	0	115	0	322	0
X + T	650	0	325	0	141	0	525	0
D	199	0	299	0	118	0	334	0
X	650	0	326	0	144	0	537	0
T	843	0	598	0	203	0	692	0
null	843	0	599	0	206	0	704	0

Table 3. Coefficient estimates for fixed effects estimated by maximum likelihood for the top model chosen by AIC for Sites 1, 4, 6 and 8 on the Harrison River, British Columbia

Site	Parameter	Estimate	Std.Error	z	P.Value
HR1	Intercept	3.17	0.37	8.47	<<0.001
	Depth	0.19	0.05	3.07	<0.001
	Distance	-0.012	0.0018	-7.01	<<0.001
	Depth*Distance	0.0016	0.00041	3.79	<<0.001
HR4	Intercept	3.31	0.26	12.70	<<0.001
	Distance	-0.008	0.00076	-11.1	<<0.001
	Tag.TypeI	0.56	0.27	2.10	0.04
	Depth*Distance	0.005	0.0007	6.79	<<0.001
HR6	Intercept	2.27	0.21	10.83	<<0.001
	Distance	-0.003	0.0001	-3.947	<<0.001
	Tag.TypeI	0.56	0.19	2.918	0.004
	Depth*Distance	0.002	0.0004	4.731	<<0.001
HR8	Intercept	4.79	0.39	12.16	<<0.001
	Distance	-0.017	0.017	-9.36	<<0.001
	Tag.TypeI	1.81	0.22	8.34	<<0.001
	Depth*Distance	0.004	0.0009	5.20	<<0.001

Table 4. Top models for each site selected from examining fixed effects of tag type (T), depth from the surface (D) and horizontal distance from the antenna (X). Models were compared using small-sample bias-corrected Akaike's Information Criterion (AICc) and model fit was estimated using R^2 values

Site	Model	Description	df	AICc	R^2
HR1	$P_{ij} \sim D_{ij} + X_{ij} + D_{ij} * X_{ij}$	D, X, D*X	5	896	0.64
HR4	$P_{ij} \sim T_{ij} + D_{ij} + X_{ij} + D_{ij} * X_{ij}$	T,D, X, D*X	6	803	0.58
HR6	$P_{ij} \sim T_{ij} + D_{ij} + X_{ij} + D_{ij} * X_{ij}$	T, D, X, D*X	6	586	0.48
HR8	$P_{ij} \sim T_{ij} + D_{ij} + X_{ij} + D_{ij} * X_{ij}$	T, D, X, D*X	6	743	0.65

6. Figures

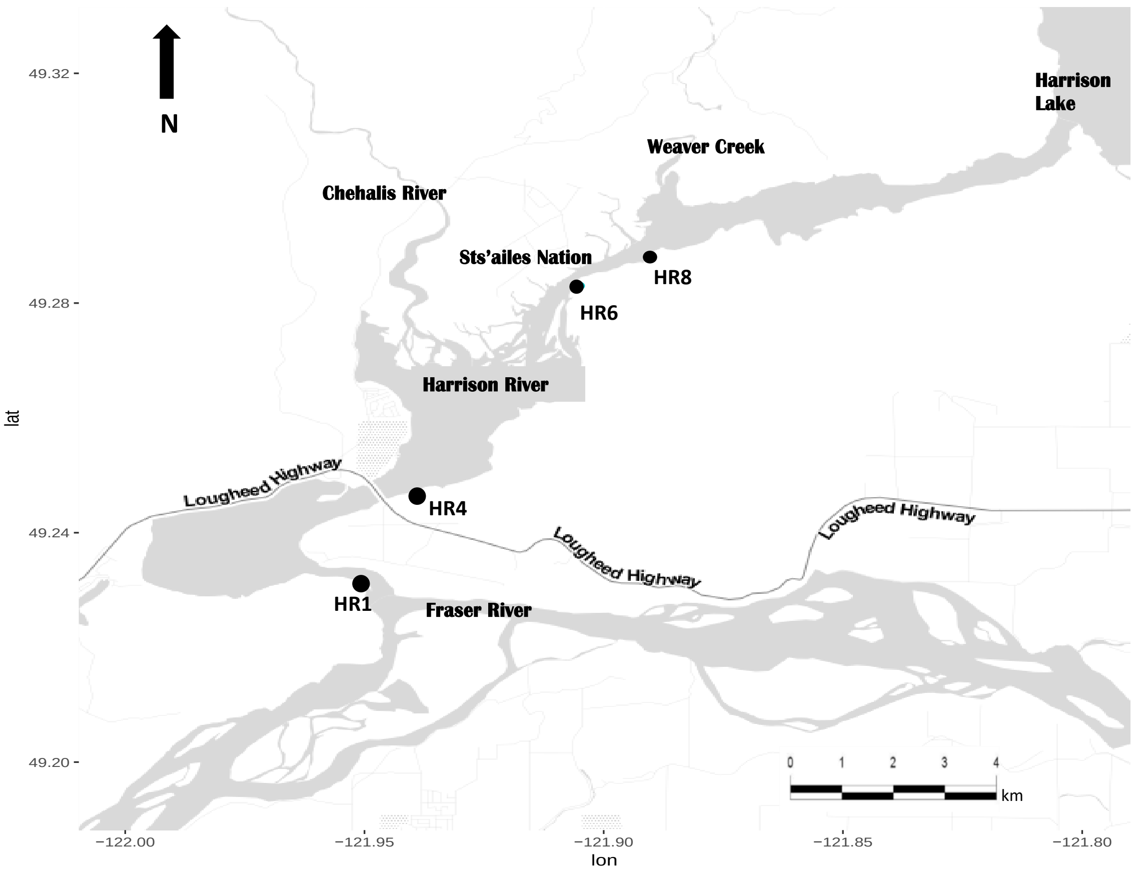

Figure 1. **Map of the Harrison River, British Columbia with tested radiotelemetry sites (closed circles).**

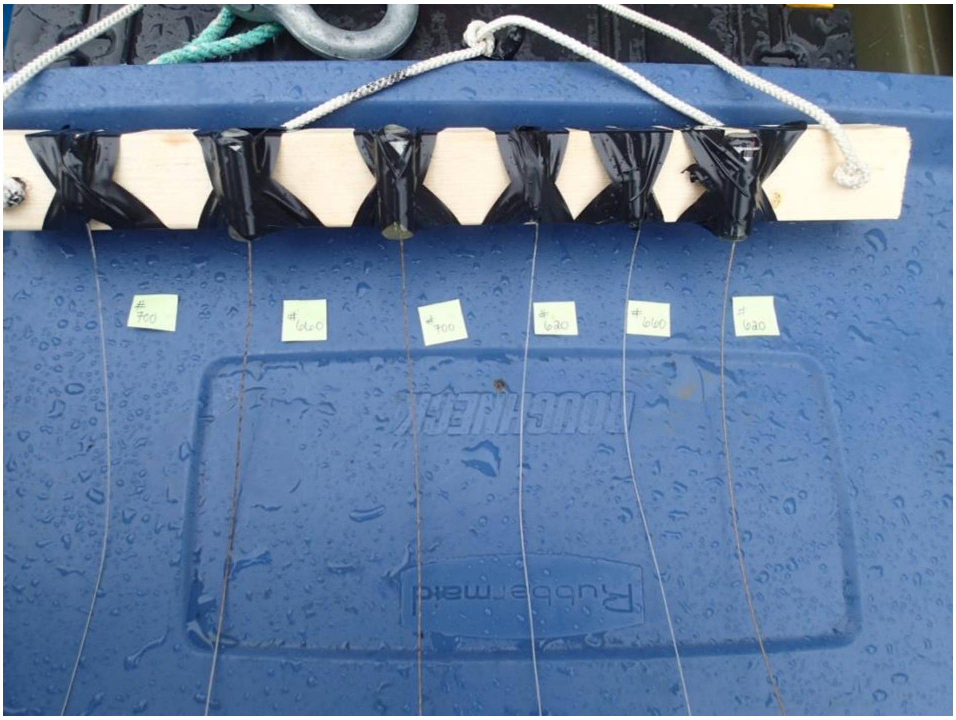

Figure 2. **Tag set up for radiotelemetry tags for drift detection probability testing. Gastric and external tags were fixed to a wooden block and towed at 1 meter depth behind the boat for a known amount of time. n = 6**

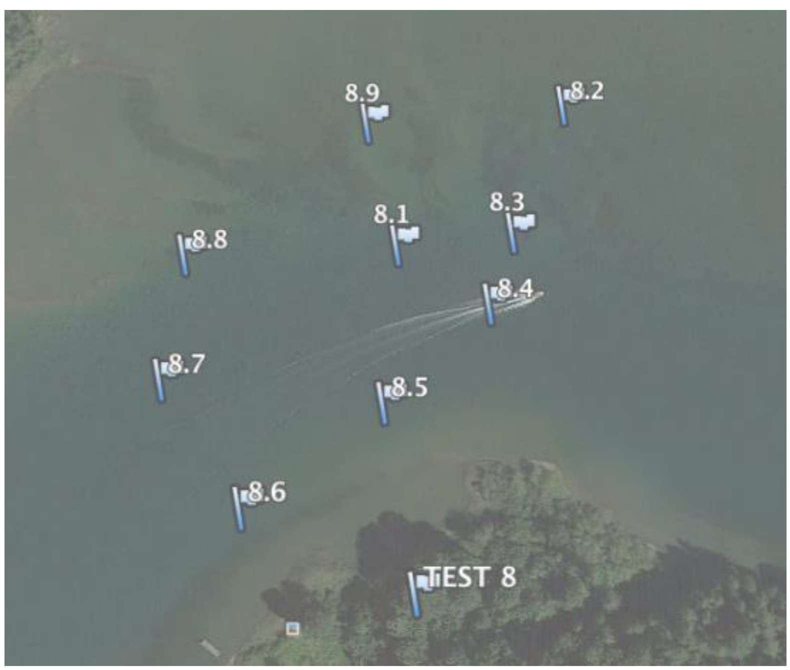

Figure 3. **Example of the grid test set-up on at site HR8 on the Harrison River, British Columbia. Six radio telemetry tags were held in the air, at 1 m depth, and at 10 cm from the bottom at each point for a three minute period.**

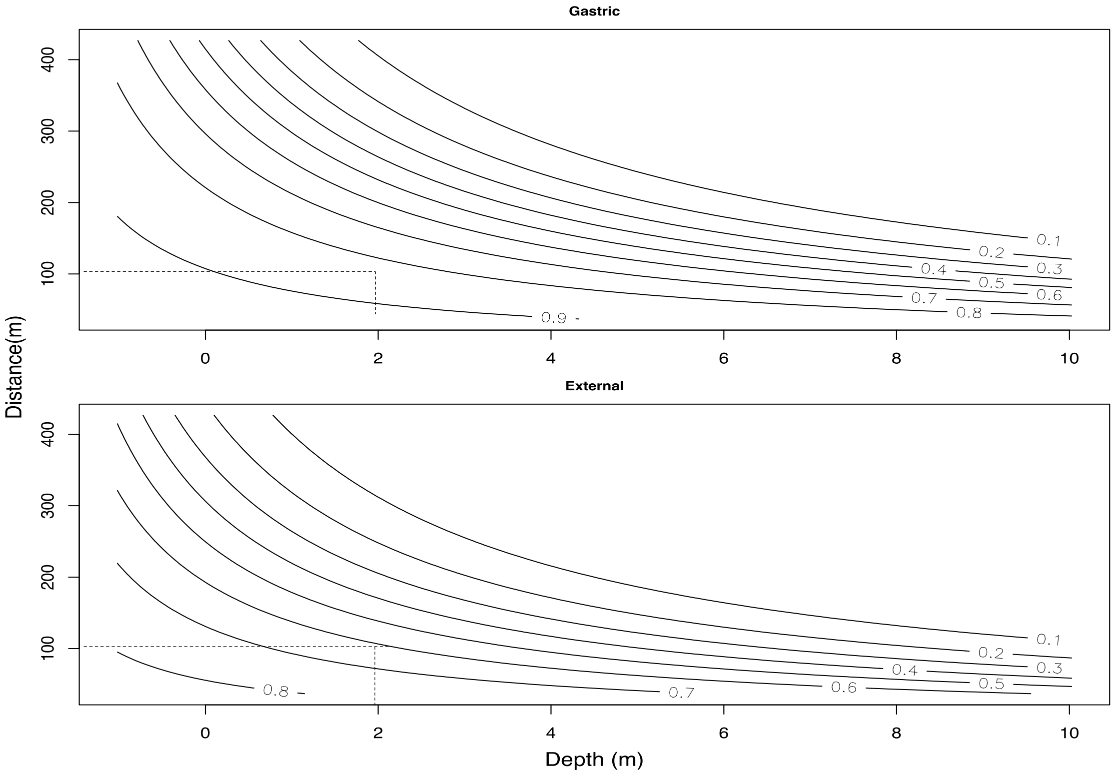

Figure 4. **Detection range for gastric (A) and external (B) tags as a function of distance and depth across all sites in the Harrison River. Contours demonstrate model estimated detection probability for both tag types. The dotted line shows the probability of detection at 100 m distance and 2 m depth for gastric and external tags (0.85 and 0.60 respectively).**

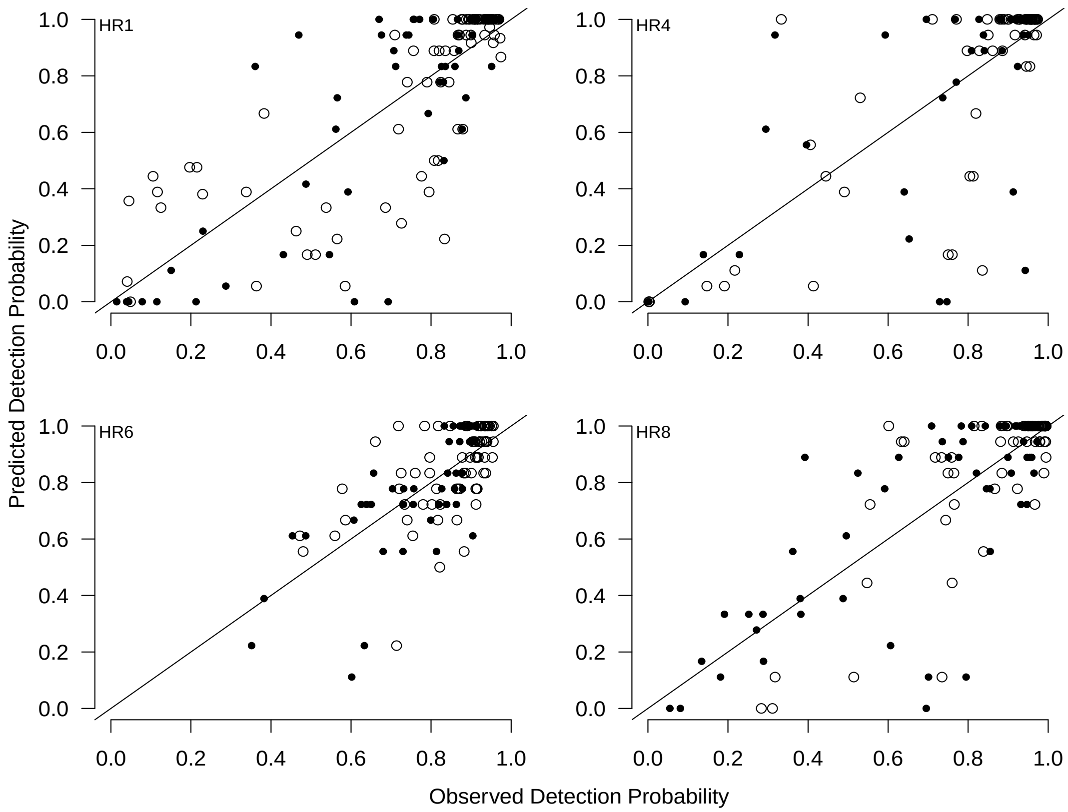

Figure 5. **Observed vs. site specific GLMM predicted probability of detection for gastric (open circles) and external (closed circles) sites HR1 (R^2 = 0.64), HR4 (R^2 = 0.58), HR6 (R^2 = 0.48) and HR8 (R^2= 0.65) in the Harrison River, British Columbia.**

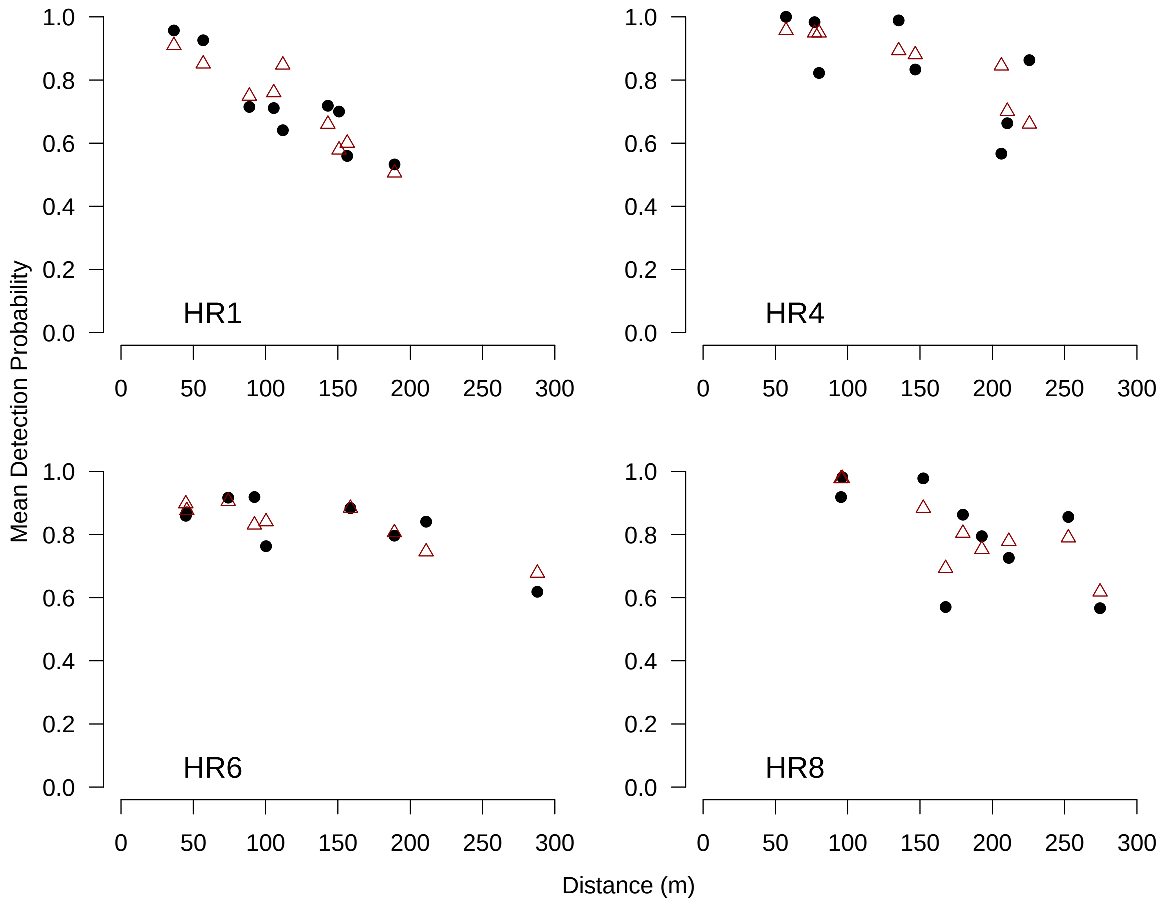

Figure 6. **Predicted (triangles) and observed (circles) mean probability of detection for all test tags as a function of distance for the four telemetry sites on the Harrison River, British Columbia over a three-minute observation period. Mean detection probability from the observed data (black dots) was calculated for each of the 9 grid points and plotted against the horizontal distance from the receiver and is the proportion of possible detections that were observed for that time period**

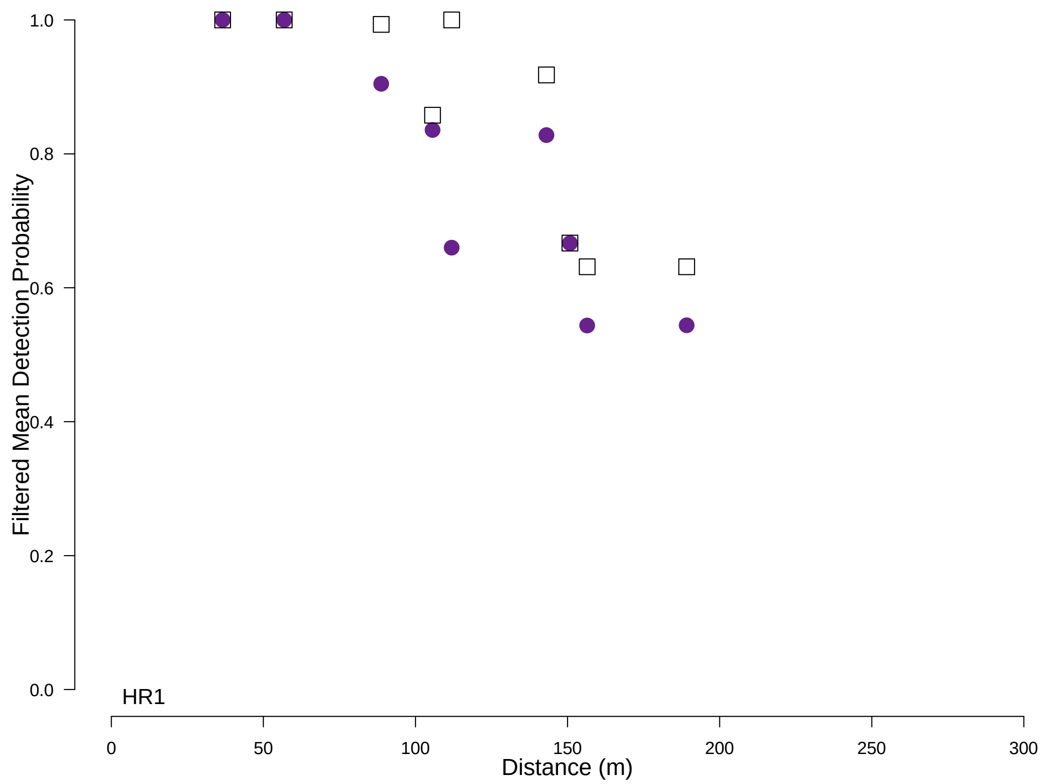

Figure 7. **Filtered mean detection probability of external tags at Site HR1 by distance (m) using a data filter of 3 detections in 1 minute (circles) and 3 detections in 2 minutes (squares) using observed tag data at each of the nine grid points tested at Site HR1.**

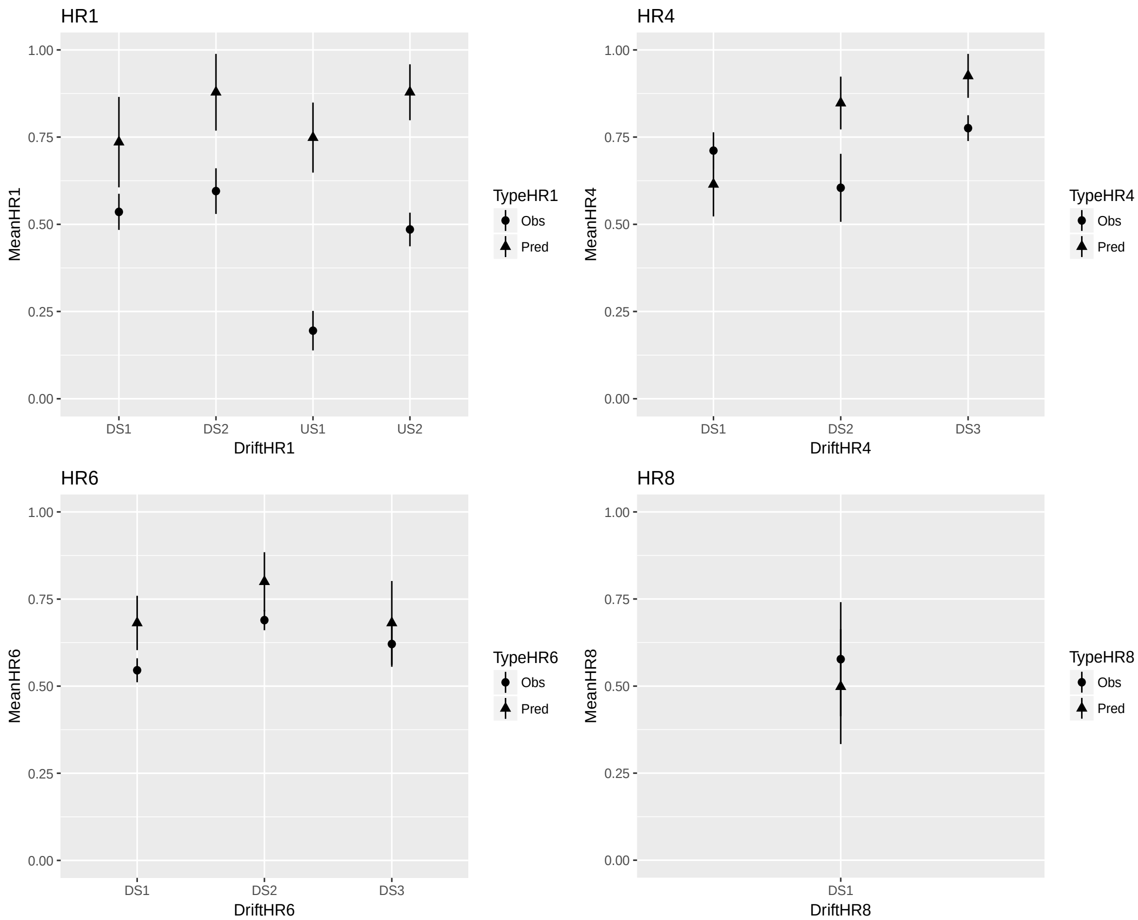

Figure 8. **Observed (circles) and GLMM predicted (triangles) estimate of probability of detection for drift data from fixed telemetry sites HR1, HR4, HR6 and HR8 in the Harrison River, British Columbia. Downstream drifts are denoted as DS and upstream drifts powered by a boat are denoted as US. Drifts are ordered by distance from furthest (DS1) to nearest (DS3). Confidence intervals around the predicted values were calculated using a 95% binomial proportion confidence interval and the bars around the observed data are standard error.**

References

Bates, D., Maechler, M., Bolker, B., and S. Walker. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1): 1-48. doi:10.18637/jss.v067.i01.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J. S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution*, *24*(3), 127–135. http://doi.org/10.1016/j.tree.2008.10.008

Cooke, S.J., Hinch, S.G., Wikelski, M., Andrews, R.D, Kuchel, L.J, Wolcott, T.G, and P.J Butler. (2004a). Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology and Evolution*. 19: 334-343

Cooke, S.J, Hinch, S.G., Lucas, M.C, and M. Lutcavage. (2012). Chapter 18- Biotelemetry and Biologging. In: A.V Zale, D.L Parrish, and T.M Sutton, editors. Fisheries Techniques. 3rd ed. American Fisheries Society, Bethesda, MD. 819-860

Crawley, M.J. (2007). Generalized Linear Models In *The R Book*. (p 511-526). John Wiley and Sons. Sussex, England

Dick, M.L., (2016). *The physiological, behavioural, and survival consequences of two radio transmitter attachment techniques on migrating adult sockeye salmon*. (Unpublished masters thesis). Carleton University, Ottawa, Canada.

Dick, M.L., E.J. Eliason, D.A. Patterson, K.A. Robinson, S.G. Hinch, and S.J. Cooke. (2018). Short-term physiological response profiles of tagged migrating adult Sockeye Salmon: a comparison of gastric insertion and external tagging methods. *Trans. Amer. Fish. Soc*

Donaldson, M. R., Hinch, S. G., Patterson, D. A., Farrell, A P., Shrimpton, J. M., Miller-Saunders, K. M., Robichaud, D., Hills, J., Hruska, K.A., Hanson, K.C., English, K.K., Van Der Kraak, and S.J Cooke. (2010). Physiological condition differentially affects the behavior and survival of two populations of sockeye salmon during their freshwater spawning migration. *Physiological and Biochemical Zoology : PBZ*, *83*(3), 446–58. http://doi.org/10.1086/649627

Drenner, S.M, Clark, T.D., Whitney, C.K., Martins, E.G, Cooke, S.J., and S.G Hinch. (2012). A synthesis of tagging studies examining the behaviour and survival of anadromous salmonids in the marine environment. *PLoS ONE*. 7(3): 1:13

English, K. K., Koski, W. R., Sliwinski, C., Blakley, A., Cass, A., & Woodey, J. C. (2005). Migration Timing and River Survival of Late-Run Fraser River Sockeye Salmon Estimated Using Radiotelemetry Techniques. *Transactions of the American Fisheries Society*, 134(5), 1342–1365. doi:10.1577/T04-119.1

Freund, J.G., & Hartman, K.J. (2002). Influence of Depth on Detection Distance of Low-Frequency Radio Transmitters in the Ohio River. *North American Journal of Fisheries Management.* 22(4): 1301-1305

Hightower, J. E., Jackson, J. R., & Pollock, K. H. (2001). Use of Telemetry Methods to Estimate Natural and Fishing Mortality of Striped Bass in Lake Gaston, North Carolina. *Transactions of the American Fisheries Society*. 130: 37–41. doi:10.1577/1548-8659

Hinch, S.G., S.J. Cooke, A.P. Farrell, K.M. Miller, M. Lapointe, and D.A. Patterson. (2012). Dead fish swimming: a review of research on the early migration and high premature mortality in adult Fraser River sockeye salmon (*Oncorhynchus nerka*). Journal of Fish Biology 81(2): 576-599.

Huveneers, C., Simpfendorfer, C.A., Kim, S., Semmens, J.M., Hobday, A.J., Pederson, H., Stieglitz, T., Vallee, R., Webber, D., Heupel, M.R., Peddemors, V. and R.G Harcourt. (2016). The influence of environmental parameters on the performance and detection range of acoustic receivers. *Methods in Ecology and Evolution*.

Gjelland, K.O. and R.D Hedger. (2013). Environmental influence on transmitter detection probability in biotelemetry: developing a general model of acoustic transmission. *Methods in Ecology and Evolution*. 4: 665 – 674

Harrison, P. M, Guowksy, L.F.G., Martins, E.G., Patterson, D.A., Cooke, S.J., and M. Power. (2014). Personality-dependent spatial ecology occurs independently from dispersal in wild burbot (*Lota lota*). *Behavioural Ecology*. 26(2): 482-492

Heupel, M. R., Reiss, K. L., Yeiser, B. G., & Simpfendorfer, C. A. (2008). Effects of biofouling on performance of moored data logging acoustic receivers. *Limnology and Oceanography-Methods*. 6: 327–335. http://doi.org/10.4319/lom.2008.6.327

J.O Thomas and Associates Ltd. (2008, 2009, 2010 & 2011). *The Chehalis/Scowlitz First Nations Harrison River Sockeye Test Fishery.* Prepared for Sts'ailes Development Corporation and Fisheries and Oceans Canada

Kessel, S.T., Cooke, S.J., Heupel, M.R., Hussey, N.E., Simpfendorfer, C.A., Vagle, S., and A.T Fisk. (2014). A review of detection range testing in aquatic passive acoustic telemetry studies. *Reviews in Fish Biology and Fisheries*.

Macdonald, J. S., Patterson, D. A., Hague, M. J., & I.C. Guthrie. (2010). Modeling the Influence of Environmental Factors on Spawning Migration Mortality for Sockeye Salmon Fisheries Management in the Fraser River, British Columbia. *Transactions of the American Fisheries Society*, *139*(3), 768–782. http://doi.org/10.1577/T08-223.1

Martins, E.G., Gutowsky, L.F.G., Harrison, P.M., Mills-Flemming, J.E., Jonsen, I.D., Zhu, D.Z., Leake, A., Patterson, D.A., Power, M., and S.J Cooke. (2014). Behavioral attributes of turbine entrainment risk for adult resident fish revealed by acoustic telemetry and state-space modeling. *Animal Biotelemetry*. 2: 1-13

Mathes, M. T., Hinch, S. G., Cooke, S. J., Crossin, G. T., Patterson, D. A., Lotto, A. G., & Farrell, A.P. (2010). Effect of water temperature, timing, physiological condition, and lake thermal refugia on migrating adult Weaver Creek sockeye salmon (Oncorhynchus nerka). *Canadian Journal of Fisheries and Aquatic Sciences*, *67*(1), 70–84. http://doi.org/10.1139/F09-158

Melnychuck, M.C and V. Christensen. (2009). Methods for estimating detection efficiency and tracking acoustic tags with mobile transect surveys. *Journal of Fish Biology*. 75: 1773-1794

Melnychuck, MC. And C.J Walters. (2010). Estimating detection probabilities of tagged fish migrating past fixed receiver stations using only local information. *Canadian Journal of Fisheries and Aquatic Sciences*. 67: 641- 658

Melnychuck MC. (2012). Detection efficiency in telemetry studies: Definitions and evaluation methods. *In* Telemetry Techniques: A User Guide for Fisheries Research (Eds. N Adams, J Beeman and J Eiler) (339-357), American Fisheries Society Books, Bethesda Maryland.

Michielsens, C. G., McAllister, M. K., Kuikka, S., Pakarinen, T., Karlsson, L., Romakkaniemi, A., Pera, I., & Mäntyniemi, S. (2006). A Bayesian state–space mark–recapture model to estimate exploitation rates in mixed-stock fisheries. *Canadian Journal of Fisheries and Aquatic Sciences*. 63: 321–334. doi:10.1139/f05-21

Patterson, D. A., Cooke, S. J., Hinch, S. G., Robinson, K. A., Young, N., Farrell, A. P., & Miller, K. M. (2016). A perspective on physiological studies supporting the provision of scientific advice for the management of Fraser River sockeye salmon (Oncorhynchus nerka). *Conservation Physiology*. 4:1–15. http://doi.org/10.1093/conphys/cow026

Payne, N.L., Gillanders, B.M., Webber, D.M., and J.M Semmens. (2010). Interpreting diel activity patterns from acoustic telemetry: the need for controls. *Marine Ecology Progress Series*. 419: 295-301

Pine, W.E., Hightower, J.E., Coggins, L.G., Lauretta, M.V., & Pollock, K.H. (2012). Design and Analysis of Tagging Studies. In A.V. Zale, D.L. Parrish, and T.M Sutton (Eds). *Fisheries Techniques 3rd ed* (521-564). Maryland, USA: American Fisheries Society

Pollock, K. H., Jiang, H., & Hightower, J. E. 2004. Combining Telemetry and Fisheries Tagging Models to Estimate Fishing and Natural Mortality Rates. *Transactions of the American Fisheries Society*, *133*(3), 639–648. doi:10.1577/T03-029.1

Powell, L. A., Conroy, M. J., Hines, J. E., Nichols, J. D., & Krementz, D. G. (2000). Simultaneous Use of Mark-Recapture and Radiotelemetry to Estimate Survival, Movement , and Capture Rates.*The Journal of Wildlife Management*, *64*(1), 302–313.

Robinson, K. A., Hinch, S. G., Gale, M. K., Clark, T. D., Wilson, S. M., Donaldson, M. R., Farrell, A.P., Cooke, S.J. & D.A Patterson. (2013). Effects of post-capture ventilation assistance and elevated water temperature on sockeye salmon in a simulated capture-and-release experiment. *Conservation physiology*, *1*(1).

Turchin, P. (1998). *Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants*. Sinauer Associates, Inc. USA.

Venables, W.N. and C. M Dichmont. (2004). GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. *Fisheries Research*. 70: 319-337

Williams, B.K., Nichols, J.D., & Conroy, M.J. (2002). Estimating Survival, Movement and Other State Transitions. In: *Analysis and Management of Animal Populations* (pp 417-493). San Diego, California: Academic Press

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and G.M Smith. (2009). Mixed Effecs Models and Extensions in Ecology with R. In*: Statistics for Biology and Health.* (pp 323-342). NY: Springer Science + Business Media